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The Northwest Atlantic fisheries have a rich history, and a great deal of research has been sponsored and encouraged by NAFO and its predecessor ICNAF. NAFO has been a leader amongst international organizations in the application of science to fishery management and in the regulation of fisheries in areas beyond national jurisdiction. In accordance with its mandate to disseminate information on fisheries research to the scientific community, the Scientific Council of NAFO publishes the Journal of Northwest Atlantic Fishery Science, which contains peer-reviewed primary papers, and NAFO Scientific Council Studies, which contains unrefereed papers of topical interest and importance to the Scientific Council. Lists of these and other NAFO publications are given on the back of this issue.

Editorial Policy

The Journal provides an international forum for the primary publication of original research papers, with emphasis on environmental, biological, economic and social science aspects of fisheries and their interactions with marine habitats and ecosystems. While the Journal is intended to be regional in scope, papers of general applicability, and methodological and review papers, irrespective of region, are considered. Space is available for notes and letters to the editor to facilitate scientific discussion of published papers. Both practical and theoretical papers are eligible. All papers are peer-reviewed to determine their suitability for primary publication. Associate Editors arrange for the peer-reviews and ensure that the papers accepted for publication meet the high standards required for the Journal. Manuscripts approved for publication are accepted with the understanding that they are not copyrighted, published or submitted elsewhere except in abstract form. There are no page charges.

Editorial Board

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NAFO CONVENTION AREA
(Showing Scientific and Statistical Subareas,
Divisions and Subdivisions)

Boundary of the Convention Area ....
Boundary of Subareas ....
Boundary of Divisions ....
200-Mile Zone Boundary ....
200-Meter Contour ....
NAFO Regulatory Area (NRA) ....

Mercator Projection Scale 1 : 8 500 000 at 60°

As shown in the chart below, 5Zc and 5Zu are sub-subdivisions of the Subdivision 5Ze established by the Scientific Council for the purpose of recording and reporting catches to NAFO from Canadian waters (5Zc) or USA waters (5Zu) (NAFO GC Doc. 86/2, 2nd revision, and GC Doc. 86/4, revised).

MASS.
CONN.
Boston
42° 20'N
66°00'W
Cape Cod
Nantucket I.
Block I.
Georges
5Zc
Georges
BK.
42°20'N
65° 40'W
4X
6A
5Zw
5
5Ze
5Zu
39° 00'N

This chart below represents the Exclusive Economic Zone (EEZ) of France (in respect of St. Pierre and Miquelon)

Newfoundland
St. Pierre and Miquelon
St. Pierre and Miquelon EEZ (France)
Canadian 200-mile Zone Boundary

Melville Bay
Baffin Bay
75° 00'N
73° 30'W

1A

BAFFIN ISLAND
0
1
0A
68° 50'N
Christianshaab
Store Hellefiske Banke
1B
66°15'N
Davis Strait
Lille Hellefiske Banke
1C
0B
64°15'N
Fyllas Banke
Godthaab (Nuuk)
1D
Fiskenaes Banke
GREENLAND
62° 30'N
Danas Banke
Frederikshaab Glacier
Hudson Strait
61°55'N
66°20'W
61°00'N
59°00'W
1E
61°00'N
60°45'N
Cape Desolation
Ungava Bay
Cape Farewell
2G
1F
59° 00'N
Cape Mugford
57°40'N
2
2H
Hopedale
55°20'N
CANADA
LABRADOR
Hamilton Bank
2J
52°15'N
52° 15'N
42° 00'W
QUEBEC
Cape Bauld
3K
Pte. Des Monts
49°25'N
64°40'W
4S
49°25'N
60°00'W
4R
Cape Freels
49°15'N
3
NEWFOUNDLAND
4T
Magdalen I.
47°50'N
60°00'W
Cape Ray
Miquelon (Fr.)
St. John's
3L
Flemish Cap
ATLANTIC OCEAN
NEW BRUNSWICK
P.E.I.
St. Pierre (Fr.)
Grand Bank
46°00'N
4Vn
3Ps
St. Pierre Bk.
MAINE
45°40'N
3M
USA
Portland
Gulf of Maine
Halifax
44°20'N
Sable I.
Scotian Shelf
44°10'N
3O
43°30'N
55°00'N
3N
44°46' 35.56"N
66°54' 11.23"W
42°20'N
66°00'W
5Y
4Vs
42°20'N
65°40'W
4W
4
6A
5Zw
5
5Ze
39° 00'N
4X
39°00'N
39°00'N
6B
6C
Cape Hatteras
6D
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6H

BERMUDA

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Contents

Age and growth of Atlantic chub mackerel (*Scomber colia*s) in the Northwest Atlantic

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Abstract

The Atlantic chub mackerel (*Scomber colias*) stock is commercially exploited throughout the Atlantic and Mediterranean and has been recently targeted by a small, but emerging, fishery off the Northeast coast of the United States. Recent efforts by the Mid-Atlantic Fishery Management Council to manage the Northwest Atlantic stock have necessitated the description of its life-history characteristics. The objectives of this study were to evaluate the utility of ageing methods, describe the length-at-age and weight-at-length relationships, and compare estimated growth parameter values to those reported from other regions. We found that whole otoliths provided the most precise method for age determination of Atlantic chub mackerel. Age estimates were derived for adult ($n = 422$) and larval fish ($n = 60$). Parameter estimates of individual growth models were determined using 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). We found that the three-parameter VBGF ($L_\infty = 33.56$ cm TL, $k = 1.75$ y^{-1}, $t_0 = 0.07$ y) was the best candidate model to describe the length-at-age relationship. A power function was used to describe the weight-at-length relationship from 1 136 individuals ($a = 0.0258$, $b = 2.72$). We found that individuals exhibit a greater rate of growth and reach smaller average maximum length when compared to published estimates in other regions. The rate of increase of weight relative to length was found to be significantly lower than that reported in other regions. These results can be used to inform assessment of the Atlantic chub mackerel stock in the Northwest Atlantic.

Key words: ageing, bayesian statistics, fishery, life history, otolith, *scomber*

Introduction

Atlantic chub mackerel (*Scomber colias*) is found throughout the warm and temperate coastal waters in the Atlantic Ocean, as well as the Mediterranean and southern Black Sea (Hernández and Ortega, 2000). It is considered a separate species from the closely related chub mackerel (*Scomber japonicus*) which is distributed throughout the Pacific Ocean (Catanese *et al*., 2010). The New England and Mid-Atlantic stock has recently been the target of a commercial fishery that also targets *Illex* spp., squid, on the eastern coast of the United States. Peak commercial harvest in New England was 239.8 mt for 2014 and 1984.2 mt in the mid-Atlantic for 2013 (NMFS, 2019). Although landings have increased in the US Exclusive Economic Zone (Fig. 1) in recent years, very little is known about the demographic characteristics of the stock. The absence of biological information on *S. colias* impedes the stock's assessment and management (Mid-Atlantic Fishery Management Council, 2017).

Information on individual growth dynamics is essential for the assessment of exploited stocks (Ballagh *et al*., 2011). The demographic characteristics of *S. colias* have been described from populations in the Northeast Atlantic (Martins 1996; Lorenzo and Pajuelo, 1996; Carvalho *et al*., 2002; Vasconcelos *et al*., 2011; Velasco *et al*., 2011; Jurado-Ruzafa *et al*., 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. These studies indicate that considerable geographic variation exists in parameter estimates of Atlantic chub mackerel growth that describe length-at-age (Table 1) and weight-at-length (Table 2) among locations. Given the range of mean parameter estimates, determining whether variations are due to geographic differences in growth or sampling practices is challenging.

Contrasts in the growth dynamics of *S. colias* reported among studies (and regions) can be attributed to several sources, including diversity of gear type used to collect the
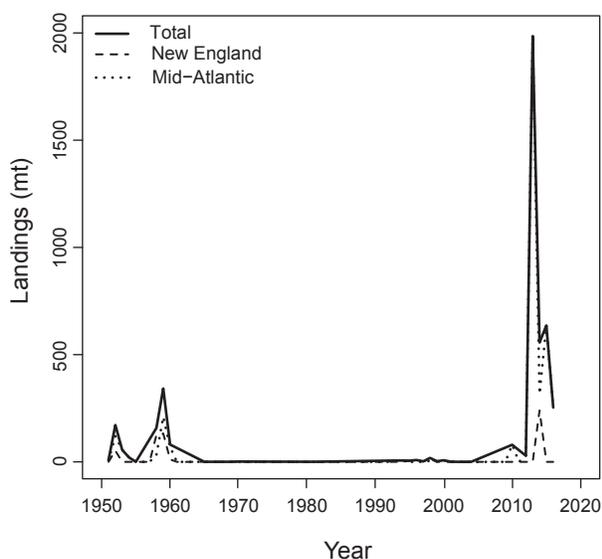
Fig. 1   Commercial catch of Atlantic chub mackerel from 1951 to 2015, (NMFS, 2019).

fish, variations in sample sizes, and temporal variability. Gear type used in commercial harvest varies widely and includes purse-seine (Martins 1996; Lorenzo and Pajuelo, 1996; Carvalho *et al*., 2002; Sinovčić *et al*., 2004; Vasconcelos *et al*., 2011; Velasco *et al*., 2011), beach seine (Sinovčić *et al*., 2004), commercial trawl (Martins 1996; Santos *et al*., 2002; Velasco *et al*., 2011; Jurado-Ruzafa *et al*., 2017), hook and line (Martins 1996; Carvalho *et al*., 2002; Velasco *et al*., 2011), longline (Santos *et al*., 2002; Moutopoulos and Stergiou 2002), traps (Santos *et al*., 2002), and a variety of other net types (Martins 1996; Carvalho *et al*., 2002; Santos *et al*., 2002; Moutopoulos and Stergiou 2002; Mendes *et al*., 2004). Sample sizes used to describe the length-at-age relationship ranged from 98 (Velasco *et al*., 2011) to 2 191 individuals (Vasconcelos *et al*., 2011) and 46 (Moutopoulos and Stergiou 2002) to 4 599 individuals (Jurado-Ruzafa *et al*., 2017) to describe the weight-at-length relationship. Sample collection also took place during different years and seasons (Martins 1996; Lorenzo and Pajuelo, 1996; Carvalho *et al*., 2002; Santos *et al*., 2002; Moutopoulos and Stergiou, 2002; Sinovčić *et al*., 2004; Mendes *et al*., 2004; Perrotta *et al*., 2005; Vasconcelos *et al*., 2011; Velasco *et al*., 2011; Jurado-Ruzafa *et al*., 2017). The majority of studies describing sex-specific length-at-age (Lorenzo and Pajuelo, 1996; Kiparissis *et al*., 2000; Perrotta *et al*., 2005; Bayhan 2007; Vasconcelos *et al*., 2011; Velasco *et al*., 2011) and weight-at-length (Lorenzo and Pajuelo, 1996; Kiparissis *et al*., 2000; Santos *et al*., 2002; Bayhan 2007; Vasconcelos *et al*., 2011; Velasco *et al*., 2011) relationships do not report significant differences between sexes, with few exceptions. Differences in sex-specific mean growth parameter estimates for the length-at-age relationship were

reported in the Adriatic Sea, however it was not reported whether these differences were statistically significant (Čikeš Keč and Zorica, 2012). Jurado-Ruzafa (2017) reported statistically significant differences between sex-specific mean weight-at-length parameters for Atlantic chub mackerel caught off the coast of Northwest Africa.

The objectives of this work are to describe the age and growth characteristics of Atlantic chub mackerel from the coastal Mid-Atlantic and New England region of the United States. We evaluated age estimates from both whole and sectioned otoliths to determine which method results in the greatest precision of age assignment. Otolith-derived age estimates were then used to determine 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.

Methods

Atlantic chub mackerel were obtained from two commercial fishing enterprises, Lund's Fisheries Inc. and Seafreeze Limited. Fish were harvested in July through September 2016 (*n* = 318) and in June, July, and October 2017 (*n* = 126), using a bottom trawl (Table 1). Additional fish were collected in September 2016 by the National Marine Fisheries Service (NMFS) Northeast Groundfish Survey (*n* = 16) in the Northwest Atlantic region (Table 1). 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. To extend the range of length for determination of growth dynamics, body lengths (BL, mm) of larval fish (*n* = 60) collected 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 two readers was evaluated using percent agreement (PA) for each structure (sectioned vs. whole). Pairs of otoliths from 50 randomly selected fish (ranging in size from 26.4 cm TL to 38.4 cm TL) were used. Left otoliths were embedded in molds using Epoxicure resin. 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. Right otoliths from each pair were left whole and fixed in trays using Flow-Texx as a mounting medium. Age estimates for whole and sectioned otoliths were assigned by

Table 1.   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.

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			
	Gulf of Mexico	January		Plankton tows	0	0.21 to 0.77	60	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)
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
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	February to September, 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, gillnet, trawl survey	0 to 12	16 to 54	883	0.10	58.52	-3.68
Lorenzo and Pajuelo, 1996	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, trawl survey	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

counting fully formed annuli at 2 × to 5 × 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 age assignment.

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 knowledge of the individual other than catch date. Otoliths that were deformed or damaged were eliminated from the analysis. PA and CV were calculated for between-reader age estimates. After independent age estimates were made for each otolith, readers reevaluated those otoliths where discrepancies existed. If agreement could not be reached, the otolith was omitted from analysis. Otoliths were read blind a second time by the first reader to determine within-reader agreement, 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 birth date of January 1st (ICES, 2015). Ages of one month were assigned to fish captured in January and ranged in length of 2.1 to 7.7 mm BL (Berrien, 1978).

The length-at-age relationship of Atlantic chub mackerel was described using four non-linear models: the two-parameter von Bertalanffy Growth Function (VBGF), three-parameter VBGF, Gompertz growth function, and logistic growth function. These models are commonly used to describe the non-linear dynamics of fish 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 parameters a and r (y^{-1}) 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 and weight-at-length relationships were fit using Bayesian methods. 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). Length measurements and age estimates adjusted by date of capture from 422 adult individuals and 60 larval fish were analyzed 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 ten. 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 MCMC chains of 1 000 000 iterations each and a thinning interval of 3 000. Informative priors were constructed for models using the distribution of published mean parameter estimates reported in previous studies (Table 1) that described the length-at-age relationship of Atlantic chub mackerel using the three-parameter VBGF. A combination of informative and uninformative priors was used to estimate growth parameters 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. L_∞ was calculated for all candidate models, with the same informative prior used to calculate L_∞ for the three-parameter VBGF. Uninformative priors with either a normal or lognormal distribution were used to calculate the remaining parameters of each model. All parameters used to describe the weight-at-length relationship were calculated using informative priors, determined from parameter estimates reported in the literature. The joint posterior for each growth model is the product of the likelihood and priors, as shown for the two-parameter VBGF:

Table 2.   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.

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
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	Gillnet, trammel net	0.0020	3.44	19.5 to 46.4	323
Santos et al., 2002	NE Atlantic	Monthly	1998 to 2000	Trawl, nets, longline, traps	0.0021	3.41	15.1 to 47.2	805
Lorenzo and Pajuelo, 1996	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	Purse-seine, hook and line, gillnet, trawl survey	0.00278	3.33	19 to 41	3,761
Moutopoulos and Stergiou, 2002	Mediterranean	Seasonally	1997, 1998	Gillnet, longline	0.0009	3.70	to 33.0	46

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

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

$$\sim \text{Normal} \ (k \mid 0, 0.0001),$$

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

the three-parameter VBGF:

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

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

$$\sim \text{Normal} \ (k \mid 0.21, 0.01),$$

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

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

the Gompertz growth model:

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

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

$$\sim \text{Lognormal} \ (a \mid 0.001, 0.0001),$$

$$\sim \text{Lognormal} \ (r \mid 0.001, 0.0001),$$

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

the Ricker growth model:

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

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

$$\sim \text{Normal} \ (a \mid 0, 0.0001),$$

$$\sim \text{Normal} \ (b \mid 0, 0.0001),$$

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

and the power function:

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

$$\sim \text{Normal} \ (a \mid 0.0038, 0.0001),$$

$$\sim \text{Normal} \ (b \mid 3.34, 0.0001),$$

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

Deviance Information Criterion (DIC) was used to compare competing non-linear growth models. 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 median and 95% credible intervals (CI) were calculated from the posterior distributions for each of the parameter estimates of the three-parameter VBGF and the weight-at-length model. Differences in predicted growth were also compared by predicting lengths at each age using estimated mean parameter estimates.

An age-length key (ALK) was computed using FSA and FSAdata packages in R. The ALK was used to identify age composition for the entire sample, by assigning age estimates to individuals based on length measurements. Length class intervals were fixed at 10 cm TL and contingency tables were used to plot the frequency (%) of individuals of a certain age in each length class.

Results

Whole otoliths provided the most precise method for age determination of Atlantic chub mackerel. Age estimates of whole otoliths yielded 72% PA and sectioned otoliths 64% PA. Of the subsample of 460 whole otoliths evaluated in this study 21 were eliminated due to poor quality. 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 for 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 age-specific 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 (Table 3). The Gompertz function had the next smallest DIC value followed by the two-parameter VBGF, and finally the logistic function. All models predict that Atlantic chub mackerel exhibit rapid growth from age zero to age one and reach asymptotic length around age two (Fig. 2). For comparison with other studies, the three-parameter VBGF was also fit without the inclusion of larval data (Table 1).

The growth of *S. colias* in the Northwest Atlantic was evaluated by describing the length-at-age (Fig. 2) and weight-at-length relationships (Fig. 4) and then compared to growth parameter estimates reported in other regions. The mean parameter estimates reported from ten previous

Table 3. 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.

Model	Equation	Growth parameters	Median estimates	95% (CI)	DIC	ΔDIC
3-P VBGF without larval data	$L_t = L_\infty\left(1 - e^{-k(t-t_0)}\right)$	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	$L_t = L_\infty\left(1 - e^{-k(t-t_0)}\right)$	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	$L_t = L_\infty a^{r^t}$	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	$L_t = \frac{L_\infty}{1 + a(e^{-bt})}$	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		

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). 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. All mean parameter estimates from previous studies used to describe the weight-at-length relationship were significantly different, falling outside the 95% CI of the median parameter estimates from this study (Table 2). The b parameter estimate for this study is smaller than other studies.

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 (Fig 3).

When lengths were predicted using mean 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 (Fig 3). 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 exceeded 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 (Fig 3).

The ALK was used to determine the distribution of ages across length classes of all individuals sampled (Table 4). The majority of individuals sampled were estimated to be age three falling in the 20 to 40 cm TL size class. Overlap of ages in each length class is particularly apparent in the 20 to 40 cm TL size class, where the majority of individuals were sampled (Fig. 5).
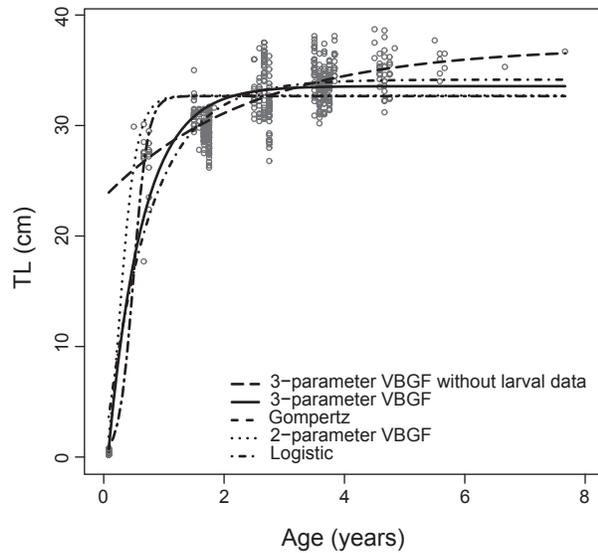
Fig. 2   Non-linear candidate models fit using a Bayesian
approach to describe the length-at-age relationship
for Atlantic chub mackerel in the Northwest
Atlantic. The three-parameter VBGF, Gompertz
function, two-parameter VBGF, and logistic
function were each fit to total length (cm) and
otolith derived 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-pa-
rameter VBGF was also fit without larval data for
comparison with other studies.

Fig 3.   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.

Discussion

Efforts to assess fish stocks require accurate estimates of
ontogenetic growth and these characteristics of Atlantic
chub mackerel in the Northwest Atlantic, have not been
described. In this study we used Bayesian statistical
methods to estimate mean growth model estimates
of length-at-age and weight-at-length. In addition to
describing the growth for *S. colias* in the Northwest
Atlantic, we found that whole otoliths are the best method
for evaluating Atlantic chub mackerel otoliths, that the
three-parameter VBGF is the best model to describe the
length-at-age relationship, and that growth parameter
estimates from this study are significantly different from
those reported in the literature from other regions.

An evaluation of ageing methodology was required
because a standardized protocol had not been reported
for age determination of Atlantic chub mackerel in the
Northwest Atlantic. The reproducibility of repeated
age estimates (Campana, 2001), was the main criterion
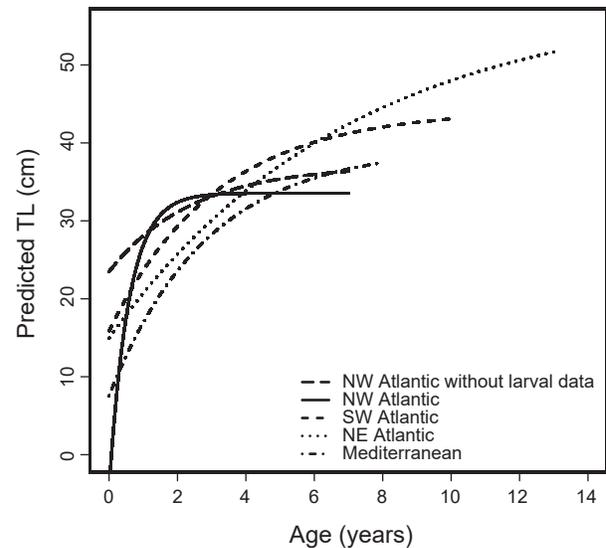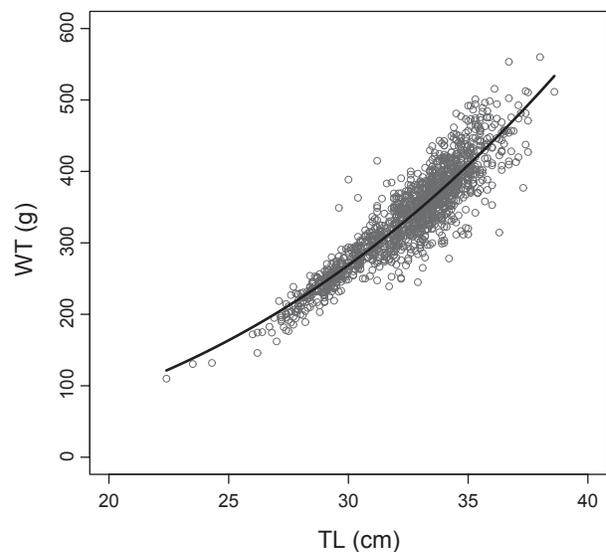we used to determine which structure should be used

Fig 4.   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).

(whole or sectioned otoliths) for age estimation. Age
determination from whole otoliths had a greater PA and
provided increased efficiency in processing relative to

Table 4. The frequency, range of total length (cm), and mean total length (cm) of individuals in each age class. Ages were assigned to total length (cm) measurements, from Atlantic chub mackerel collected in the Northwest Atlantic, using an age-length key.

Age	n	Mean	sd	Min	Median	Max
0	95	10.14	13.08	0.21	0.30	30.1
1	327	29.92	1.33	26.2	29.7	35.0
2	282	32.91	2.06	26.8	33.0	37.5
3	682	33.71	1.33	30.2	33.7	38.1
4	107	34.46	2.02	31.2	34.2	46.5
5	20	35.20	1.14	34.0	35.2	37.7
6	1	35.30	NA	35.3	35.3	35.3
7	1	36.70	NA	36.7	36.7	36.7

Fig 5. Frequency of Atlantic chub mackerel in the Northwest Atlantic with each length category for ages zero to seven.

sectioned otoliths. The continuation of the use of whole otoliths, the primary ageing structure in other studies on Atlantic chub mackerel growth dynamics, provides the additional benefit of maintaining consistency in methodology among studies.

The precision of age assignment was evaluated using PA and CV. 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 chub mackerel (WKARCM) of 57%. The total CV of age estimates in this study was 20%. In a review of 117 age and growth studies, Campana and Thorrold (2001) suggests that 5% CV or lower be used as a target for fishes that exhibit moderate longevity and ease of otolith readability. The CV attained in this study is much higher than this suggested target, but is an improvement to the 30% CV reported from the 2015 WKARCM (ICES, 2015). 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; Jurado-Ruzafa *et al*., 2017) and results in inconsistent age estimates. Inconsistency in age estimates are a source of observation error and manifest in biases in the estimation of growth model parameters.

We recommend the three-parameter VBGF be used to describe the length-at-age relationship of *S. colias* in the Northwest Atlantic. Of the four non-linear models
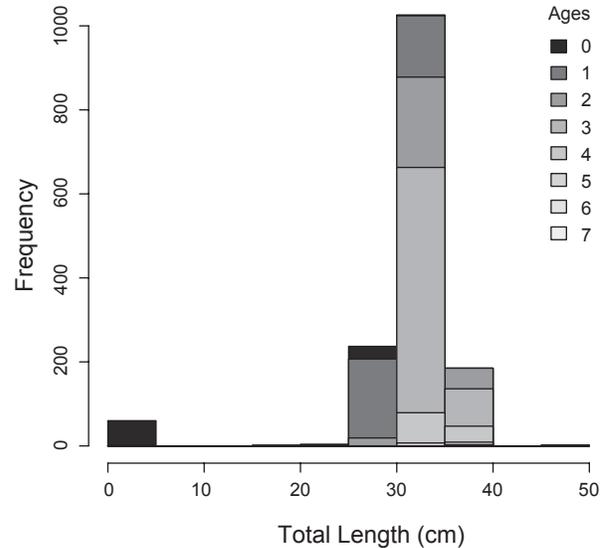
evaluated using objective criteria to reduce errors of model misspecification (Burnham and Anderson, 2004), the three-parameter VBGF was selected as the "best" candidate model. The multi-model approach has been widely used to evaluate candidate length-at-age models (Cope and Punt, 2007; Thorson and Simpfendorfer, 2009; Pardo *et al*., 2013; Dippold *et al*., 2016). Previous studies on Atlantic chub mackerel have primarily used the three-parameter VBGF to model the length-at-age relationship (Carvalho *et al*., 2002; Velasco *et al*., 2011). Continued use of this model here, and in the future, will serve to maintain consistency in regional comparison of the growth of *S. colias*.

An ALK was also used to address the potential for bias resulting from a length stratified sampling plan. This arises as a result of fish at a given age potentially straddling several length classes. An ALK provides an estimate of the proportion of individuals in each length class at a given age, rather than an estimate of age. As Morgan and Hoenig (1997) show this must be taken into consideration when using the length-at-age relationship to estimate maturity-at-age. Using the age-length key resolves this issue by explicitly assigning ages to all individuals sampled (Isermann and Knight, 2005).

The description of the length-at-age relationship in this study suggests that individuals in the Northwest Atlantic grow faster and reach a smaller asymptotic length than in other regions. We note that differences in mean growth

model parameter estimates have multiple sources of uncertainty and though we primarily focus this analysis on differences in regional growth dynamics, bias can arise from sampling (Goodyear, 1995) and methods of age determination. Spatial and temporal differences among regions exhibit variability in temperature and productivity, which may be responsible for differences in growth. Although temperature has been reported to impact 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 very limited number of commercial vessels in the United States that are capable of capturing Atlantic chub mackerel. It is possible that larger fish are present in the region but are able to swim at speeds that allow them to evade capture. Together, regional patterns of selectivity and availability lead to contrasts in the length and age ranges of fish among studies and it is likely that the narrow length range of adult fish in this study is a result of gear selectivity. The range of lengths was extended in this study by including larval fish captured in ichthyoplankton tows. These smaller individuals ranged from 2.1 to 7.7 mm BL. Without the inclusion of smaller individuals, the three-parameter VBGF predicted length-at-age zero to be 23.5 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 biologically realistic description of growth in the Northwest Atlantic, other studies on Atlantic chub mackerel have not included these data.

The range in mean weight-at-length parameter estimates among regions indicates the existence of geographic variation. The scaling exponent *b* estimated in this work is smaller than reported estimates in all previous studies. This suggests that weight-at-length is depressed in the Northwest Atlantic, relative to that exhibited in other regions. Some of the observed contrast may be due to sampling error, individuals were collected during different months and years in each study, which are likely to vary in temperature and productivity. These factors impact growth and condition of fish (Martin, 1949; Houde, 1974; Powell *et al*., 2004; Martins, 2007) and lower *b* values have been reported during the colder parts of the year (Čikeš Keč and Zorica, 2012). Some regions, such as the Canary Islands, exhibit seasonal fluctuations in weight-at-age of Atlantic chub mackerel (Lorenzo and Pajuelo, 1996) with the greatest values from March to September and reductions in October to February.

A small number of studies in other regions have validated annuli formation of Atlantic chub mackerel. Vasconcelos, *et al*. (2011) reported that one translucent and one opaque

band were deposited each year for Atlantic chub mackerel collected off Madeira Island and used marginal increment analysis to validate annuli formation for individuals aged zero to four years. We were unable to collect samples throughout the year in this study to conduct marginal increment analysis due to the absence of fishery-dependent and fishery-independent catch in the Northwest Atlantic. Mark-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 requires extensive resources.

The research presented here provides a description of Atlantic chub mackerel growth in the Northwest Atlantic. Description of length-at-age allows the development of age-length keys and an understanding of the age-composition of harvest in the commercial fishery. This information can be implemented into age-structured models and allow reconstruction of population dynamics which is 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 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.

Acknowledgements

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Diverse migratory behaviors of Atlantic halibut (*Hippoglossus hippoglossus*, L.) based on the 2000–2017 Maine halibut tagging program

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Abstract

Accurately delineating the spatial extent of fish stocks and the degree to which stocks mix is important for understanding the effects of fisheries management and environmental change. This paper describes migratory behaviors of Atlantic halibut (*Hippoglossus hippoglossus* L.) tagged with conventional wire tags in the U.S. portion of the Gulf of Maine between 2000 and 2017. There were 412 recaptures reported out of 2 573 releases, a return rate of 16.0%. These returns illustrate that although most fish are recaptured close to the release point with a median distance at recapture of 38 km, Gulf of Maine Atlantic halibut also engage in dispersive behavior with some fish travelling at least 1 564 km. Returns from Canadian waters accounted for 43.2% of total recaptures. A generalized linear model found greater distances at recapture related to greater days at liberty and during winter. Fish size explained a negligible proportion (<1%) of the variability in recapture distance. Most (76%) recaptures were from waters of the Gulf of Maine and the Western Scotian Shelf off Canada, suggesting a higher level of mixing within this transnational boundary area than to elsewhere. This contrasts common assumptions about stock structure made for assessment and management purposes.

*Keyword*s: partial migration, halibut, *hippoglossu*s, tagging, Gulf of Maine

Introduction

A key assumption when defining a fish stock is that the spatial bounds described for the stock reflect actual behavioral phenomena related to distribution so that fisheries science and regulation within those boundaries produce meaningful results. Recent advances in technology related to genetics and electronic tagging (Hauser and Carvalho, 2008; Seitz *et al*., 2017) have shown that many fish populations are in fact metapopulations (*sensu* Kritzer and Sale, 2004) comprised of smaller, local units within which demographically meaningful processes occur. Even where stocks are well-defined, there may be multiple "contingents" within a local unit stock, where each contingent displays different migratory behaviors, such as the resident and coastal contingents of the Hudson River striped bass (*Morone saxatalis*) (Secor, 1999). The presence of multiple contingents, including partial migration, can allow for greater fitness across individuals within a population, but also creates difficulties for traditional fisheries stock assessments that assume closed populations (Kerr *et al*., 2009). Further complicating assessment, tagging studies for some species such as tunas (Block *et al*., 2005) and large pelagic sharks (Mejuto *et al*., 2005) have shown that enough individuals regularly cross ocean basins, hemispheres, and multiple international boundaries to necessitate international cooperation for science and fisheries regulation. If spatial boundaries to delineate a demographically-meaningful stock unit are unknown, understudied, or ignored, the tasks of fisheries assessment and management become less tractable (Stephenson, 1999).

Atlantic halibut (*Hippoglossus hippoglossus*) is a long-lived and commercially important flatfish found across the North Atlantic. We refer to *H. hippoglossus* as "halibut" for the remainder of this paper. Waters of the United States contain halibut from Cape Cod and Georges Bank into the Gulf of Maine, though there are records of the species present as far south as Virginia (Bigelow and Schroeder, 1953; Cargnelli *et al*., 1999). The fishery for halibut in the Gulf of Maine has existed for almost two

centuries. Although at one time they were a nuisance to be avoided on the cod-fishing grounds of the Northwest Atlantic (Bigelow and Schroeder, 1953), a directed fishery for halibut had begun by the 1840s (Grasso, 2008). By the 1880s, the fishery was effectively over in U.S. and adjacent waters (Goode and Collins, 1887), with the remaining vessels in the fishery having to travel to Iceland to make profitable trips (Grasso, 2008). Over a century later, the U.S. stock is still considered overfished despite recent small increases in a handful of indices (Rago, 2017).

Because they can migrate long (>1,000 km) distances, currently halibut are considered to belong to a single unit stock in the U.S. (Rago, 2017). In federal waters of the U.S., multispecies groundfish vessels are limited to landing one halibut per trip as non-targeted bycatch by gillnet and otter trawl vessels, with all other halibut discarded. These vessels catch halibut throughout the year (Portland Fish Exchange, 2019). The State of Maine allows a targeted longline fishery in the months of May and June within state waters (out to 3 miles), with a 250 hook per vessel limit, a yearly limit of 25 fish per vessel, and hook size limits (Maine Department of Marine Resources, 2018). Federal waters catches have fluctuated between 47.8 and 60.7 mt from 2012 to 2016, while Maine's state waters longline catch has increased from 13.3 to 47.9 mt during the same time (New England Fisheries Management Council, 2017).

Across the U.S./Canada transnational boundary in the Gulf of Maine known as the Hague Line, the Scotian Shelf and Southern Grand Banks stock assessed by the Department of Fisheries and Oceans (DFO) Canada is at high biomass levels and continues to experience high recruitment (Trzcinski and Bowen 2016; DFO 2018). This disparity in status between adjacent stocks, one certified as sustainable by the Marine Stewardship Council and the other considered overfished, has been hypothesized to be in part due to a separation of the U.S. and Canadian stocks. This hypothesis is supported by electronic tag data (Seitz et al., 2016) and consistent differences in site occupancy of available modeled habitat (Shackell et al., 2016). Specifically, continued low biomass levels of U.S. halibut may support this hypothesis of a separation of stocks, as U.S. fish do not appear to be limited by habitat availability and yet are consistently less abundant on the U.S. side, despite extensive Canadian recovery (Shackell et al., 2016).

As Atlantic halibut recovers in the Northwest Atlantic (Trzcinski and Bowen, 2016), understanding the relative proportion, magnitude, and ontogenetic timing of different migratory behaviors will be important for understanding the dynamics of stocks both within (Boudreau et al.,

2017) and across (Shackell et al., 2016) the exclusive economic zones of Canada and the U.S. For Atlantic halibut, management at too great of a scale may result in persistent localized depletions (Boudreau et al., 2017), and serial depletion of halibut stocks in the northwest Atlantic has happened before (Grasso, 2008). Therefore, the objectives of this study are twofold: 1) to examine the types of migratory behaviors Gulf of Maine halibut display, 2) to examine whether there are ontogenetic or seasonal effects on movement. To address these objectives to the extent possible, this study looks at recaptures from Atlantic halibut tagged in the Gulf of Maine using conventional wire tags over the period 2000–2017.

Methods

Data and sample collection

This study reports on 412 reported recaptures through January 2018 from 2 573 Atlantic halibut tagged and released in the Gulf of Maine between 2000 and 2017. The State of Maine's Department of Marine Resources began a conventional halibut tagging program as part of an experimental longline fishery that occurred in federal waters off eastern Maine between 2000 and 2004 (Kanwit, 2007). A total of 844 fish smaller than the minimum size at the time, 36 inches (91.4 cm), was tagged by onboard observers or participating fishermen and released.

Following the success of the tagging from this initial program, the Department expanded the conventional tagging program to the state waters directed fishery and regional fisheries surveys. At public meetings, the Department distributed tags and tag applicator needles, and concurrently trained halibut fishermen on how to tag fish and record pertinent data. Through state waters commercial fishermen, another 1 290 sublegal fish were reported as tagged during 2001–2016. As the minimum size was increased to 41 inches (104.1 cm), the size of tagged fish increased. Additional stakeholder groups were trained to perform tagging, leading to a further 271 tagged fish of all sizes that were released by the Maine/New Hampshire inshore trawl survey from 2001 through 2013, and 45 released by a 2007–2008 halibut longline survey in federal waters off coastal Maine. Other participants included the Massachusetts trawl survey, the Gulf of Maine cod tagging program, and federally-permitted commercial multispecies fishermen, who collectively tagged an additional 123 fish. Maine state waters commercial fishermen recaptured 27 tagged fish that were still under the legal size, and these subsequently re-released fish were recorded as both a recapture and a release. Federal fishery harvesters did not report any re-

release of juvenile fish or discarding of tagged legal fish released due to their one fish limit. Most tagging occurred during the Maine state commercial halibut season of May and June, regardless of stakeholder. All but eight (0.3%) of the releases occurred within 24 miles of the coast of the state of Maine, with the majority of tagged fish released within or adjacent to Maine state waters in the eastern half of the state where the state waters commercial fishery is concentrated. Thus, the primary tagging area was adjacent to Canadian waters, and the median distance for all releases from the U.S.-Canadian maritime boundary was 72 km.

During tagging, fish length was recorded and a stainless-steel tag coated with yellow plastic was inserted through the outside of the first operculum using a purpose-built applicator needle, with the tag ends then twisted to form a loop. The spaghetti tags used in this program were 16 cm in total wire length with 14 cm of the central portion coated in clear plastic, the most central 7.5 cm in yellow plastic. The plastic was inscribed with "H00001 Return to DMR // PO Box 8 W Boothbay Hbr, ME 04575 PH: 207-633-9535." From 2000 to 2001, deployed tags were manufactured by Floy Tag Inc. From 2002 to present, deployed tags were made by Hallprint Pty Ltd.

To encourage the reporting of recaptures, the Department instituted a reward program for returned tags, providing the returnee with a hat or coffee mug and a letter with information on the tagging program and where and when their fish was released. As tags were returned, a Department employee would reach out to the returnee and attempt to gather any missing biological or spatiotemporal information on the recapture. We did not investigate what percentage of tags from recaptured fish were ultimately reported, or the shedding rate of tags.

Data quality control

To be included for data analyses, tag recaptures were screened in a quality control process. Out of the 412 recaptures, only 378 included spatial and temporal information of what was determined to be adequate quality, while 351 also included high quality release length information. The analysis in this paper therefore made use of either the subset of 378 or 351 recaptures, as appropriate. None of the recaptures for the 35 tags that we do not describe were from outside of the general recapture area reported in the results.

Many returns had land masses between the points of release and recapture, including smaller islands but also Newfoundland and Nova Scotia. Distance was therefore calculated as the shortest path between points travelling only via ocean waters. To determine ocean-only distance, we first created a 1 000 by 1 000 cell raster within the spatial extent of the tag releases and recaptures. A high-definition raster of coastal landmasses within the extent was used to assign costs to cells, with land and a land buffer of 1 km assigned a value of 999 and ocean a value of 1. We then determined the least-cost path using the shortest path function from the gdistance package (van Etten, 2018). Due to the size of the cells, precision of computed distances is limited to 0.56 km.

Analysis of seasonal effects

To determine whether minimum distance travelled between release and recapture locations was related to season, time of recapture was assigned to two seasons and season was incorporated as a two-level factor into a generalized linear model (GLM) described below. Seasons were split into winter (October to March) and summer (April to September) based on the presumed winter spawning period in Canada (Neilson et al., 1993; Armsworthy et al., 2014; Murphy et al., 2017) and a summer foraging period (Godo and Haug, 1988a; Le Bris et al., 2018). To ensure that this analysis examined comparisons of summer releases to summer or winter recaptures, we removed 10 recaptures from analysis that were from fish released in winter months.

Analysis of ontogenetic effects

To examine whether there were possible ontogenetic effects on minimum distance, the relationship between release length against distance travelled was incorporated into the GLM described below. For comparability to two previous Canadian conventional tagging studies in adjacent waters (Stobo et al., 1988; den Heyer et al., 2012), movement by fish both under and over 80 cm total length, the L50 for Gulf of Maine male halibut, were compared (Sigourney et al., 2006) using a one-way ANOVA with no assumption of equal variances. In addition, the effect of overall days at liberty on distance was examined as a rough proxy for ontogenetic development as part of the GLM.

Generalized linear model design

To examine potential drivers of movement, seasonal, size and time-at-liberty factors were included in regression analysis to determine if these were related to movement (defined here as ocean-only distance at recapture in km) based on the subset of data with high quality spatial, temporal, and release length information, from summer

releases (*n* = 341). An initial multiple regression using fish length at release, days at liberty, and season as explanatory variables failed a Shapiro-Wilk normality test of the residuals (p< 2.2e⁻¹⁶). To aid in resolving issues with the error distribution, we built a generalized linear model (GLM) to better accommodate the error structure around the response variable. With the continuous, positive response variable of distance we chose a Gamma distribution with a log link for the GLM as most appropriate (Quinn and Keough, 2009). We included as predictors in the model days at liberty, fish length at release, and season of recapture. Because seasonal fish movement could be influenced by maturity, we included an interaction term for release length and season. All explanatory predictors were continuous, except season was a two-level factor consisting of winter and summer (see above). Prior to modeling, the response variable of distance was transformed by adding one meter to remove false zeroes occurring due to imprecise reporting of release and recapture locations when fishermen recaptured fish at the same underwater feature where released.

After building the GLM, we examined relative model fit based on the Akaike Information Criterion (AIC; Akaike 1974). The AIC uses the number of parameters in the model and the maximized value of the model likelihood function to compute an AIC score (Akaike, 1974). For this GLM, the scores served as a basis for comparing explanatory variables in different model formulations based on how much each predictor contributed to the goodness-of-fit against how much complexity each added to the model. We report here on the complete model, as well as a subset of model combinations following AIC-based stepwise removals from the stepAIC function in the R package MASS (Venables and Ripley, 2002). For model validation, we looked at the model with the lowest AIC value, and examined fitted values against the Pearson residuals. All data analyses including calculating minimum swimming distance, descriptive statistics and modelling were done in the R statistical software (R Core Project Team, 2018).

Results

Between April 28, 2000 and August 13, 2017 a total of 2 573 Atlantic halibut were tagged and released in the Gulf of Maine. Most releases occurred during 2000–2010, while most recaptures occurred by 2013 (Table 1). Of the tagged fish, length information was available for 97.4% at release, with mean and median total fish lengths of 78 and 81 cm (range 22–173 cm), respectively.

By January 2018, there were 412 (16.0%) reported recaptures, including 378 with full location data, 351 with location and release length data, and 320 with full location and growth data (see methods). Of the 378 fish with high-quality location recapture data, 332 were tagged in May or June, and 36 were tagged in April, July, August, or September. Only 10 were tagged during October–March. Recapture lengths included 374 records, with a range of 61 to 163 cm, and a mean of 102 cm (median=99 cm). The greatest reported increase in TL for a tagged fish while at liberty was 91 cm. Days at liberty ranged from a few hours to 4 433 days (12.1 years). Median days at liberty was 674, and the mean was 772 days.

Movement

Distance between release and recapture points ranged from a few meters to 1 564 kilometers. Most fish were recaptured close to their release point (Fig. 1), as indicated by a median distance of 38 km, while a number were

Table 1.   Number of total releases and recaptures of Atlantic halibut in and adjacent to the Gulf of Maine by year.

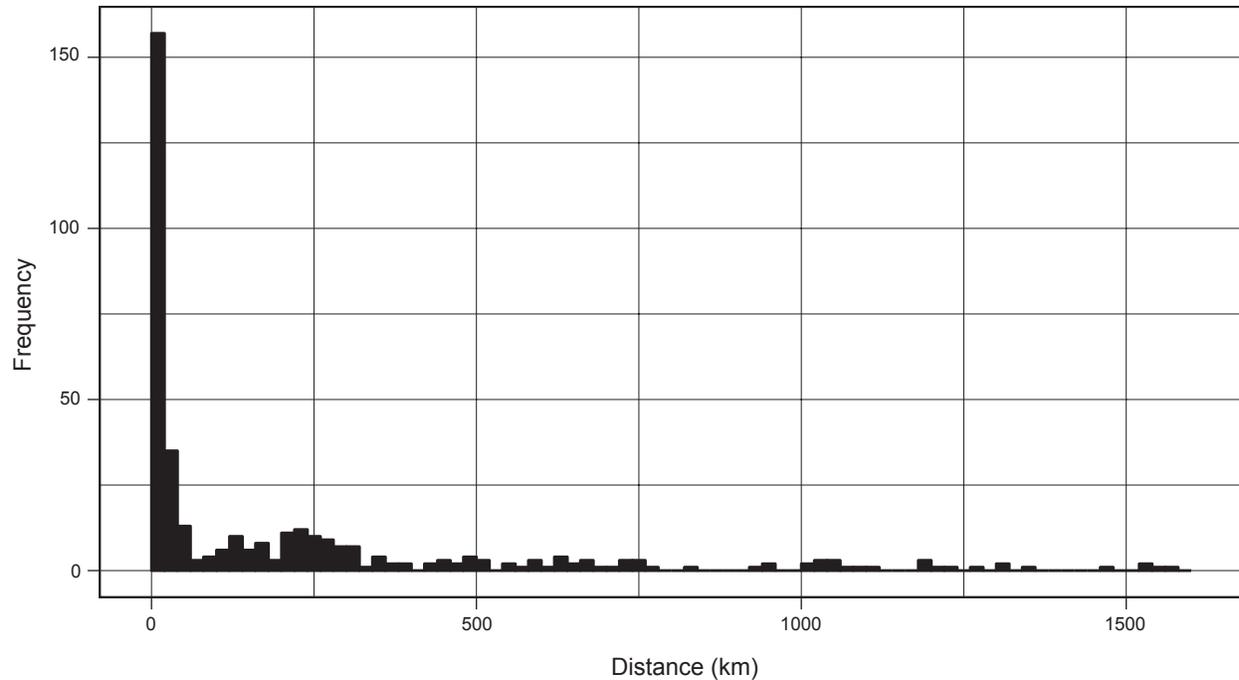| Year	Releases	Recaptures	Year	Releases	Recaptures
2000	69	1	2009	205	50
2001	46	2	2010	154	36
2002	282	20	2011	200	27
2003	440	40	2012	60	21
2004	219	42	2013	27	22
2005	85	23	2014	0	8
2006	207	36	2015	0	7
2007	252	32	2016	1	4
2008	304	37	2017	22	4

Fig. 1.   Histogram of ocean-only swimming distances of Atlantic halibut between release and recapture locations ($n = 378$) in and adjacent to the Gulf of Maine.

recaptured at much greater distances, leading to the larger mean of 219 km (1 SD = 338 km). The Canadian fishery recaptured 43.2% of the tagged fish. Although international emigration was common, a considerable proportion of these halibut were recaptured relatively short distances away in the Bay of Fundy or off southwestern Nova Scotia (Fig. 2). Recaptures west of 65º West longitude represented 76% of total returns.

Ontogenetic effects on movement

Small and large fish were recaptured over a similar range of distances, and fish of all sizes were recaptured close to their release point (Fig. 3). With increasing days at liberty, there were more recaptures at greater distances, however some fish were still recaptured close to the release site across the range of days at liberty (Fig. 4).

Seasonal effects on movement

Distance at recapture was greater for winter recaptures (median=317 km; mean=438 km; $n = 61$) than for summer recaptures (median =20 km; mean=176 km; $n = 317$), with May and June having the lowest median distances (13 and 11 km, respectively), but close to the greatest ranges (1 310 and 1 564 km, respectively; Figs. 4,5). Although winter returns had higher median and mean distances, 9 of the

10 largest distance returns were from summer recaptures. Only three of the 61 returns from winter months were from inside U.S. waters (Fig. 2). Returns from winter months included fish reported as captured off the continental slope by the Scotian Shelf, however all but one of the fish recaptured near the slope of the southern Grand Banks were recaptured in summer (Fig. 2).

Generalized linear model

Based on AIC, the model with the best goodness-of-fit discounted by complexity was the model that included days at liberty, season, and release length (Table 2). Including the interaction term for season and release length in the complete model explained very little (0.09%) additional deviance. Release length had a positive effect on distance (Fig. 3) but similarly to the interaction term explained only a small proportion of the deviance when added to the model (0.57%). Most of the deviance explained came from the addition to the model of days at liberty (9.38%) and season (5.75%), both of which had a positive effect on distance (Fig. 4).

Looking at a cutoff roughly similar to that examined in previous studies which looked at fish above and below 75 and 81 cm TL (Stobo *et al*., 1988; den Heyer *et al*., 2012), there were only small differences in recapture distance between fish over 80 cm total length at release
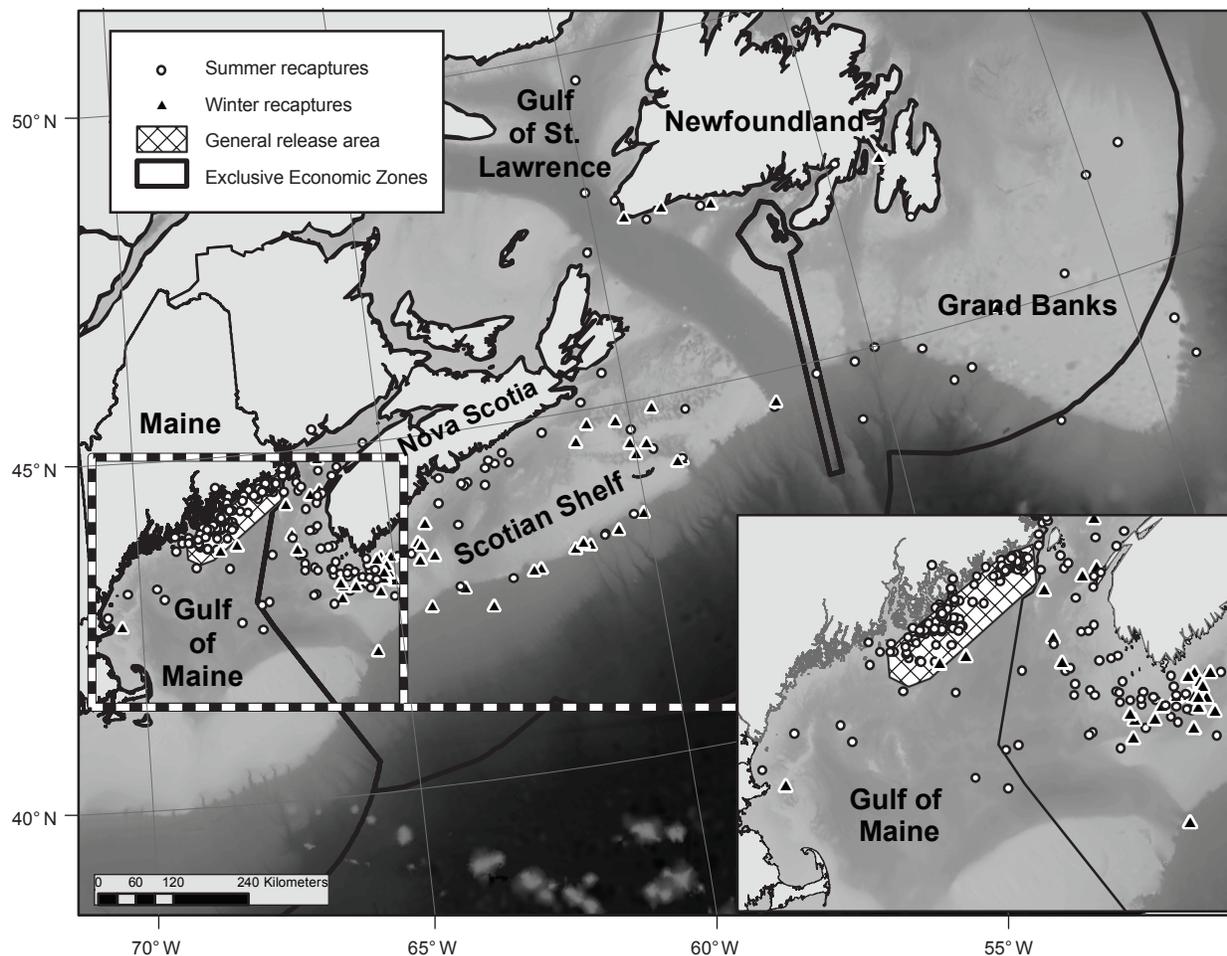
Fig. 2.   Recapture locations of Atlantic halibut by season (*n* = 378). Bathymetry data from General Bathymetric Chart of the
             Oceans. The release area is a general illustration to adhere to State of Maine confidentiality rules.

Discussion

(median=29 km; mean=222 km; *n* = 164) and under 80 cm
total length (median=38 km; mean=196 km; *n* = 187),
and these were not significant (one-way ANOVA, no
assumption of equal variances, *p* = 0.47).

Discussion

Atlantic halibut from the Gulf of Maine exhibit a range
of migratory behaviors. Although total days at liberty
and season in particular may both drive the extent of this
movement, fish of all sizes, recaptured at all times of the
year and a variety of days at liberty exhibited a range of
recapture distances and locations. There is evidence here
that halibut tagged in the Gulf of Maine display dispersive
behavior and site fidelity, either representing homing or
sedentary behavior. This could indicate that if the Gulf
of Maine is in fact a discrete population, then multiple
contingents (Secor, 1999) are present exhibiting dispersive
and site fidelity behaviors, *i.e.* partial migration (Kerr

et al., 2009). Due partially to the short distance required
to pass international boundaries from the general release
area, a notable proportion of fish was recaptured in the
Canadian fishery. Most recaptures of tagged fish occurred
within the area stretching from the Gulf of Maine to the
Western Scotian Shelf, with limited (24%) dispersion
outside of this area.

The 18-year dataset used in these analyses provides
different conclusions from those based on earlier analyses
from the first six years of this tagging project. Based on
just the returns from 2005 and earlier, Kanwit (2007)
reported median days at liberty of 384 days and a median
distance travelled of 12 km. Thirteen years later, the
median days at liberty is 674 days and median distance
is 32 km, suggesting that for long-lived fishes with
complex life histories, it may be premature to report on
returns without multiple years of data. Additionally, the
proportion of tagged fish recaptured outside of the U.S.

EEZ was 28% when considering the first six years of data (Kanwit, 2007), but with an additional twelve years of data that number is 43%. These basic findings highlight the value of long-term tagging studies.

Ontogenetic effects

Ontogenetic development does not appear to be an important factor for driving migratory behavior. The GLM found release length to have a positive effect (Fig. 3), though it explained very little of the deviance in the model (Table 2). In contrast, Stobo and colleagues (1988) found greater movement on the Scotian Shelf and Grand Banks by juveniles, which they defined as less than 75 cm, compared to that of adults and proposed that fish were moving to the northeast as part of a compensatory migration hypothesis in which they were returning to their natal locations to counter drift in their egg and larval stages from spawning grounds to the northeast. However, a more recent study in the same area using a similar size cutoff does not support this hypothesis (den Heyer *et al.*, 2012). The results reported here found no significant difference between fish above and below the L50 cutoff for males in the Gulf of Maine of 80 cm (Sigourney *et al.*, 2006) when using a simple one-way ANOVA, and furthermore

the GLM with release length as a continuous variable found a weak positive effect on swimming distance. The weak, positive effect in the GLM means that the issue is likely not related to using an inaccurate threshold for size-at-maturity for the ANOVA modeling in this or previous studies. At the same time, there is a positive relationship between days at liberty and distance that could point to compensatory migration. Given the lack of a strong size effect, Atlantic halibut in the Gulf of Maine may not exhibit compensatory migration to distant spawning grounds, but rather show general dispersion to adjacent suitable habitat throughout the period of ontogeny represented by tagged fish. The lack of ontogenetic effects in den Heyer's (2012) study promotes this interpretation.

Seasonal effects

Greater distance at recapture during the winter season could reflect movement to spawning areas on the continental slope, while low summer recapture distances could represent sedentary behavior or homing to summer feeding areas. A mixture of conventional and electronic tagging studies have shown halibut may move to forage in the summer and migrate to spawning grounds in winter, while other fish stay resident (Godo and Haug,

Fig. 3.   Ocean-only swimming distance of Atlantic halibut between release and recapture locations in and adjacent to the Gulf of Maine by length of fish at release for tags with complete location and size data (*n* = 320). Lengths have been rounded to the nearest centimeter and distance to the nearest 10 km for ease of interpretation of the bubble plot. Generalized Linear Model presented here is the model with the best fit, including days at large, season, and release length as predictors.

1988a, b; Armsworthy *et al*., 2014; Le Bris *et al*., 2018; for *Hippoglossus stenolepis* Nielsen and Seitz, 2017). With most of the fish tagged in this study during summer months, the fish in this study may also have been tagged at a summer feeding location where they were again recaptured, leading to lower mean summer recapture distances (Figs. 2, 4, 5). However, as 9 out of 10 of the recaptures with the greatest distances were from the summer period, it appears that some fish are engaging in dispersive behavior beyond just seasonal movements related to spawning or foraging.

Types of migratory behavior

The results illustrate that Atlantic halibut tagged off the coast of Maine exhibit a variety of migratory behaviors. It is likely that a sizable proportion of fish from the Gulf of Maine either display site fidelity, disperse, or undertake seasonal movements. Electronic tagging studies with Pacific halibut have shown that fish can occupy release locations at a later time both due to sedentary and homing behavior, and this may relate to whether fish undergo spawning migrations (Loher and Seitz, 2008; Nielsen and Seitz, 2017). Within our data, evidence of site fidelity is shown by the low median distance between release and recapture and the large number of fish recaptured near

the release area (Figs. 1,2). However, this study also provides evidence that a portion of Gulf of Maine fish travel long distances, as shown by the large range in distances year-round (Fig. 5). While some fish exhibit site fidelity to the release area in May and June, others are recaptured at the same time over 1 000 kilometers distant and may represent permanent emigrants or migrants that do not follow a seasonal pattern (Fig. 5). If fish tagged in the Gulf of Maine do migrate to Canada to spawn in winter, this dispersive behavior could fall under seasonal mixing if fish from multiple feeding areas mix on common spawning grounds (*e.g.* Le Bris *et al*. 2018) or year-round emigration to the slope if these fish stay in the proximity of the spawning area once mature (Armsworthy *et al*., 2014).

This diversity in migratory behaviors by halibut in the Gulf of Maine may indicate that there are multiple contingents present, potentially including residential and migratory (Secor, 1999). If fish that are large enough to be caught by commercial fishing gear are already at a life stage to begin employing one or the other strategy, then the presence of contingents is supported by the existence of fish of all sizes recaptured across the entire range of distances. The finding that days at liberty was a significant variable and explained more deviance than the other variables in the GLM (Table 2; Fig. 4) may suggest that there is a general trend for disperserive behavior to become a more common
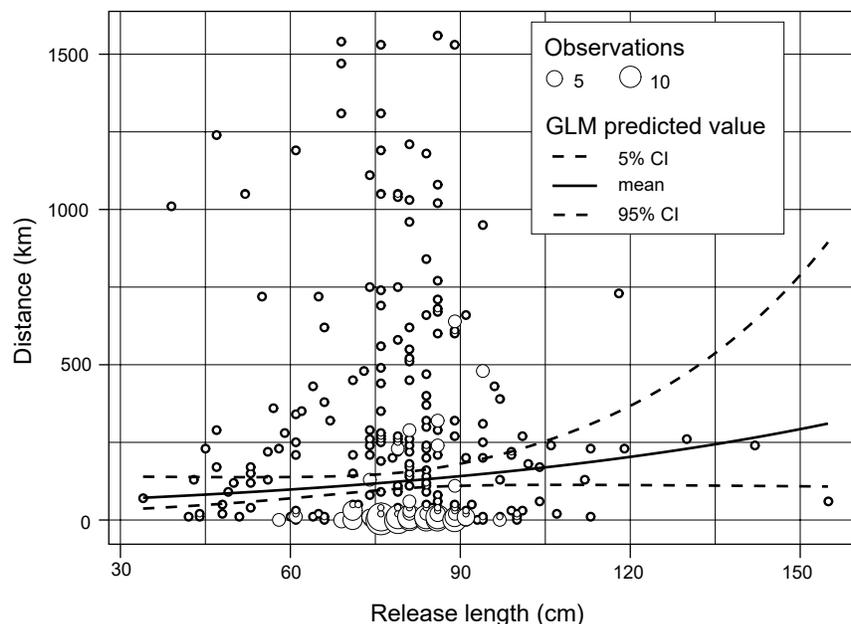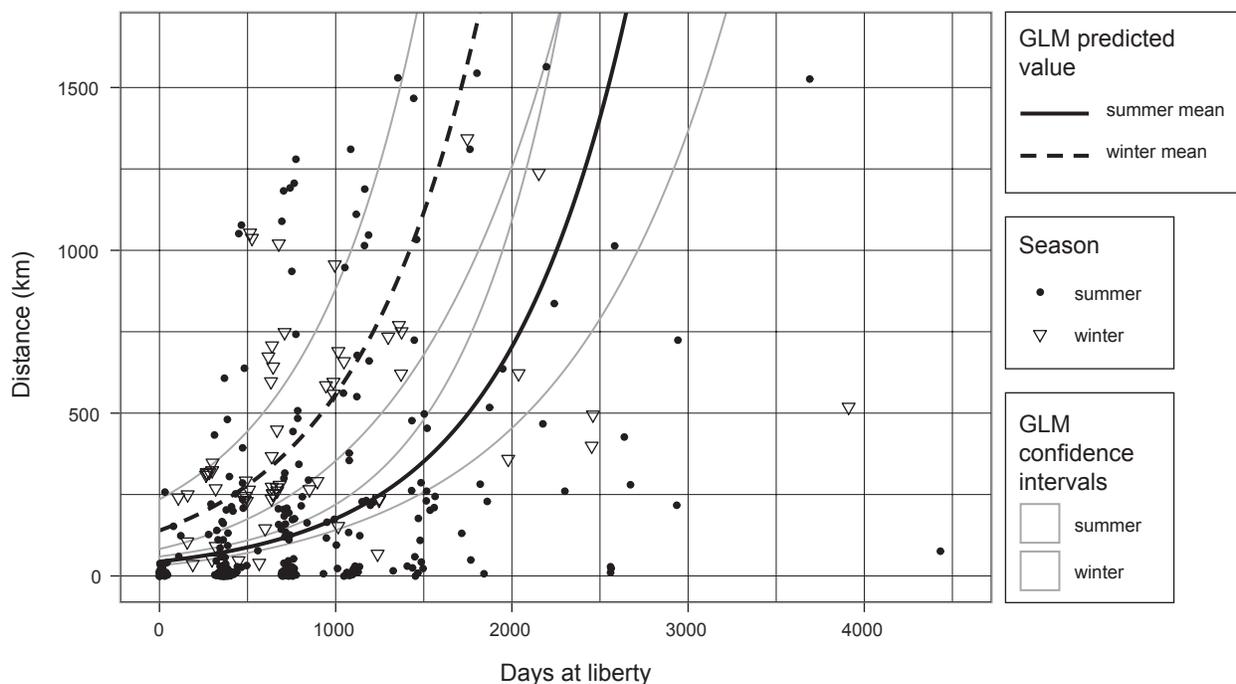

Fig. 4.   Ocean-only swimming distance of Atlantic halibut between release and recapture locations in and adjacent to the Gulf of Maine for tags with complete location data (*n* = 378) compared to days at liberty and season of recapture. The Generalized Linear Model presented here is the model with the best fit, including days at large, season, and release length as predictors.
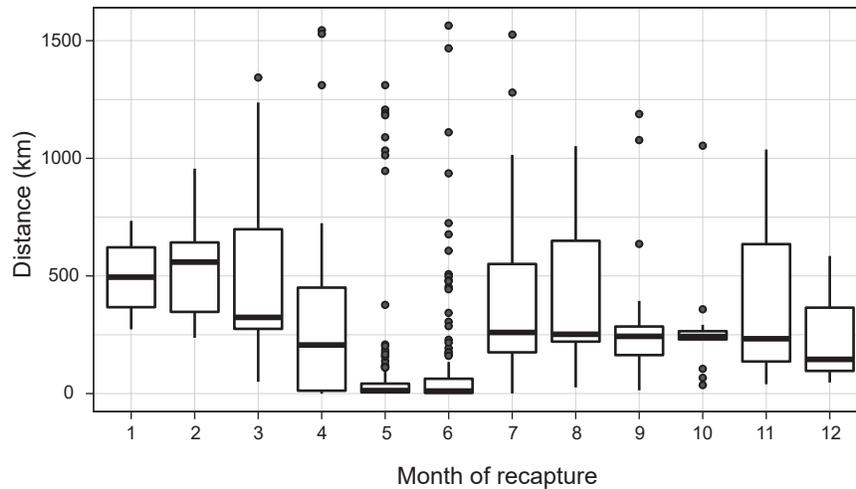
Fig. 5.   Boxplots of minimum distance travelled by Atlantic halibut between release and recapture locations in and adjacent to the Gulf of Maine for tags with complete location data (*n* = 378) compared to month of recapture. Note that sample sizes for November, December, and January recaptures are very small (*n* = 3, 3, 5 respectively). Boxplots include median (solid line), interquartile range (hinges), closest point to 1.5*interquartile range (whisker), and outliers (points).

behavior for Atlantic halibut from the Gulf of Maine given enough time, while resident (sedentary and homing) behavior decreases in frequency. The results reported here support the continued persistence of both contingents.

Conventional tagging studies and biases

The use of conventional tags warrants careful interpretation of results. Recovery of conventional tags depends on capture efforts and subsequent reporting, which when inconsistent over time and space may result in biases (Webster *et al.*, 2013). Therefore, the relatively large proportion of tag returns from Canada since the early 2000s is difficult to interpret as it may reflect greater fishing effort in the targeted Canadian halibut fishery compared to that in U.S. Federal and Maine state waters, rather than a true behavioral phenomenon. Specifically, Canadian landings have increased from a yearly average of 1 484 mt in 2000–2009 to 3 263 mt in 2016 (DFO, 2018) whereas U.S. catch, consisting mostly of non-target bycatch from the multispecies fishery but also including targeted longline catch from Maine state waters, was 108 mt in 2016 (New England Fisheries Management Council 2017). Alternatively, the increase in recaptures from Canada does agree with the finding that days at liberty has a positive effect on distance at recapture, and the increased timeframe during which recaptures are reported in this study allowed halibut to move into Canadian waters. In addition, as the Hague Line separating U.S. and Canadian waters was only a short distance from

most releases the slight increase in median distance at recapture from 12 to 32 km since the previous study likely has resulted in more fish recaptured across a border that was only a median distance of 72 km away for tagged and released fish. Any future study that seeks to establish mixing rates between the two jurisdictions will need to estimate fisheries-dependent effects (Webster *et al.*, 2013), as well as reporting rates (Rago, 2017). This work with conventional tags does establish that, at a minimum, 43% of fish released in the U.S. Gulf of Maine are at some time vulnerable to the Canadian fishery, and this could greatly confound a U.S. stock assessment that must estimate discard and fishing mortality (Rago, 2017).

The presence of a seasonal effect on recapture distance adds to the uncertainty over the relative extent of mixing between the U.S. and Canada. As most of the tagged fish were released and recovered in the Maine state waters commercial fishery, which only occurs in May and June, estimates of small distance movement are likely inflated and summer-to-winter recaptures are likely relatively undetected. The U.S. federal waters multispecies fishery does land fish in Maine throughout the year, though landings are generally lower in winter (Portland Fish Exchange, 2019) and most of the effort in this fishery occurs outside of the tagging release area (New England Fisheries Management Council, 2017). This likely leads to inflated estimates of winter movement if some tagged fish did not leave the summer tagging area where they would not be vulnerable to winter recapture. While the

Table 2.   Different formulations and associated AICs and residual deviances for generalized linear models (Gamma
          distribution, log link) with swimming distance of Atlantic halibut tagged in the Gulf of Maine as response variable.
          DAL = Days at liberty.

Model predictors	AIC	Residual deviance	Null deviance	Residual d.f.	Null d.f.
NULL	3897.5	1392.3	1392.3	340	340
DAL, Season, Release length, Season: Release length	3823.1	1172.4	1392.3	336	340
DAL, Season, Release length	3821.6	1173.6	1392.3	337	340
DAL, Season	3822.7	1181.6	1392.3	338	340
DAL	3852.0	1261.7	1392.3	339	340

number of returns from Canada could be enhanced by more directed fishing effort overall, the relative magnitude of winter migrations into Canadian waters could also be an underestimate if fish tagged in the Gulf of Maine are more likely to be present in Canadian waters during winter as the directed Canadian fishery is less active in winter months (Themelis and den Heyer, 2015). However, these examples of potential biases, seasonal and otherwise, are neither comprehensive nor conclusive in their direction, and there may be further issues presented by any unknown effects on reporting rates by gear type, season, or year. We would suggest that what appears to be a seasonal effect in these results should not be interpreted beyond providing a clue regarding potential movement patterns. These patterns could be a basis for future studies that can better avoid these biases, such as with electronic tagging (*e.g.* Le Bris *et al.*, 2018).

Implications for assessment, management

These results provide evidence that the current management boundary between U.S. and Canadian stocks does not represent a strict population boundary. It is clear from these results that a large proportion of fish tagged in the U.S. waters of the Gulf of Maine spend at least part of their lives in Canadian waters where they are vulnerable to the Canadian fishery. This could reflect the existence of a demographically-meaningful stock boundary extending across the Hague Line, conflicting with current assumptions used for assessment (Rago, 2017; DFO, 2018). Additionally, it appears that a contingent of Gulf of Maine halibut from U.S. waters displays residency there. Data from this study cannot give precise estimates of stock boundaries or mixing rates, but nevertheless do provide evidence that current assumptions surrounding halibut stocks need to be readdressed in both science and management.

If future studies confirm that stock boundaries cross the Hague Line, it is possible to assess and manage Atlantic

halibut through a Transboundary Resource Assessment Committee (TRAC), as has been done for eastern Georges Bank cod, haddock, and yellowtail flounder (Martin *et al.*, 2017; Barrett *et al.*, 2017; Legault *et al.*, 2017). Simply incorporating some estimate of mixing may alleviate certain issues with the U.S. assessment, and allow for a formal assessment beyond the current "Plan B" approach (Rago, 2017). However, just as the current unit stocks are not assessed together, they are not surveyed together. Without DFO halibut longline survey coverage in the Gulf of Maine, it may not be plausible to extend their assessment methods to the west (DFO, 2018). The National Marine Fisheries Service bottom trawl survey, which extends to the Western Scotian Shelf, may offer a unified survey for juvenile biomass. Regardless of how a possible cross-boundary stock unit would be assessed and managed, failure to acknowledge the underlying biological population structure occludes the ability to do either, and bears an increased risk of depletion (Boudreau *et al.*, 2017).

In conclusion, this study illustrates that fish tagged in the Gulf of Maine exhibit a spectrum of migratory behaviors including site fidelity and dispersive movements, and this could have ramifications for how we delineate stock boundaries. Fish are recaptured at greater distances in winter and with more days at liberty, but at all sizes, in all seasons, and over the course of days or many years some fish are caught close to the release point while others are caught 1 000 km or more away, suggesting the presence of resident and migratory or exploratory contingents. At an absolute minimum, 43.2% of fish tagged in the U.S. portion of the Gulf of Maine spend at least some time in Canadian waters. This number is substantially higher than the mixing rate found by Kanwit (2007) when reporting earlier results of this study, underlining the importance of many years of returns for tagging of long-lived fish with complex life histories. Given the high level of fishing mortality in the Canadian fishery for fish released by American fishermen, there is a need for managing the

fish across international boundaries through the TRAC process (Shackell *et al*., 2016), as well as potentially at a finer-scale in Canada (Boudreau *et al*., 2017). Further research into genetic relations among spawning groups sampled during spawning season, as well as young of year fish including those present in the Gulf of Maine (Beaty and Chen, 2017), may help to describe the extent to which metapopulations in the Northwest Atlantic are demographically discrete. In addition, further electronic tagging with finer temporal sampling intervals could help to show if and where fish from the Gulf of Maine and Western Scotian Shelf are spawning and what this means for stock definition.

Acknowledgements

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

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Abstract

The NAFO divisions 3NOPs4VWX5Zc Atlantic halibut (*Hippoglossus hippoglussus* 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 hippoglussus* 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-Macphee, 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

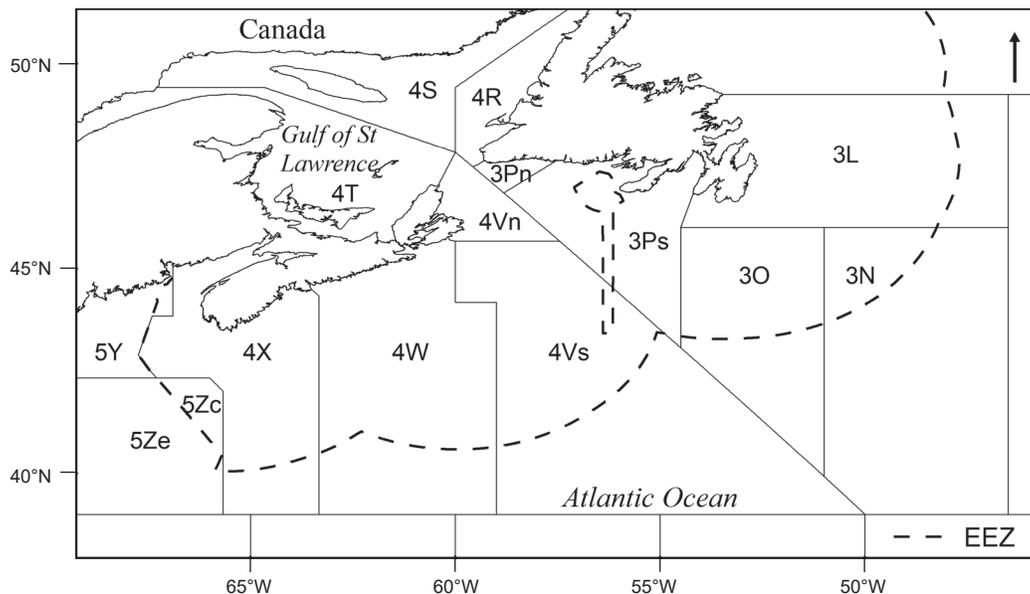Fig. 1.   Northwest Atlantic ocean showing NAFO divisions 3NOPs4VWX5Zc, the stock unit for Atlantic Halibut (DFO, 2015). Dashed line represents exclusive economic zone (EEZ). NAFO shapefile obtained from: https://www.nafo.int/Data/GIS, EEZ shapefile obtained from: http://www.mari-neregions.org/gazetteer.php?p=details&id=8493, and world map shapefile obtained from: 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 ~7°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 °C*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°C over the 12 month period (Fig. S2). The lower threshold of 3°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
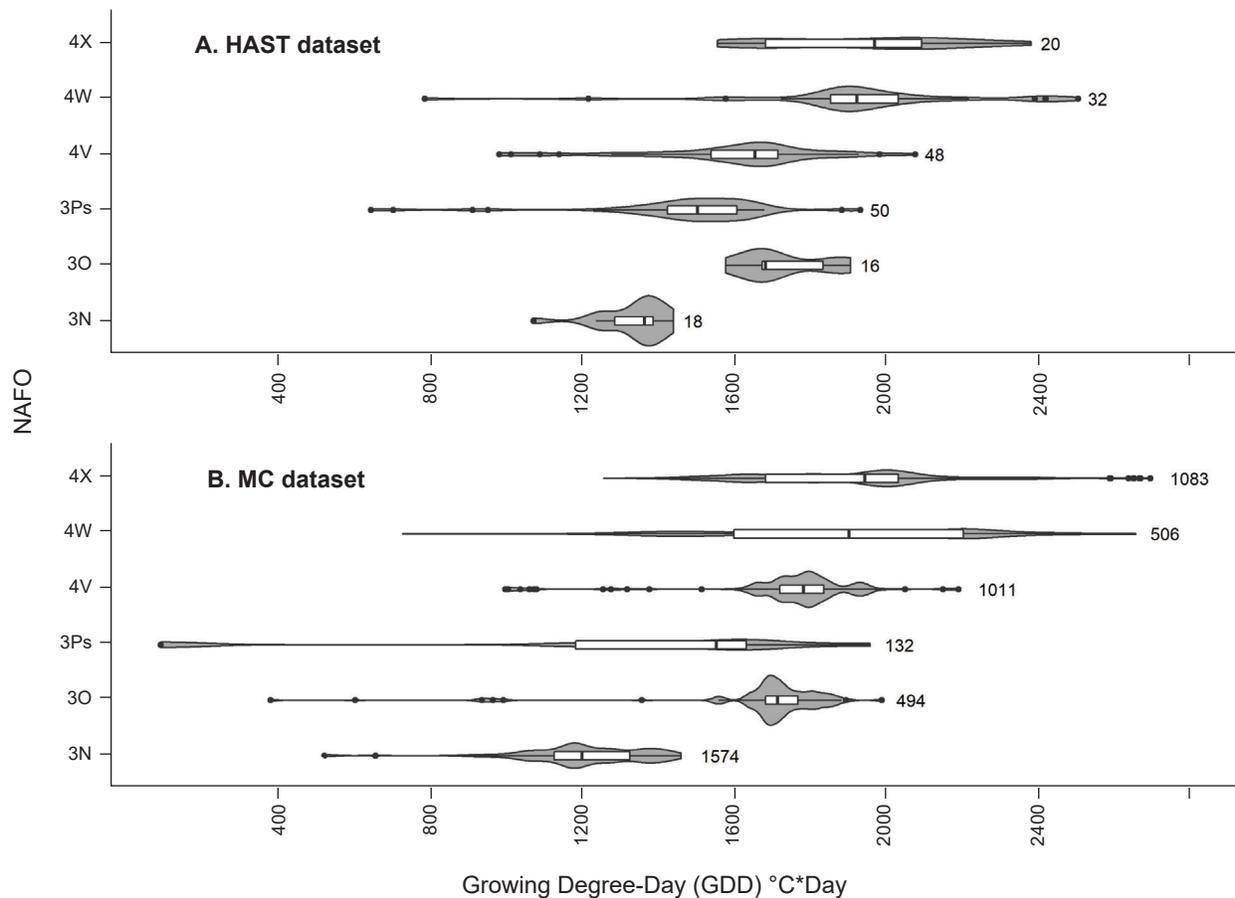
Fig. 2.   Boxplots overlaying violin plots of annual Growing Degree-Day (GDD °C*day) across NAFO divisions for **(A)** HAST dataset used to estimate growth rate and **(B)** MC dataset used to estimate LM50%. Sample sizes within each NAFO division/dataset are inset. Boxplot lines represent the lower and 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.

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

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).

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

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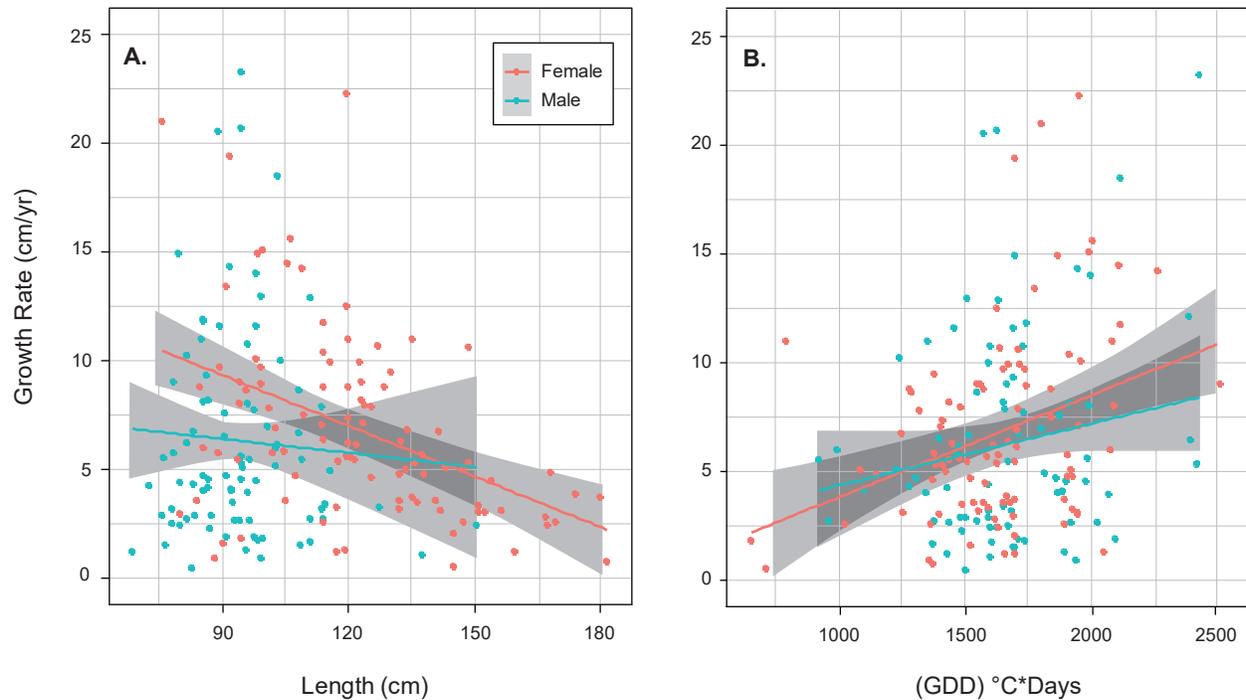
Fig. 3.   Growth rate of males (blue) and females (red) as **(A)** a function of length (cm) and **(B)** growing degree-day
          (GDD °C*day). Lines are the fitted linear model. The grey shading represents the 95% confidence intervals.

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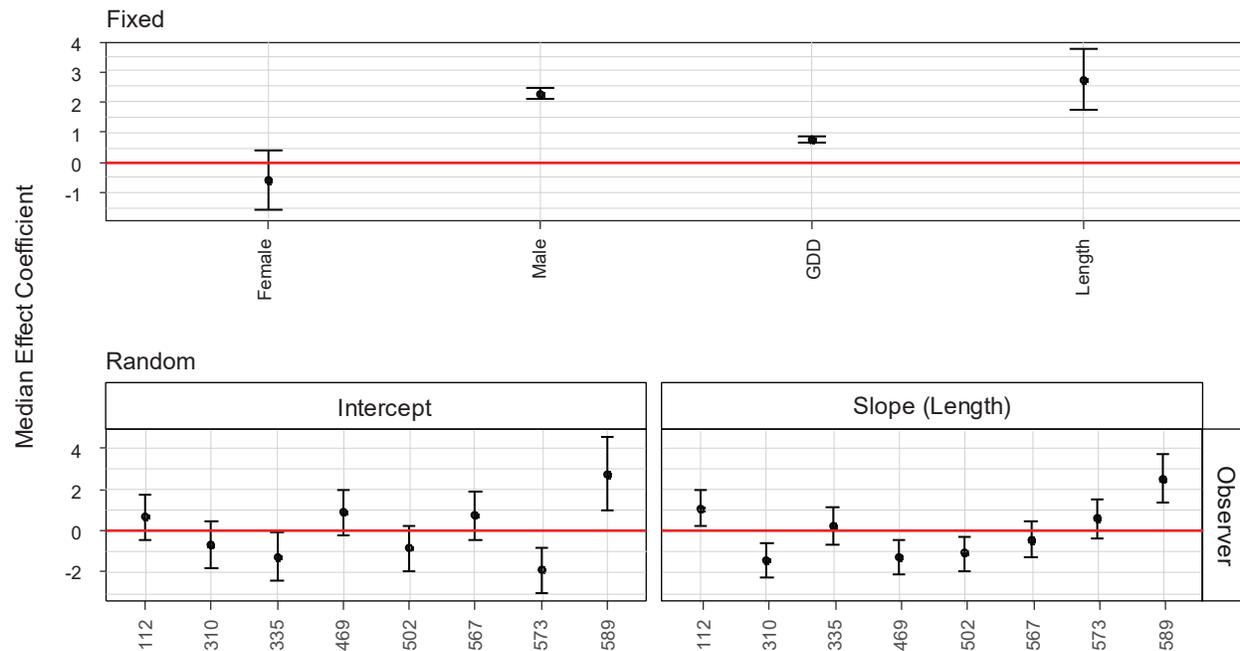
Fig. 4.   Simulated median estimates (*n* = 1 000) of fixed (top) and random (bottom) effects parameters of final Maturity Status model derived from posterior distributions. Median estimates that overlap 0 are not significantly different from 0, or each other. Observer numbers are displayed on X axis.

Discussion

Female halibut grew faster and matured at larger sizes than males reflecting the sexual dimorphism of the species (Kohler, 1967; Collette and Klein-Macphee, 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
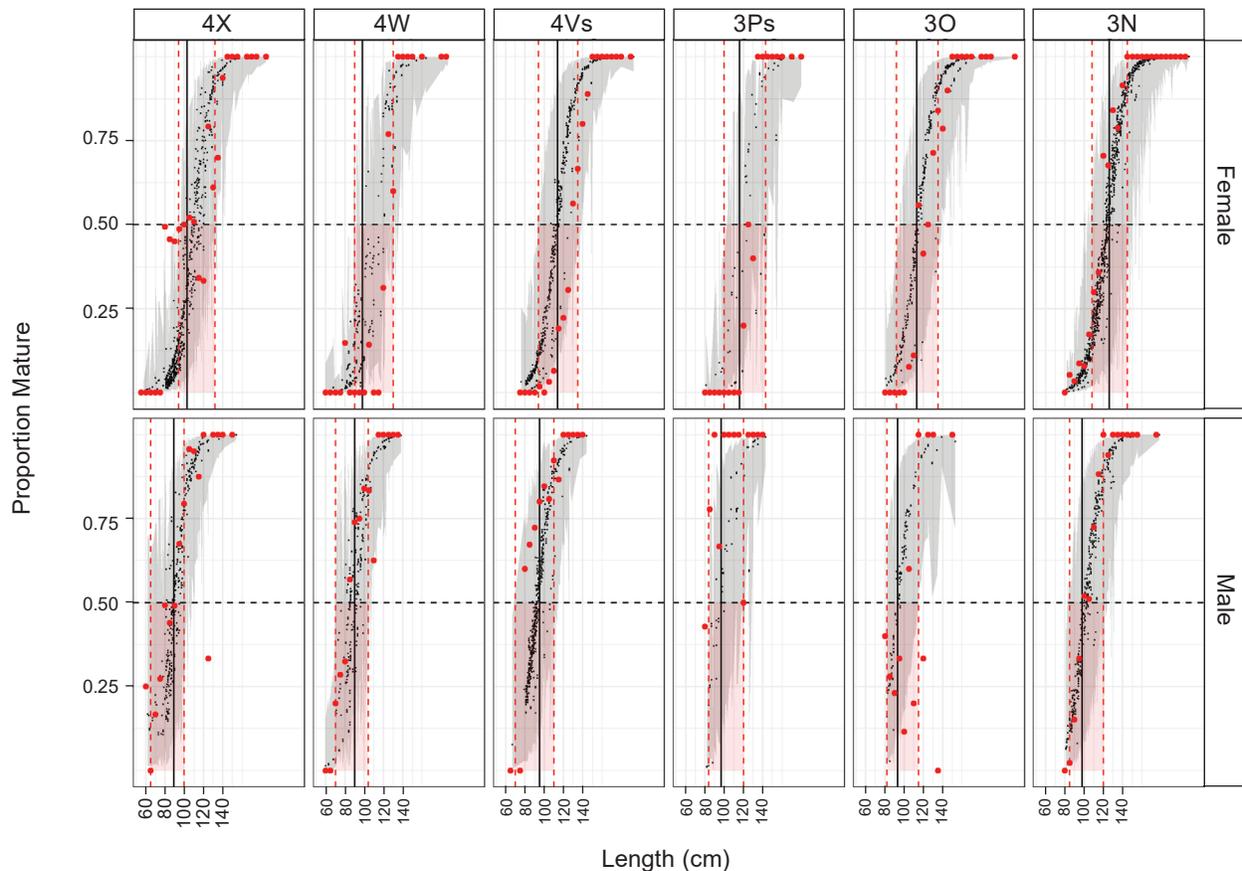
Fig. 5.   Proportion Mature in each NAFO division for each sex. Model predictions (black points) and intervals generated by simulation (*n* = 1000). Red points represent observed proportion mature. Horizontal dashed line shows proportion mature of 0.5, vertical solid black line is the LM50%. Pink shaded area refers to length range of LM50%, estimated as the lengths corresponding to the intersection when upper/lower prediction interval is ~0.5.
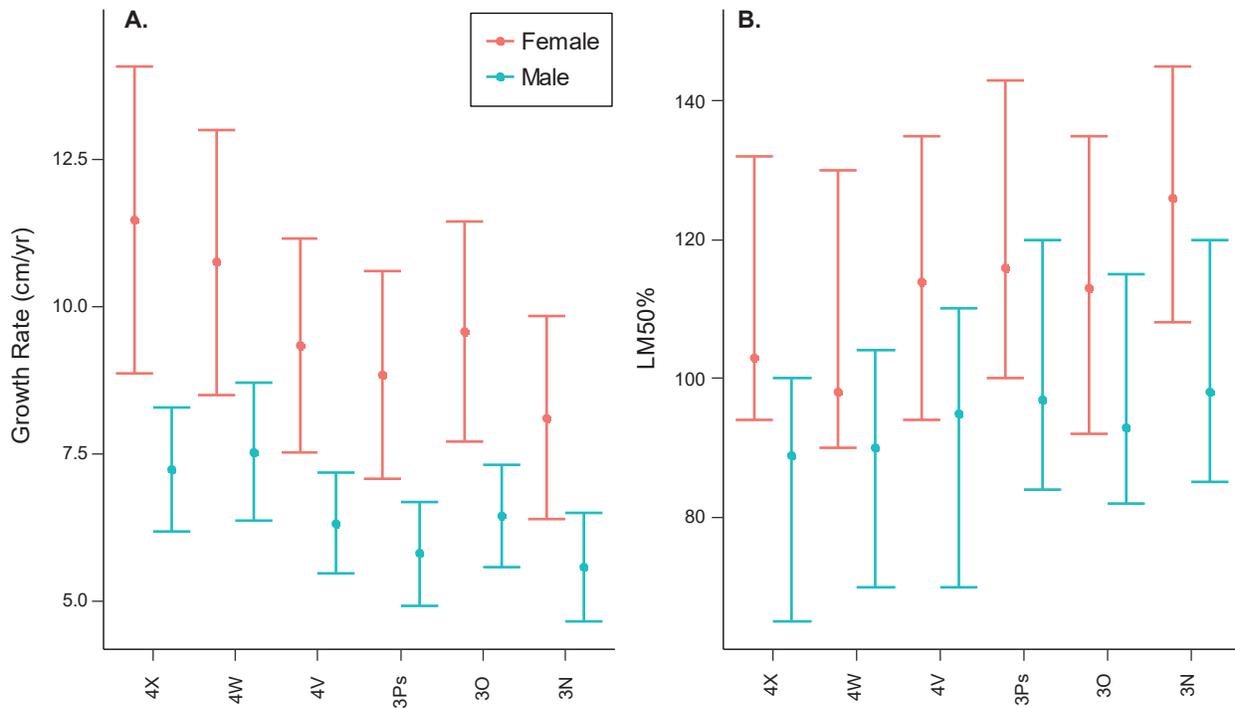
Fig. 6.   Predicted **(A)** growth rate of males (blue) and females (red) at 90 cm and **(B)** Length at Maturity (LM50%) for each NAFO division.

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.

Acknowledgements

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Development of a climate-niche model to evaluate spatiotemporal trends in *Placopecten magellanicus* distribution in the Gulf of Maine, USA

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Abstract

We developed a climate-niche species distribution model to evaluate spatiotemporal trends in Atlantic sea scallop (*Placopecten magellanicus*) along the coastal waters of the Gulf of Maine. We used a Tweedie-generalized additive model (GAM) to quantify the relationships between scallop abundance and key environmental variables. A boosted regression tree was used to identify significant interactions among environmental variables to integrate within the Tweedie GAM and a regional circulation model was incorporated with the Tweedie GAM to hindcast projections of scallop distribution and assess the impacts of environmental change on this species. Additionally, we evaluate two common model fitting and variable selection methods for GAMs to ensure high model performance. A classic backward variable selection procedure was compared to penalized thin plate regression splines. Projections from the climate-niche species distribution model show higher scallop density along inshore areas relative to those farther offshore. An increasing temporal trend in scallop density was observed along inshore areas and a decreasing temporal trend was observed in areas farther offshore. Additionally, we found that the GAM incorporating thin plate regression splines outperformed the widely used backwards stepwise procedure. This modeling framework will help to inform adaptive management strategies for the scallop fishery within the context of a changing Gulf of Maine ecosystem.

Keywords: Species distribution models, generalized additive models, model selection, *Placopecten magellanicus,* Gulf of Maine

Introduction

Atlantic sea scallops (*Placopecten magellanicus*) support a highly valuable fishery in the United States. However, the scallop fishery within Maine state waters is relatively depleted. The fishery there bottomed out in 2005 when only 33 000 lb was taken, about 1% of what was landed in the early 1990s (Kelly 2012). However, recent years have shown an increasing trend in scallop abundance, with over 800 000 lb landed in 2018, allowing for an opportunity to establish a persistent, valuable fishery through research-informed management and conservation efforts (Kelly, 2012).

The distribution and abundance of species are central concepts to ecological research and vital components of conservation planning and fisheries management (Franklin, 2010). Species distributions are influenced by many interacting biotic and abiotic processes that can manifest as complex occurrence-environment relationships (Boulangeat *et al*., 2012; Merow *et al*.,

2014). Thus, a key step in understanding the biogeography of species is identifying environmental factors that regulate the distribution of a species (Merow *et al*., 2014). Like most benthic species*,* scallop abundance and distribution are influenced by an array of interacting variables such as depth, current, temperature, and salinity (Stokesbury and Himmelman 1995, Hart and Chute 2004).

Throughout their geographic range, scallops occur mainly at depths of 15 to 110 m, but can be found as shallow as 2 m in the northern part of its range (Naidu and Anderson 1984, Carsen *et al*., 1995). Temperature is an important environmental factor influencing growth rates of this species with adult scallops showing optimal growth at temperature between 10–15°C and temperatures above 21°C being lethal (Stewart and Arnold 1994). This species prefers full strength seawater (~35 ppt), with salinities of 16.5 ppt or lower being lethal (Stewart and Arnold, 1994). Scallops are usually found in environments with strong currents (Hart and Chute, 2004), and flow velocity has been shown to be a key factor controlling waste removal,

oxygen uptake, feeding, and growth rates (Stewart and Arnold, 1994; Shumway and Parsons, 2006). Optimal growth for this species occurs near 0.1 m s⁻¹ (Wildish and Saulnier, 1992) and feeding inhibition has been observed to start at ~0.25 m s⁻¹ (Pilditch and Grant, 1999). While the influence of key environmental variables on bivalve ecology is apparent, quantitative evaluations of scallop-environment relationships and spatiotemporal trends of distribution are uncommon (Shumway and Parsons, 2006; Mendo *et al.*, 2014).

Water temperatures within the Gulf of Maine (GoM) have increased over the past 35 years at an average rate of 0.026°C yr⁻¹ (Mills *et al.*, 2013; Pershing *et al.*, 2015). Rapidly increasing temperatures are changing the distribution of numerous marine species (Overholtz *et al.*, 2011, Howell and Auster, 2012, Hollowed *et al.*, 2013), with many fish stocks undergoing a poleward shift in their center of biomass and/or an increase in depth (Nye *et al.*, 2009). Scallop distribution has also been shown to be impacted by climatic variability (Frank *et al.*, 1990, Kurihara 2008). Dickie (1955) and Caddy (1979) demonstrated that higher temperatures in the Bay of Fundy were correlated with changes in scallop abundance. Additionally, climactic changes may alter larval development as well as the survival of juvenile and adult scallops (Dickie, 1955; Caddy, 1979). Considering a changing GoM ecosystem (Mills *et al.*, 2013; Pershing *et al.*, 2015), it is important to document the importance and potential synergistic effects of climate forcing on the dynamics of species abundance and distribution.

In this study, we use data describing the distribution of scallops in the GoM to develop a climate-niche species distribution model (SDM). This SDM predicts the spatial distribution of scallops within the inshore Gulf of Maine across unsampled areas and hindcasts spatiotemporal changes in the distribution of scallops from 2005–2013 to evaluate the effects of shifting environmental conditions on this species. We used Tweedie-generalized additive models (GAMs) to quantify the relationships between scallop abundance and key environmental variables. Additionally, we evaluate two prevalent model fitting and variable selection methods for GAMs to ensure high model performance. A classic backward variable selection procedure was compared to penalized thin plate regression splines following Wood (2003, 2006). This modeling framework will help to inform adaptive management strategies for the scallop fishery within the context of a changing GoM ecosystem.

Materials and Methods

Study Area and survey data.

Dredge-based fishery-independent scallop surveys conducted over 15 years, from 2005 to 2017, by the Maine Department of Marine Resources were used for this modeling effort (DMR: Kelly, 2012; Fig. 1). Survey coverage extends out to 3 nm from shore from southern Maine to the Maine-Canadian border, USA (Fig. 1). This dataset comprised two annual random systematic surveys,
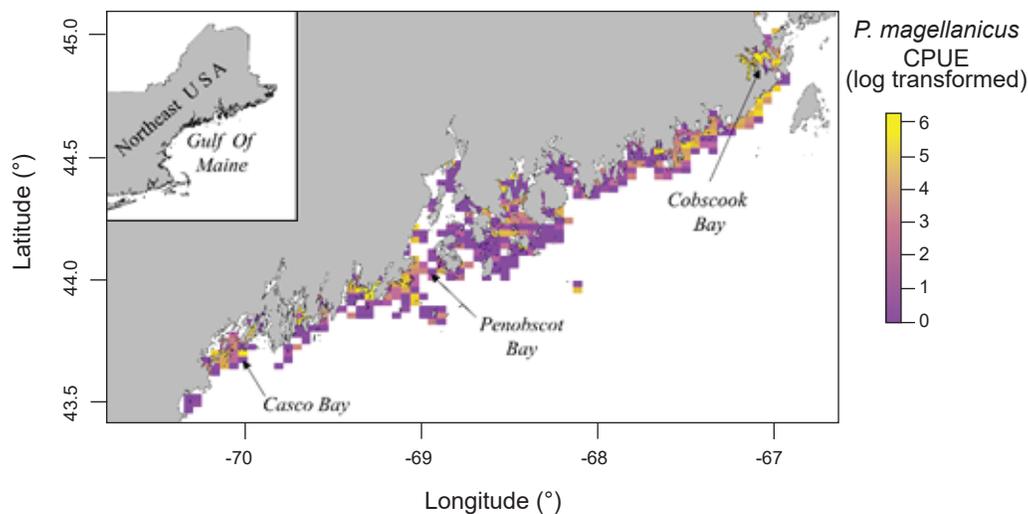
Fig. 1.　　Spatial distribution of natural log standardized scallop (*Placopecten magellanicus*) density from the Maine Department of Marine Resources Scallop Dredge Survey from 2005–2017. The study area encompasses nearshore waters of Gulf of Maine from Casco Bay to the Maine-Canada border.
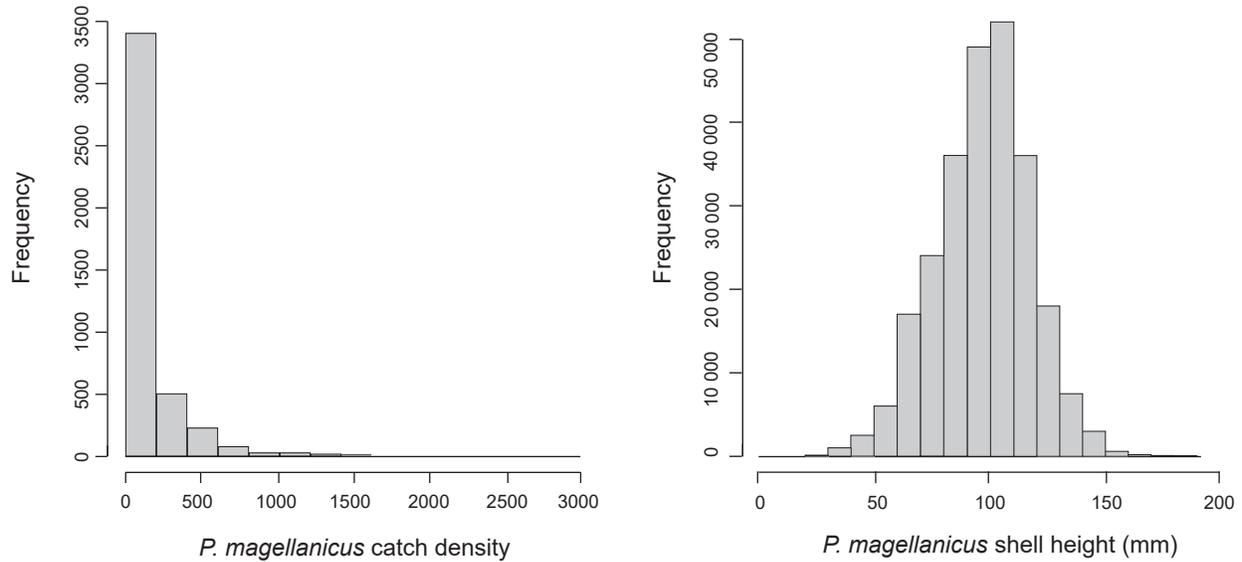
Fig. 2.   Frequency plots of scallop (*Placopecten magellanicus*) density (left) and size frequency (right) in the density data from the Maine Department of Marine Resources Scallop Dredge Survey.

one in the spring survey covering alternating portions of inshore Maine waters and one in the fall covering select coastal areas. The gear used for both surveys is an unlined, 7 ft. New Bedford style drag with 2 in rings, 1.75 in head bale, 3.5 in twine top, 10 in pressure plate and rock chains. Since scallops <65 mm in shell height were not efficiently sampled with the 2 in rings (Kelly 2012), these were excluded from all analyses. Tows were conducted at 3.5–4 knots and lasted ~ 2.5 minutes. A total of 4 321 tows were made yielding 507 911 total observed scallops in this dataset (Fig. 2). All tows from the survey were included within the modeling framework. Scallop abundance from each tow was standardized to catch-per-unit-effort (CPUE) over a 2.5-minute tow.

The GoM is characterized by a mixture of oceanic influences directly affected by the Labrador Current, the Gulf Stream, and the freshwater discharge from the St. Lawrence River (Tremblay 1997; Drinkwater and Gilbert, 2004). As such, water temperature follows a gradient moving up the coast and offshore. Within the study area, scallops were found where maximum yearly temperature ranged from 8°C in deeper areas to 16°C in shallow areas. Salinity ranged from 26 ppt in areas subject to freshwater inputs to full seawater (35 ppt) in offshore locations. The Maine covered depths to ~110 m, since scallops are uncommonly found outside of this depth range (Hart and Chute, 2004), with the majority of tows occurring in <60 m.

Environmental data

Because the DMR surveys did not measure temperature, salinity, or current velocity, the Finite-Volume Community Ocean Model (FVCOM), a regional ocean circulation model developed by the University of Massachusetts-Dartmouth and the Woods Hole Oceanographic Institution (Chen *et al.*, 2006) was used to simulate monthly estimates of bottom temperature, salinity, and current velocity from 2005 to 2013. It has a horizontal resolution ranging from 0.02 km to 10 km and captures complex and irregular coastal geometry, making it suitable for physical and biological studies in coastal regions and estuaries (Chen *et al.*, 2011). FVCOM predictions were matched to survey tows from the nearest neighboring FVCOM node during time of sampling (Fig. 3). Horizontal current velocity was calculated to approximate the magnitude of water flow at a given FVCOM node. Current velocity C was estimated at station i, and year y from FVCOM predictions using the following equation:

$$C_{i,y} = \sqrt{(u_{i,y}^2 + y_{i,y}^2)}$$

where C is the magnitude of the predicted current velocity and u and y are the x and y vector components of the velocity(Chen *et al.*, 2011; Torre *et al.*, 2018). Bathymetry data were obtained from the U.S. Coastal Relief Model (CRM) (National Geophysical Data Center, 1999).

Response variable

Maine DMR Scallop Dredge
Survey (2006–2007)

↓

P. Magellanicus catch density

Environmental predictors

Button temperature (C)
Bottom salinity (ppt)   ←   Finite Volume Community
Current speed (m/s)   Ocean Model (FVCOM)
Depth (m)
                               ←   Coastal Relief Model
                                   (CMR)

Identify potential covariates

Boosted regression tree (BRT)

Model building

Generalized Additive Model (GAM)   →   **Use best**   →   **Visualization of spatiotemporal**
using Tweedie distribution   **preforming model**   **distribution of *P. Magellanicus***

                                                                 Spatial distribution of
Model fitting and variable selection   *P. Magellanicus* catch density

Stepwise backward selection   Temporal change in
Thin plate regression splines   *P. Magellanicus* catch density

Model evaluation

AIC & BIC
Cross validation

Fig. 3.   Schematic diagram of the modeling framework implemented in this study. All data exploration
and modeling procedures were conducted within the R programming environment.

Generalized additive models

A generalized additive model (GAM) was used to make spatiotemporal predictions of scallop distribution in the inshore GoM (Fig. 3). Conceptually, GAMs are generalized linear models with a linear predictor upon which smooth functions are applied to covariates (Guisan *et al*., 2002, Marra and Wood, 2011). The strength of GAMs lie in their ability to handle, in a multivariate regression setting, non-linear and non-monotonic relationships between the response and covariates that arise often in nature (Guisan *et al*., 2002). Resulting from their ability to deal with a variety of distributions that occur in ecological data, the use of GAMs has been extensively applied to species distribution modeling efforts (Guisan *et al*., 2002, Sagarese *et al*., 2014, Young and Carr, 2015).

Terms included within the full model were selected according to boosted regression tree (BRT) analysis (Elith *et al*., 2008), and bivariate interaction terms were also identified and included based on this analysis. BRT models

were used to determine the relative importance of each environmental variable with relation to scallop density. Bivariate terms were included when interaction between two variables in the BRT was considered high (>100).

Formulation of the GAM for the estimate of scallop CPUE can be expressed as follows:

$$g(n) = \alpha + \sum_{j=1}^{p} S_j(\chi_j) + \varepsilon$$

where $g(.)$ is a log link function between the response variable, n, and each additive predictor, x_j; α is the intercept term; s_j are smooth functions of the predictors, represented by either cubic splines, that are linear or nonlinear, or thin plate regression splines with a penalty; ε is the residual error (Wood, 2003; Marra and Wood, 2011). Predictors comprised either a single variable or interacting pair of variables that are thought to relate to scallop distribution (Table 1). Smooth terms were used in

Table 1.   Variables used in generalized additive modeling of scallop (*Placopecten magellanicus*) density in the nearshore Gulf of Maine.

Variables	Description
Longitude (°)	Measurement of longitude of tow starting location
Latitude (°)	Measurement of latitude of tow starting location
Bottom Temperature (°C)	bottom temperature at tow location (imported from FVCOM)
Bottom Salinity (ppt)	bottom salinity at tow location (imported from FVCOM
Current Velocity (m s^{-1})	current velocity at tow location (imported from FVCOM)
Depth (m)	depth at tow location

FVCOM: Finite Volume Community Ocean Model

conjunction with a pair of variables to model interactions. Where cubic splines were used, the maximum value for degrees of freedom were set at 5 for univariate functions and 30 for bivariate functions. These values were chosen as a balance between over generalization and over-fitting as suggested in the literature (Zuur *et al.*, 2009, Sagarese *et al.*, 2014). Statistical analyses were carried out within the R programming environment (R Core Team Development 2016). Boosted regression tree analysis was done using the *dismo* package (Hijmans *et al.*, 2017) and GAMs were fitted using the *mgcv* package (Wood, 2011).

A Tweedie distribution was used as the likelihood to measure GAM fit to account for a high proportion of zero-catch tows and skewness in the CPUE data (Fig. 2). The Tweedie distribution handles zero and positive values simultaneously, and works as a Poisson-Gamma compound distribution when the power parameter *p* is greater than 1 but less than 2 (Li *et al.*, 2011; Wood 2011). This distribution has been shown to outperform other methods for dealing with zero inflated data (Shono, 2008; Li *et al.*, 2011). Tweedie GAMs were fitted through a process of optimizing its profile likelihood. Power parameter *p* was estimated with the range of $1 < p < 2$ during the fitting process (Shono, 2008; Wood, 2011; Tanaka *et al.*, in review).

Final GAMs were used to predict the density of scallops at every FVCOM node in the study area during 2005–2013. Predictive fields were interpolated using ordinary kriging with a semivariogram function to produce continuous model outputs (Bailey and Gatrell, 1995, R Core Team Development 2016). Predicted density of scallops was aggregated temporally by obtaining the median density value over the 8-year study period at each FVCOM node. Median values were used as opposed to means because they provide a clearer interpretation of the tendency over the study period, *i.e.* not susceptible to skewing in rare cases of outliers. Linear regression was performed at every

FVCOM node and the derived slope (*β*) coefficient was used to evaluate temporal change in predicted density of scallops over the 8-year study period.

Model selection

In this modeling framework, two methods of fitting and variable selection were performed to assess their relative performance (Fig. 3). Here, performance signifies both a balance between goodness of fit and parsimony, and maximizing prediction accuracy while maintaining model interpretability (Marra and Wood, 2011). The first method of model fitting and variable selection was a conventional backwards stepwise procedure (BSP), where terms were removed iteratively from an initial full model using AIC (Akaike, 1974). This method is widely used in ecological modeling due to its simplicity and demonstrated effectiveness (Burnham and Anderson, 2002; Marra and Wood 2011). During each step, the variable with the lowest *p*-value was removed and AIC was recalculated for the reduced model. This iterative process was repeated as long as variable removal lowered AIC.

The second method of model fitting and variable selection was a shrinkage approach where each variable in the full model was fitted with a thin plate regression spline including a thin plate spline penalty (TPRS). These are low rank isotropic smoothers of covariates that include a modification to the smoothing penalty, so that whole terms can be reduced to zero, effectively removing superfluous variables (Wood 2003; Marra and Wood, 2011). Unlike the stepwise algorithm from BSP, this procedure is carried out in a single step.

Model Validation

The performance of final models from BSP and TPRS was evaluated using multiple evaluation criteria (Fig. 3).

Two traditional model evaluation criteria, AIC and BIC (Burnham and Anderson 2002, Wood 2006), were used to compare relative performance of BSP and TPRS. AIC and BIC are widely used as model evaluation criteria. AIC is an estimator of the relative quality of statistical models based on goodness of fit. BIC is closely related to AIC, but has been shown to penalize complexity to a higher degree than AIC (Hastie, 2009).

A cross-validation study was implemented to evaluate predictive performance of final GAMs, where a randomly selected subset, training data, (80% of all data) was used for GAM development, while the remaining 20%, testing data was used for the evaluation of performance (Smith 1994; Wood 2006; Zuur *et al.*, 2007; Tanaka and Chen, 2015, 2016). The GAM-predicted CPUE values based on training data were compared against observed CPUE values, based on testing data, and linear regression analysis was performed to evaluate the predictive performance of the GAM. The cross-validation procedure was repeated 100 times using random data selection in each round to obtain 100 sets of linear regression parameters (intercept, slope, and R^2). Good model performance was indicated by an intercept parameter close to zero, a slope close to one and an R^2 close to one.

Results

GAM performance

Full GAMs included nine terms in total (Tables 2 and 3). Single terms included latitude (°), longitude (°), depth (m), bottom temperature (°C), bottom salinity (ppt), and current velocity (m/s). BRT analysis identified strong two-way interactions (value >100) between three pairs of variables, depth-latitude (163.13), salinity-temperature (112.79), and longitude-latitude (125.10) (Table 2). All three of these two-dimensional terms were significant and included in both full and final GAMs (Table 3, Fig. 4 and 5).

Model fitting and variable selection using BSP went through two iterations of term removal. Depth was removed during the first round and bottom temperature was removed during the second round. Deviance explained for the parsimonious BSP model was 48.60 %. Model fitting and variable selection using TPRS, similarly, penalized depth to a high degree (edf = 0.05, Table 3, Fig. 4) to where it had a negligible effect on predictions. The effect of both bottom temperature (edf = 0.91) and longitude (edf = 0.94) on scallop density were reduced to almost linear relationships (Table 3, Fig. 4). Deviance explained for the parsimonious TPRS model was 49.70% (Table 3).

While overall model performance was similar between the parsimonious BSP and TPRS GAMs, TPRS model slightly outperformed BSP model across all evaluation criteria (Table 3, Fig. 6). AIC and BIC were lower in the TPRS model (AIC = 42 274.97, BIC = 42 888.10), suggesting its superior performance over the BSP model (Table 3). Assessed by cross validation, the TPRS model showed higher predictive performance (α = -0.60, β = 1.02, R^2 = 0.42) compared to the BSP model (α = -2.278, β = 1.04, R^2 = 0.41; Fig. 6). Therefore, the TPRS model was determined to be more appropriate than the BSP model in this study.

Model predictions.

The parsimonious TPRS GAM was used to map model predictions over the inshore GoM. Model results show that nonlinear relationships commonly exist between environmental variables and scallop density; however, both bottom temperature and longitude were reduced to decreasing, near-linear relationships by the TPRS model. The response curves for scallop density as a function of bottom salinity and current velocity were dome shaped, with salinity peaking between 27–32 ppt and current velocity peaking between 0.10–0.17 (m/s). Because depth

Table 2.   Results from boosted regression tree analysis. Higher values are associated with stronger interaction between variables. Variable pairs with a value > 100 were considered to have a "strong" interaction and included as terms in the generalized additive models.

	Longitude	Latitude	Bottom Temperature	Bottom Salinity	Current Velocity	Depth
Longitude	0	125.1	13.33	46.73	5.34	30.65
Latitude	0	0	60.15	12.93	8.55	163.13
Bottom Temperature	0	0	0	112.79	24.78	44.98
Bottom Salinity	0	0	0	0	49.63	27.83
Current Velocity	0	0	0	0	0	4.77
Depth	0	0	0	0	0	0
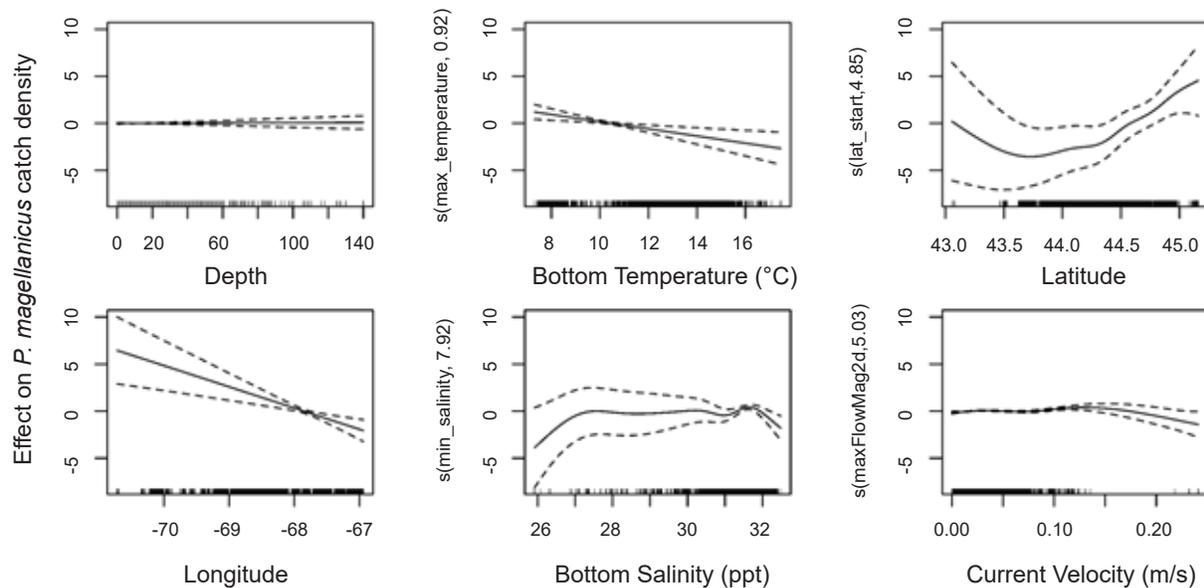
Fig. 4.   Plots describing the partial effect of significant univariate explanatory variables in the thin plate regression spline generalized additive model. The response curves describe the relationship between a given environmental term and smoothed density of scallops (*Placopecten magellanicus*). Tick marks on the x-axis correspond to number of observations.

was penalized out of the TPRS model, this response curve was flat.

Interactions included in this model (latitude-longitude, latitude-depth, bottom temperature-bottom salinity), identified using BRT analysis, were included to capture the common effect of single environmental variables operating within a more complex composite of factors directly controlling species distribution (Austin, 2007, Araujo and Peterson, 2012). For example, salinity in this model acts as a proxy for broad spatial patterns in scallop distribution which is shown by the strong interaction between salinity and temperature detected within the model, and likely corresponds to the origin of water mass existing in a given area (MacDonald and Thompson, 1985a, 1985b; Macdonald *et al*., 1987).

Predicted scallop density was higher (>20 scallops per m^2), in general, along inshore areas relative to offshore areas (<5 scallops per m^2) (Fig. 7). Select estuaries along the Maine coast show significantly higher (>60 scallops per m^2) predicted scallop density relative to other inshore areas. In particular, the Cobscook Bay area shows high predicted density (>100 scallops per m^2) relative to surrounding areas (Fig. 7). Additionally, offshore waters in Western Maine show slightly higher predicted density (10–20 scallops per m^2) relative to Eastern Maine (<10 scallops per m^2) (Fig. 7). Over the 8-year study, predicted

density shows a strong increasing trend along inshore areas and a decreasing trend in offshore areas (Fig. 8). Cobscook Bay and Penobscot Bay show stronger increasing trends relative to other inshore areas and offshore waters in Western Maine show a stronger decreasing trend in predicted density relative to Eastern Maine.

Discussion

Decision-making associated with conservation planning and fisheries management should use as much information and knowledge as possible to maximize the benefits of management actions (De Ornellas *et al*., 2011). The model developed in our study was designed to use an existing dataset describing both the abundance and distribution of Atlantic sea scallops to develop a climate-niche species distribution model (SDM). Our Tweedie GAM approach produced high quality predictions of abundance for scallops. Model outputs agree generally with consensus of the distribution of scallops along coastal Maine according to fishermen knowledge, the distribution of fishing effort in the area, as well as landings information (not able to be shown here due to confidentiality agreements). Thus, we consider this modeling effort a successful approach to predict the distribution of scallops across unsampled areas.

This study provides a regional projection in the distribution of scallops within the inshore GoM and hindcasts these
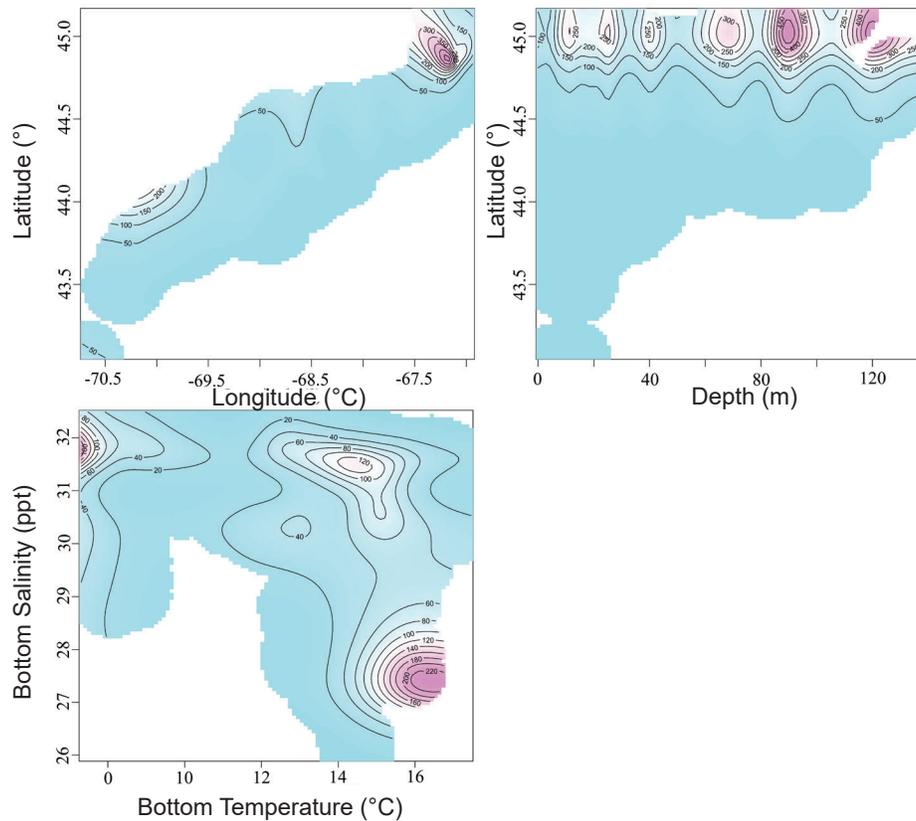
Fig. 5. Partial generalized additive model plots depicting the significant interaction effects of bivariate environmental variables included in the modeling framework.

projections back eight years. A dominant spatial trend made apparent by this climate-niche SDM is a decline in predicted density moving from inshore to offshore locations. This finding corresponds with habitat value for scallops being higher among inshore areas relative to offshore areas likely attributed to deteriorating food availability moving offshore (Torre *et al.*, 2018). This is thought to represent a natural gradient of habitat quality (Sarro and Stokesbury, 2009).

An increasing temporal trend in climate-driven scallop density was observed for inshore areas with a decreasing trend in offshore areas (Fig. 8). Any change in density over time results from changes in dynamic environmental variables (bottom temperature, bottom salinity, and current velocity), suggesting that the composite of these three factors has changed favorably regarding scallop abundance from 2005–2013 in inshore areas and has changed unfavorably in offshore areas. These trends assume that scallop-environment relationships have remained consistent over the study period (Pearson and Dawson, 2003, Crisp *et al.*, 2009, Catullo *et al.*, 2015). This general temporal trend is reflected in a recent study

which depicts the spatiotemporal distribution of available scallop habitat in the GoM using a bioclimate envelope model (Torre *et al.*, 2018).

The TPRS GAM, incorporating a Tweedie distribution for zero-inflated catch data was shown to be a useful prediction tool according to cross validation. The response curves in general agreed with known information about drivers of scallop distribution (Naidu and Anderson, 1984; Thouzeau *et al.*, 1991; Wildish and Kristmason, 1993; Stewart and Arnold, 1994; Pilditch and Grant, 1999; Hart and Chute, 2004; Torre *et al.*, 2018).

Depth in the case of this modeling framework was not significant, and so was penalized out of the TPRS model. In other studies, scallops have been shown to grow more slowly (MacDonald and Thompson, 1985; Thouzeau *et al.*, 1991) and occur at reduced densities (Schick *et al.*, 1988; Shumway and Parsons, 2006) at deeper depths; however, the example given here is comprised of areas that were surveyed in less than 100 m, as opposed to scallops occupying deep areas in other studies (up to 170 m in the case of Schick *et al.*, 1988). Since, within the current

Table 3. Generalized additive models for scallop (*Placopecten magellanicus*) density in the nearshore Gulf of Maine with deviance explained by the model (Dev. Exp.), Akaike Information Criterion (AIC), and Bayesian Information Criterion (BIC). The terms in models are latitude (La), longitude (Lo), depth (De), bottom temperature (Bt), bottom salinity (BS), and current velocity (Cv). Edf = estimated degrees of freedom. Greyed out terms are variables that were removed from the model. *Denotes the highest performing model from each category (thin plate regression spline and backwards stepwise).

Model	edf	Dev. explained	AIC	BIC
Thin plate regression spline w/ penalty				
*s(La) + s(Lo) + s(De) + s(Bt) + s(Bs) + s(Cv) +s(La*Lo) + s(Bt*Bs) + s(De*La)	4.84, 0.94, 0.05, 0.91, 7.92, 5.03, 24.21, 21.11, 20.16	49.70%	42 274.97	42 888.10
Backwards stepwise				
s(La) + s(Lo) + s(De) + s(Bt) + s(Bs) + s(Cv) +s(La*Lo) + s(Bt*Bs) + s(De*La)	2.64, 1.00, 1.00, 1.00, 3.47, 3.85, 25.04, 21.12, 20.03	48.60%	42 361.42	42 919.23
s(La) + s(Lo) + s(De) + s(Bt) + s(Bs) + s(Cv) +s(La*Lo) + s(Bt*Bs) + s(De*La)	2.644, 1.00, 1.00, 3.47, 3.85, 25.04, 21.12, 21.03	48.60%	42 358.74	42 908.00
*s(La) + s(Lo) + s(De) + s(Bt) + s(Bs) + s(Cv) +s(La*Lo) + s(Bt*Bs) + s(De*La)	2.644, 1.00, 3.47, 3.85, 25.04, 22.16, 21.03	48.60%	42 357.53	42 902.99
s(La) + s(Lo) + s(De) + s(Bt) + s(Bs) + s(Cv) +s(La*Lo) + s(Bt*Bs) + s(De*La)	2.654, 1.00, 3.85, 25.07, 24.41, 21.09	48.40%	42 370.16	42 905.51

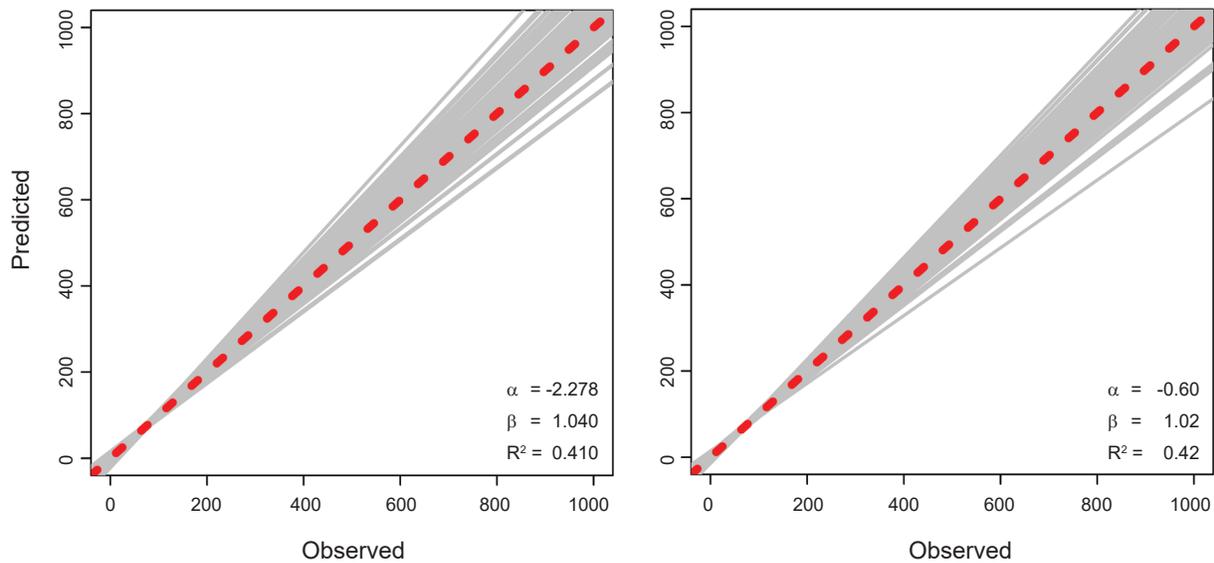

Fig. 6.   Diagnostic plots depicting the comparison of model performance between the parsimonious generalized additive model produced by backwards selection and thin plate regression splines. Predictive performance was assessed by cross validation. A graphical summary of observed vs predicted scallop (*Placopecten magellanicus*) density based on 100 runs of random data sampling are displayed.

study, the dataset describing scallop distribution has low contrast in depth, it follows that depth is not a critical environmental component in this modeling framework.

The results show that, overall, a shrinkage approach where each variable in the full GAM was fitted with a thin plate regression spline including a thin plate spline penalty (TPRS) performed better across all model evaluation criteria than a classic, backwards selection procedure (BSP) for predicting scallop density. These results support findings from Marra and Wood (2011), which used simulated data to show that shrinkage approaches perform significantly better than competing approaches (including BSP) in terms of predictive ability, and are competitive in terms of variable selection performance. However, when using simulated data, the advantage of one modeling approach over another depends on the underlying structure of the simulated data, which makes it difficult to select a "best procedure" for all situations (Binder and Tutz, 2008). For example, Marra and Wood (2011) suggest that BSP would be preferred over shrinkage approaches in situations where the data have particularly high information content. Hence, using real-world data to evaluate the utility of model fitting and variable selection methods, as they apply to species distribution modeling, adds an important dimension to comparisons made with simulated data.

In addition to direct model performance benefits offered by TPRS, compared to BSP, shown here and in Marra

and Wood (2011), there are other considerations that need to be taken into account when choosing an appropriate method for model fitting and variable selection. Stepwise procedures, such as BSP, have the potential to be inconsistent due to high sensitivity to small variability in the response data, which can sometimes lead to very different subsets of chosen variables. Additional variation in application of stepwise procedures results from a dependence on the initial starting path chosen through the variable space (Marra and Wood, 2011). Another downside of these procedures is that during variable selection and hypothesis testing using the selected model, p-values associated with model terms do not take into account variable selection uncertainty, and can therefore be misleading (Marra and Wood, 2011). Conversely, shrinkage approaches have been shown to be a valid alternative to stepwise procedures in terms of consistency among iterations of application, and increased robustness to variability in the data (Marra and Wood, 2011). Moreover, since variable selection in shrinkage approaches is carried out within a single step these methods are less computationally demanding, especially when using larger datasets (Leathwick *et al.*, 2006, Hesterberg *et al.*, 2008).

An important limitation of this modeling framework is that the development of species distribution models relies upon environmental data, and as with any environmental data there are several possible sources of error that could cause misrepresentation of model predictions. The
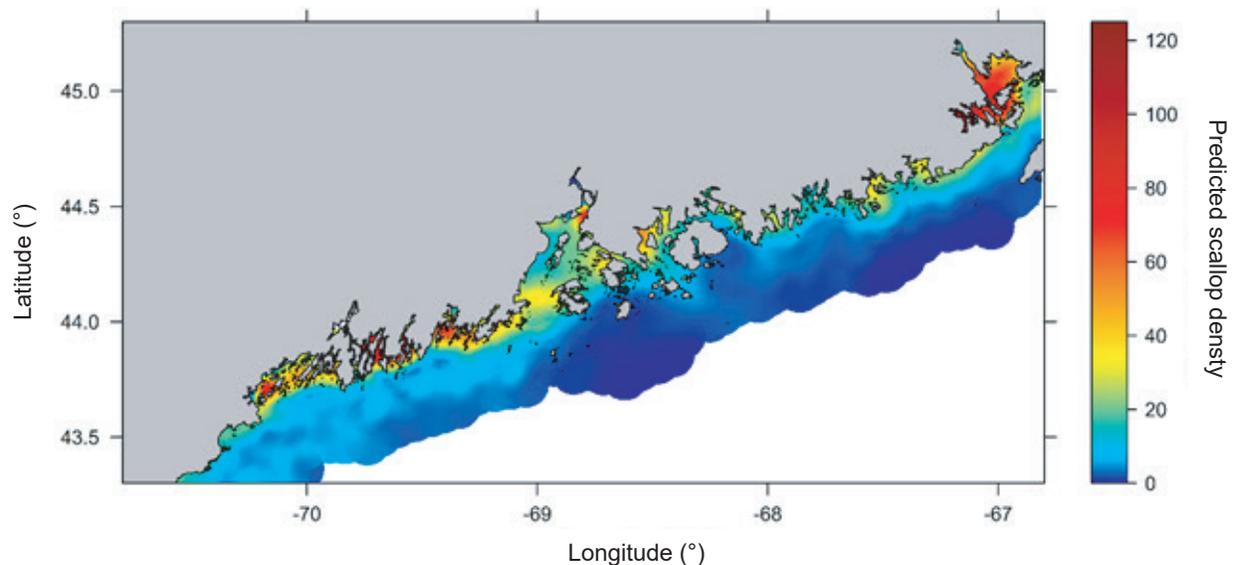
Fig. 7.   Map showing the spatial distribution of median predicted density of scallops (*Placopecten magellanicus*) in the nearshore Gulf of Maine from 2005–2013. The color ramp corresponds to predicted density (scallops per m²), where blue indicates low catches and red indicates high catches.
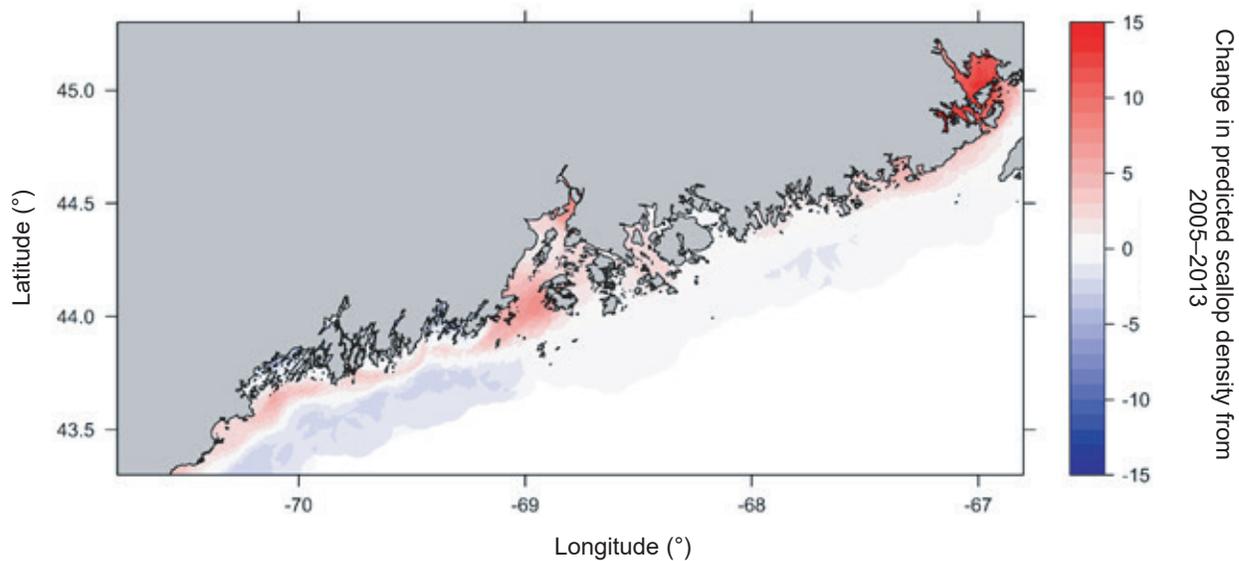
Fig. 8.   Map showing the temporal change in predicted density of scallops (*Placopecten magellanicus*) in the nearshore Gulf of Maine waters from 2005–2013. The color ramp corresponds to the degree of change in predicted density. Red areas have a positive change and blue areas have a negative change.

current modeling framework relies particularly heavily upon FVCOM predictions. To evaluate performance of FVCOM within the study area, Tanaka and Chen (2016) and Li *et al.,* (2017) performed comparisons between environmental monitors on observed temperature data to and FVCOM predictions. They found that in general, FVCOM adequately captured broad spatial and temporal trends in bottom temperature and salinity which adds validity to the quality and accuracy of FVCOM predictions.

In this study, environment-density relationships for scallops were defined upon only four environmental variables when, many physical, biological, and chemical conditions likely factor into the life history and distribution of this species. However, variables used to train the generalized additive model may have functioned as surrogates for factors directly controlling scallop distribution through physiological mechanisms (Austin, 2007; Araujo and Peterson, 2012). From the associations between variables we can infer the relationship between spatiotemporal variability of environmental factors, habitat quality, and resulting scallop distribution. For example, salinity in this model may act as a proxy for broad scale spatial patterns in scallop distribution due to the inherent relationship between salinity and the origin of water mass existing in a given area. Environmental predictors in this study were selected based on availability and assumed correlation with scallop density. As more

comprehensive environmental data becomes available in the future, studies to develop a further detailed species distribution modeling approach could include additional variables such as pH, dissolved oxygen, predator-prey, and other food-web interactions to capture a more comprehensive representation of scallop ecology (Araújo and Luoto, 2007).

The climate-niche SDM developed in this study establishes the ability to quantify relationships between a commercially important fish stock and the surrounding environment, which provides a tangible tool to visualize species distribution over space and time as well as to evaluate potential impacts of a changing GoM ecosystem. Also, our real-world evaluation of two common GAM selection and fitting procedures provides insights into the effectiveness of each method and can be incorporated into further research using GAMs. This modeling approach is highly generalizable to a variety of commercially important species and can advise conservation efforts for the scallop fishery in the GoM to help ensure the implementation of adaptive management strategies under uncertain climate conditions.

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Ávila de Melo, A. M., Power, D. , and Alpoim, R. MS 2005. An assessment of the status of the redfish in NAFO Division 3LN, *NAFO SCR Doc.*, No. 52, Serial No. N5138, 19 p.

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