Investigating the Impact of Multiple Factors on Gray Meats in Atlantic Sea Scallops (Placopecten magellanicus)

Authors: Liese A. Siemann, Luisa M. Garcia, Carl J. Huntsberger, and Ronald J. Smolowitz

Source: Journal of Shellfish Research, 38(2) : 233-243

Published By: National Shellfisheries Association

URL: https://doi.org/10.2983/035.038.0203

Journal of Shellfish Research, Vol. 38, No. 2, 233–243, 2019.

INVESTIGATING THE IMPACT OF MULTIPLE FACTORS ON GRAY MEATS IN ATLANTIC SEA SCALLOPS (*PLACOPECTEN MAGELLANICUS*)

LIESE A. SIEMANN,[1]* LUISA M. GARCIA,[1] CARL J. HUNTSBERGER[1,2] AND RONALD J. SMOLOWITZ[1]

[1]*Coonamessett Farm Foundation, Inc., 277 Hatchville Road, East Falmouth, MA 02536;* [2]*Darling Marine Center, University of Maine, 193 Clarks Cove Road, Walpole, ME 04573*

ABSTRACT The Atlantic sea scallop fishery is the one of the most valuable fisheries in North America. There is concern about scallops with low-quality adductor muscles, referred to as gray meats, impacting the fishery and the overall health of the stock because an apicomplexan parasite has been linked to gray meats and a mass mortality event that led to the collapse of the Icelandic scallop fishery. Yet, changes in scallop meat color have also been linked to the depletion of energy reserves in the adductor muscle following spawning. Seasonal scallop dredge surveys were conducted across Georges Bank, collecting data on scallop meat quality, scallop abundance, mortality, and reproductive cycles, as well as environmental parameters, including bottom depth and temperature. To investigate multiple causes for gray meats, a set of models were developed to examine the impact of biotic and abiotic factors on gray meat prevalence and meat quality of individual scallops. Model results indicate that different factors influence gray meat prevalence on the southern and northern parts of Georges Bank. In the south, location was a significant factor for predicting the presence of gray meats, highlighting Closed Area I where an outbreak of gray meats occurred after the area reopened to fishing. Yet in the north, reproductive stage was a significant factor, with scallops more likely to have discolored meats after spawning. Study results suggest that gray meats may be a symptom of poor condition that was caused by multiple factors and isolating a single cause may not be possible. Improved screening tests and continued monitoring of scallop health through targeted disease surveys is recommended.

KEY WORDS: apicomplexan parasite, gametogenesis, Georges Bank, scallop dredge, seasonal surveys, *Placopecten magellanicus*

INTRODUCTION

The Atlantic sea scallop *Placopecten magellanicus* (Gmelin, 1791) fishery is the one of the most valuable fisheries in North America, with 2016 landings worth more than $488 million (NMFS 2017). In recent years, there has been increasing concern about scallops with low-quality adductor muscles, commonly referred to as gray meats, impacting the fishery and the overall health of the sea scallop stock (Inglis et al. 2016, Levesque et al. 2016). Because an apicomplexan parasite has been linked to gray meats and contributed to a mass mortality event that led to the collapse of the Icelandic scallop fishery (Kristmundsson et al. 2015), understanding the cause of gray meats and potential impacts on the Atlantic sea scallop population has become a management priority.

Gray meats were first reported in the literature from sea scallops found in Canadian waters in the Bay of Fundy in the 1930s, with the condition being attributed to senescence (Stevenson 1936). Medcof (1949) later reported observations of gray meats in scallops with shell parasites during surveys off Nova Scotia. In U.S. waters, scallops with stringy gray meats and boring sponge infestations were caught by fishermen in the Nantucket Lightship Closed Area in 2004–2005 (Stokesbury et al. 2007). More recently, when Closed Area I (CAI) on Georges Bank was reopened to scallop fishing in 2011, after an extended closure to protect groundfish, there was a short period of high-intensity fishing when high numbers of scallops with gray meats were observed, limiting the harvest of scallops from this area (Levesque et al. 2016). This recent event, coupled with gray meats being observed in the Habitat Area of Particular Concern (HAPC) at the northern edge of Closed Area II (CAII) led to concerns that prolonged area closures could result in high incidences of gray meats that could adversely impact the fishery (Rudders et al. 2013, 2014).

Gray meats have been linked to the presence of an apicomplexan parasite (Kristmundsson et al. 2011, Kristmundsson et al. 2015, Inglis et al. 2016, Levesque et al. 2016, Kristmundsson & Freeman 2018). The parasite *Merocystis kathae* (Dakin, 1911) was originally identified in common whelks *Buccinum undatum* (Linnaeus, 1758) and later found in Iceland scallops *Chlamys islandica* (Müller, 1776), queen scallops *Aequipecten opercularis* (Linnaeus, 1758), and king scallops *Pecten maximus* (Linnaeus, 1758) (Patten 1935, Kristmundsson et al. 2011). More recently, the same apicomplexan parasite was identified in Atlantic sea scallops (Inglis et al. 2016). The parasite has been identified in all colors of field-collected scallops, with higher numbers of the parasite present in scallops with discolored meats than in those with white meats (Inglis et al. 2016, Levesque et al. 2016, Garcia et al. 2018). A two-mollusc life cycle that includes the common whelk and a scallop has been hypothesized, with the apicomplexan parasite passing through the gastrointestinal tract of both hosts (Kristmundsson & Freeman 2018). In Iceland scallops, higher grades of infection, scored by the presence and numbers of apicomplexan zoites, were correlated with decreased adductor muscle and gonad indices (Kristmundsson et al. 2015).

Changes in scallop meat color have also been linked to the depletion of energy reserves and breakdown of adductor muscle following spawning, when discolored meats of low quality are routinely observed (Fisher 2000). Scallops store energy reserves in the adductor muscle as glycogen and protein, with both used during gonad development (Robinson et al. 1981, Barber & Blake 2016). The utilization of energy stored in the adductor

*Corresponding author. E-mail: lsiemann@cfarm.org
DOI: 10.2983/035.038.0203

muscle is less pronounced in environments with adequate food supply available during gametogenesis (Barber & Blake 1983, Luna-González et al. 2000), and this change in glycogen storage and muscle catabolism has been linked to depth for *Placopecten magellanicus* (Gould et al. 1988, Barber & Blake 2016).

Because Georges Bank is a highly productive area for the scallop industry, Coonamessett Farm Foundation has conducted seasonal scallop dredge surveys across the bank since 2011, and scallop meat quality, including meat color and condition, has been a focus since 2013. The survey also collects information on scallop abundance, mortality, and reproductive cycles, as well as environmental parameters, including bottom depth and temperature. The primary objective of this study was to develop a model to examine the impact of biotic and abiotic factors on gray meat prevalence in scallops from Georges Bank. The meat color of sampled scallops was also modeled to investigate the impacts of the same factors on individual health. The inclusion of factors such as reproductive stage and scallop mortality allowed investigation of multiple causes for gray meats in Georges Bank sea scallops.

MATERIALS AND METHODS

Sample Collection and Assessment

Five survey trips were conducted between August 2013 and March 2014 on the southern portion of Georges Bank and 15 survey trips between August 2015 and June 2017 on the northern portion of Georges Bank aboard commercial sea scallop fishing vessels. Surveys were performed every 6 wk in 2013–2014 and during preselected months in 2015–2017 (Table 1). The sampling locations were in areas open to fishing, the scallop access area in CAI, and in CAII on Georges Bank (Fig. 1). During each survey, two dredges were towed from the vessel: a standardized 4.6-m-wide Turtle Deflector Dredge and a 4.6-m-wide New Bedford–style dredge in 2013–2014 and two 4.6-m-wide Turtle Deflector Dredges with different aprons (seven row versus five row) in 2015–2017. Each tow passed through the center of the predetermined grid cell from a random start point. Under ideal conditions, the tows were 30 min long at 4.8 knots (8.89 km/h). Tow track locations were recorded every minute using the vessel navigation system and a GPS module included in the tablet used for data collection. Depth and bottom temperature were recorded every 30 sec by using a Star-Oddi DST milli-TD temperature-depth logger attached to the dredges.

After each tow, scallops and commercially important bycatch species were sorted, counted, and measured. Scallops were sorted into bushel baskets, and one representative bushel was selected for length-frequency measurements in 5-mm-size bins. In addition, the number of clappers, dead scallops, or shells with intact hinges in the measured bushel was recorded. Total scallop catch at each station was measured in bushels unless the catch was less than a bushel; in these cases, catch was recorded as a fraction of a bushel based on the number of scallops in the measured bushel and an average full bushel count of approximately 100 scallops. In 2013 and 2014, up to 20 scallops were collected to measure shell heights and meat weights and assess reproductive stage and meat quality at a subset of stations. Beginning in 2015, up to 30 scallops were collected at every station for these measurements and assessments unless fewer than 30 scallops were caught in the dredges overall. Meat quality was assessed based on a qualitative color scale with three categories with colors ranging from white to

TABLE 1.

Totals numbers of scallops assessed during each survey month.

Survey month and year	Number of scallops sampled
September 2013	396
October 2013	380
December 2013	364
January 2014	363
March 2014	399
August 2015	411
September 2015	558
October 2015	557
November 2015	605
January 2016	563
March 2016	654
May 2016	641
June 2016	527
July 2016	530
October 2016	517
November 2016	385
January 2017	483
March 2017	520
May 2017	628
June 2017	502

Surveys were performed every 6 wks in 2013–2014 and during preselected months in 2015–2017. Larger numbers of scallops were sampled starting in August 2015 because the number sampled per station increased from 20 to 30 scallops.

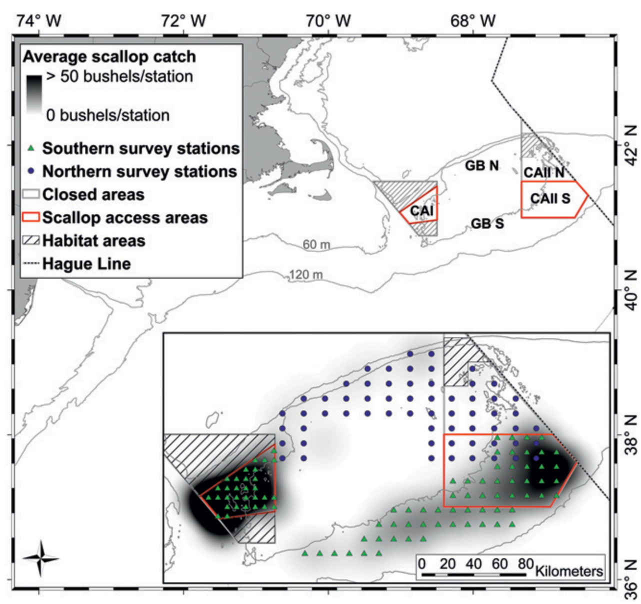

Figure 1. Map of survey location and defined survey areas, with (inset) smoothed average scallop catch and the locations of survey stations. CAI, Closed Area I; CAII S, Closed Area II south of 41° 30′ N; CAII N, Closed Area II north of 41° 30′ N; GB S, area open to scallop fishing on the southern portion of Georges Bank; and GB N, area open to scallop fishing on the northern portion of Georges Bank.

brown to gray (Fig. 2). Scallop reproductive stage was classified as developing, ripe, partially spent, or spent based on visual criteria including color, texture, and fullness (Naidu 1970). Because scallops were collected year round, sexually mature scallops were sampled before, during, and after spawning.

Data Analysis and Modeling

Total numbers of gray, brown, and white meat scallops observed during each trip were summarized by area (CAI = Closed Area I, CAII S = Closed Area II south of 41° 30′ N, CAII N = Closed Area II north of 41° 30′ N, GB S = area open to scallop fishing on the southern portion of Georges Bank, and GB N = area open to scallop fishing on the northern portion of Georges Bank). Because sampling methodologies changed between the 2013–2014 southern Georges Bank and 2015–2017 northern Georges Bank surveys, these areas were modeled separately.

Before running any models, the gray meat prevalence, percentage of spent scallops, clapper ratio, and scallop density were calculated for each station during each trip. The gray meat prevalence was estimated as follows:

$$\text{GM prevalence} = \frac{\text{No. of gray or brown scallops per station and trip}}{\text{total no. of scallops per station and trip}}.$$

Similarly, the percentage of spent scallops was calculated as follows:

$$\text{Spent percentage} = \frac{\text{No. of spent scallops per station and trip}}{\text{total no. of scallops per station and trip}}.$$

Both of these values were determined from the subset of scallops (≤30 animals) that were collected for meat quality analysis. The clapper ratio, used as a proxy for scallop mortality at each station (Merrill & Posgay 1964, Stokesbury et al. 2007), was calculated using totals from the entire measured bushel.

$$\text{Clapper ratio} = \frac{\text{No. of clappers in the measured bushel per station and trip}}{\text{No. of live scallops in the measured bushel per station and trip}}.$$

Scallop density (bushels/km^2) was calculated using the entire catch and dredge swept area, with the dredge width and the estimated tow length based on tow track coordinates (great circle distance using the haversine formula) used to compute dredge swept area (Robusto 1957).

Because it has been suggested that gray meat outbreaks may be linked to disease reservoirs in closed areas with older scallops (Inglis et al. 2016), the downstream distance from a closed area was calculated for each station. This was determined by measuring the distance between each station and the closest closed area boundary along bottom current streamlines. Measurements were made in ArcGIS, with distance vector orientation determined using a shapefile of Georges Bank bottom currents downloaded from the Northeast Ocean Data portal (http://www.northeastoceandata.org/data/data-download/). Distances were then categorized as within a closed area (distance = 0), less than 5 km from a closed area, between 5 and 10 km from a closed area, or greater than 10 km from a closed area.

The gray meat prevalence at each station for each survey trip was modeled using a quasibinomial distribution in the R package "mgcv" (generalized additive model function "gam" with family = "quasibinomial," link = "logit," and thin plate splines), with prevalence modeled separately for southern and northern stations because of the survey area shift between 2014 and 2015 (R Core Team 2017, Wood 2011). A quasibinomial distribution was used because the data was overdispersed with a

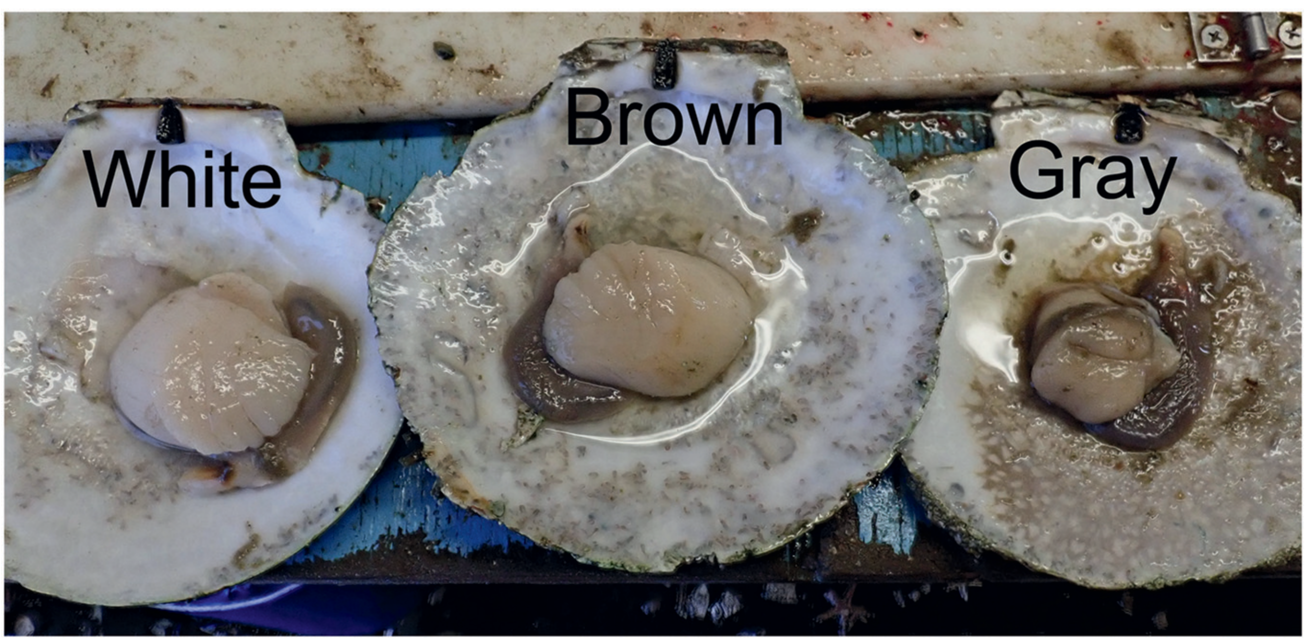

Figure 2. Image of scallops of approximately the same shell height with white, brown, and gray meats collected during the December 2018 trip, highlighting the changes in color and meat quality used to categorize scallops.

high proportion of zero values (Bolker 2017). Fixed effects available for modeling gray meat percentages included location (''easting'' and ''northing'' with latitude and longitude coordinates projected into UTM space using the R package ''rgdal''), bottom depth (29–106 m), bottom temperature (4–19°C), scallop density, clapper ratio, spent percentage, average shell height, area, and downstream distance from a closed area (km) (Bivand et al. 2015). Before running the models, fixed effect data that was highly skewed was log-transformed. Random effects for survey trip and station were added to the initial model (random effect smooth) to account for differences in gray meat state because of changes in survey vessels or survey protocol and any differences between survey stations. The final model was selected based on quasi-Akaike information criteria (qAIC) scores derived using the R package ''bbmle'' (Wood 2011, Shadish et al. 2014, Bolker 2017). The significance of the fixed effects in the final model were assessed using the function ''anova.gam'' in the R package ''mgcv,'' a function that uses a Type III ANOVA to assess model terms (Wood 2011).

Meat color of individual scallops, as gray meat presence (gray or brown) or absence (white), was modeled using a binomial distribution in the R package ''mgcv'' (generalized additive model function ''gam'' with family = ''binomial,'' link = ''logit,'' and thin plate splines), with meat color modeled separately for southern and northern stations (Wood 2011, R Core Team 2017). Fixed effects available for modeling gray meat state included survey station location, bottom depth, bottom temperature, scallop density, clapper ratio, shell height (60–193 mm), downstream distance, area, and reproductive stage. Random effects for survey trip and station were added to the initial model (random effect smooth) to account for differences in gray meat state due to changes in survey vessels or survey protocol and any consistent differences between survey stations. The final model was selected based on AIC scores (Akaike 1973), and the significance of fixed effects were determined using ''anova-gam'' (Wood 2011).

Model results were plotted using the R packages ''ggplot2'' and ''visreg'' (Wickham 2016, Breheny & Burchett 2017). Model fit was assessed based on the deviance explained by and histograms of observed predicted values from each final model. To visualize the geographical distribution of the prevalence model outputs, the observed gray meat prevalence and the predicted gray meat prevalence estimates were calculated for each station and mapped in ArcGIS.

TABLE 2.

Summary of the values of parameters included in the models. Gray meat prevalence was included as the dependent variable for one set of models, whereas the other variables were included as independent variables.

Variable	Mean	Range of values
Gray meat prevalence	4.1%	0%–100%
Scallop density	110.9 bushels/km^2	0.4–640.6 bushels/km^2
Shell height	132.7 mm	60–193 mm
Clapper ratio	2.6%	0%–93.3%
Spent percentage	3.4%	0%–100%
Depth	66.3 m	29.2–106.3 m
Bottom temperature	9.5°C	4–19°C

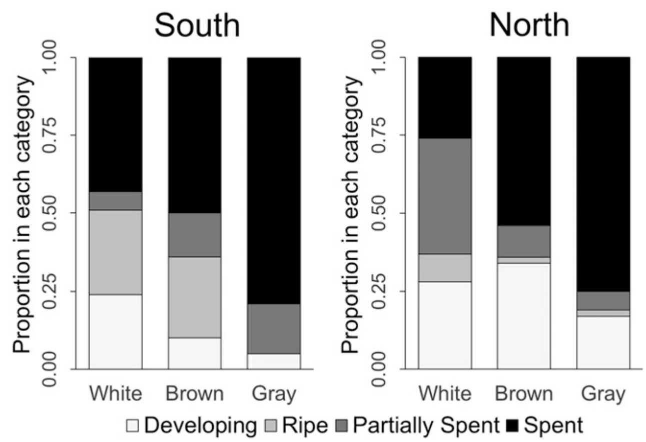

Figure 3. Proportion of scallops in each reproductive stage category by meat color for the southern and northern Georges Bank stations. Scallops of all sizes are included in this analysis, and all scallops were large enough to be sexually mature.

RESULTS

The mean values and ranges of the continuous variables used in the models are shown in Table 2. Observed gray meat prevalence spanned the whole range from 0% to 100%, with a mean prevalence of 4.1. Scallop densities ranged from 0.38 to over 640 bushels/km^2, with a mean of 110.9 bushels/km^2. Scallop shell heights ranged from 60 to 193 mm, and because scallops reach sexual maturity at age two (35–75-mm shell height), all scallops were large enough to be sexually mature (NEFSC 2018). The mean clapper ratio was 2.6% (0%–93.3%), with the highest ratios at stations with low scallop densities. The mean percentage of spent scallops was 3.4% (0%–100%). This value ranged from 0 to 2.0 (mean = 0.03), with the highest values observed in November and December. On both southern and northern Georges Bank, there was an increasing proportion of spent scallops as meat color progressed from white to brown to gray (Fig. 3).

Total counts of white, brown, and gray meat scallops by survey trip and area are summarized in Table 3. In 2013 and 2014, the highest numbers of gray and brown meats were observed in CAI where 14.93% of sampled scallops had discolored meats (5.14% gray and 9.79% brown). Moderate numbers of gray and brown meats were observed in CAII S (0.79% gray and 5.68% brown), whereas low numbers were observed in the open areas on southern Georges Bank (2.59% brown). From 2015 through 2017, low numbers of gray meats were observed overall, with higher numbers in CAII N (1.65% gray and 2.86% brown) than in the open areas on northern Georges Bank (0.75% gray and 1.31% brown).

For the southern stations surveyed in 2013 and 2014, the final model for predicting the prevalence of gray meats during each trip included fixed effects for location, clapper ratio, average shell height, and area (Table 4). Examination of model smoothed fit lines indicated that gray meat prevalence increased with increasing clapper ratio and shell height and that gray meats were more common in CAI than CAII or open areas (Fig. 4). Clapper ratio, average shell height, and area were highly significant predictors ($P < 0.001$), whereas location was likely to have an effect on gray meat prevalence ($P = 0.063$) (Table 5). The model accounted for more than two-thirds of the observed variation in gray meat prevalence (deviance explained = 68.5%), with

TABLE 3.

Total numbers of gray, brown, and white meat scallops observed during each trip in Closed Area I (CAI), Closed Area 2 (CAII S and CAII N), and the open areas on Georges Bank (GB S and GB N). Totals for each area and the percentages of scallops in each color category are included to summarize the data.

	CAI			GB S			CAII S		
	Gray	Brown	White	Gray	Brown	White	Gray	Brown	White
September 2013	3	29	130	0	2	69	2	23	138
October 2013	5	14	143	0	3	68	3	10	134
December 2013	7	6	146	0	2	65	1	5	132
January 2014	14	16	115	0	2	67	0	5	144
March 2014	12	13	144	0	0	70	0	0	160
Subtotals	41	78	678	0	9	339	6	43	708
Totals		797			348			757	
Percentages	5.14%	9.79%	85.07%	0	2.59%	97.41%	0.79%	5.68%	93.53%
					GB N			CAII N	
August 2015	–	–	–	0	3	230	6	8	164
September 2015	–	–	–	7	18	338	4	8	183
October 2015	–	–	–	11	9	322	7	23	185
November 2015	–	–	–	11	8	361	6	17	202
January 2016	–	–	–	5	11	337	7	10	193
March 2016	–	–	–	0	0	415	6	6	227
May 2016	–	–	–	3	3	394	2	6	233
June 2016	–	–	–	0	3	343	0	2	179
July 2016	–	–	–	0	7	342	0	3	178
October 2016	–	–	–	0	0	350	1	2	164
November 2016	–	–	–	0	0	183	0	0	202
January 2017	–	–	–	0	0	293	6	1	183
March 2017	–	–	–	1	1	343	1	0	174
May 2017	–	–	–	0	2	382	0	0	244
June 2017	–	–	–	0	1	305	4	1	191
Sub-totals	–	–	–	38	66	4,938	50	87	2,902
Totals	–	–	–		5,042			3,039	
Percentages	–	–	–	0.75%	1.31%	97.94%	1.65%	2.86%	95.49%

98% of the predicted prevalence values differing from observed values by less than equal to 10% (Fig. 5). Overall, the model successfully predicted locations with high gray meat prevalence, but it also predicted the presence of low numbers of gray meat scallops in areas where none were observed in the deeper parts of CAI and in the open waters south of CAII (Fig. 6).

The final model for predicting the prevalence of gray meats at the northern stations surveyed from 2015 through 2017 included fixed effects for shell height, clapper ratio, and percentage of spent scallops (Table 4). Like the model for the southern stations, gray meat prevalence increased with increasing clapper ratio and shell height (Fig. 4). In addition, gray meat prevalence was higher when at least 50% of the scallops were in spent condition (Fig. 4). The model accounted for most of the observed variation in gray meat prevalence at the northern stations (deviance explained = 84.5%), and 85% of the predicted prevalence values differed from observed values by less than equal to 10% (Fig. 5). The model successfully predicted locations with high gray meat prevalence near the northern part of CAII (Fig. 6).

The models for predicting meat color in individual scallops had similar trends to those for predicting gray meat prevalence, although measures of model fit were lower in both areas (Georges Bank S deviance explained = 35.6%, Georges Bank N deviance explained = 50%). At southern and northern stations, the likelihood of a scallop having discolored meats (gray or brown) increased with shell height and clapper ratio, and scallops were more likely to have discolored meats at lower scallop densities (Table 6, Fig. 4). Scallops in southern Georges Bank were significantly more likely to have discolored meats in CAI, whereas scallops in the northern stations were significantly more likely to have discolored meats when they were spent (Tables 6 and 7, Fig. 4). Neither model predicted that a white scallop would be discolored. Yet, both of the models underestimated the number of scallops that had discolored (gray or brown) meats, with both correctly predicting the color of gray/brown scallops less than one-third of the time in both regions (Georges Bank S: 32% correct, Georges Bank N: 35% correct) (Fig. 5).

DISCUSSION

The phrase ''gray meat disease'' has appeared in recent articles and management documents discussing Georges Bank scallops (Levesque et al. 2016, NEFSC 2018), and in some scallops, discolored meats have been linked to the presence of an apicomplexan parasite that can negatively impact scallop survival and reproduction (Kristmundsson et al. 2015, Inglis et al. 2016, Levesque et al. 2016). Because the parasite has been found in sea scallop meats of all colors (Kristmundsson et al. 2015, Inglis et al. 2016, Levesque et al. 2016, Garcia et al. 2018), isolating a single cause for or assessing the risks associated with discolored meats may not be possible. The results from this

TABLE 4.

Summary of the quasi-binomial generalized additive mixed-model analysis for gray meat prevalence at each station during each trip.

Gray meat prevalence (quasibinomial)			
Full model: GM ~ *f*(Location) + *f*(Bottom depth) + *f*(Scallop density) + *f*(Clapper ratio) + *f*(Bottom temperature) + *f*(Shell height) + *f*(Spent percent) + downstream distance + area + *f*(Trip)			
Model fixed effects	**Edf**	**qAIC**	Δ_{qAIC}
Southern Georges Bank			
f(L) + *f*(CR) + *f*(SH) + Area	7.00	316.92	
f(L) + *f*(D) + *f*(SCD) + CR + *f*(SH) + *f*(SP) + Area + DownD	12.00	323.86	6.94
f(L) + *f*(D) + *f*(SCD) + *f*(CR) + *f*(BT) + *f*(SH) + Area + DownD	12.00	333.46	16.54
f(L) + *f*(D) + *f*(CR) + *f*(BT) + *f*(SH) + *f*(SP) + Area + DownD	12.00	333.47	16.55
f(L) + *f*(D) + *f*(SCD) + *f*(CR) + *f*(BT) + *f*(SH) + *f*(SP) + Area	11.00	333.82	16.90
f(L) + *f*(SCD) + *f*(CR) + *f*(BT) + *f*(SH) + *f*(SP) + Area + DownD	12.00	336.32	19.40
f(L)+*f*(D)+*f*(SCD)+*f*(CR)+*f*(BT)+*f*(SH)+*f*(SP)+Area + DownD	13.00	337.32	20.40
f(L) + *f*(D) + *f*(SCD) + *f*(CR) + *f*(BT) + *f*(SP) + Area + DownD	12.00	342.25	25.33
f(D) + *f*(SCD) + *f*(CR) + *f*(BT) + *f*(SH) + *f*(SP) + Area + DownD	11.00	345.40	28.48
f(L) + *f*(D) + *f*(SCD) + *f*(CR) + *f*(BT) + *f*(SH) + *f*(SP) + DownD	11.00	347.56	30.64
f(L) + *f*(D) + *f*(SCD) + *f*(BT) + *f*(SH) + *f*(SP) + Area + DownD	12.00	350.62	33.70
Northern Georges Bank			
f(CR) + *f*(SH) + *f*(SP)	5.33	302.32	
f(L) + *f*(D) + *f*(SCD) + *f*(CR) + *f*(SH) + *f*(SP) + Area + DownD	12.05	310.19	7.87
f(L) + *f*(D) + *f*(SCD) + *f*(CR) + *f*(BT) + *f*(SH) + *f*(SP) + Area	10.73	313.45	11.13
f(L) + *f*(D) + *f*(SCD) + *f*(CR) + *f*(BT) + *f*(SH) + *f*(SP) + DownD	12.55	313.81	11.49
f(L) + *f*(D) + *f*(SCD) + *f*(CR) + *f*(BT) + *f*(SP) + Area + DownD	11.84	316.13	13.81
f(D) + *f*(SCD) + *f*(CR) + *f*(BT) + *f*(SH) + *f*(SP) + Area + DownD	10.66	317.17	14.85
f(L) + *f*(D) + *f*(SCD) + *f*(CR) + *f*(BT) + *f*(SH) + *f*(SP) +Area + DownD	12.83	317.86	15.54
f(L) + *f*(D) + *f*(CR) + *f*(BT) + *f*(SH) + *f*(SP) + Area + DownD	11.09	326.14	23.82
f(L) + *f*(D) + *f*(SCD) + *f*(CR) + *f*(BT) + *f*(SH) + Area + DownD	11.79	326.47	24.15
f(L) + *f*(SCD) + *f*(CR) + *f*(BT) + *f*(SH) + *f*(SP) + Area + DownD	12.61	332.65	30.33
f(L) + *f*(D) + *f*(SCD) + *f*(BT) + *f*(SH) + *f*(SP) + Area + DownD	12.00	386.62	84.30

BT, bottom temperature; CR, clapper ratio; D, bottom depth; DownD, downstream distance; Edf, estimated degrees of freedom; GM, gray meat prevalence; L, location; SP, spent percent; SCD, scallop density; SH, average shell height. The full model, final model, and the models with each effect dropped from the full model are shown. Trip was included as a random effect.

study indicate that multiple factors differentially influence gray meat prevalence on the southern and northern parts of Georges Bank. In the south, location was a significant factor for predicting the presence of gray meats, with the model highlighting CAI where an outbreak of gray meats occurred after the area reopened to fishing. Yet in the north, reproductive stage was a significant factor, with scallops more likely to have discolored meats after spawning. Scallops with gray meats have been reported along the eastern United States and Canada since the 1940s, with likely causes ranging from old age to bacterial infections to boring sponges (Medcof 1949, Gulka et al. 1983, Stokesbury et al. 2007). Coupled with these reports, the results from this study suggest that gray meats are a symptom of poor condition that could be caused by multiple factors, including pathogens, costly reproduction, poor habitat, or other stressors.

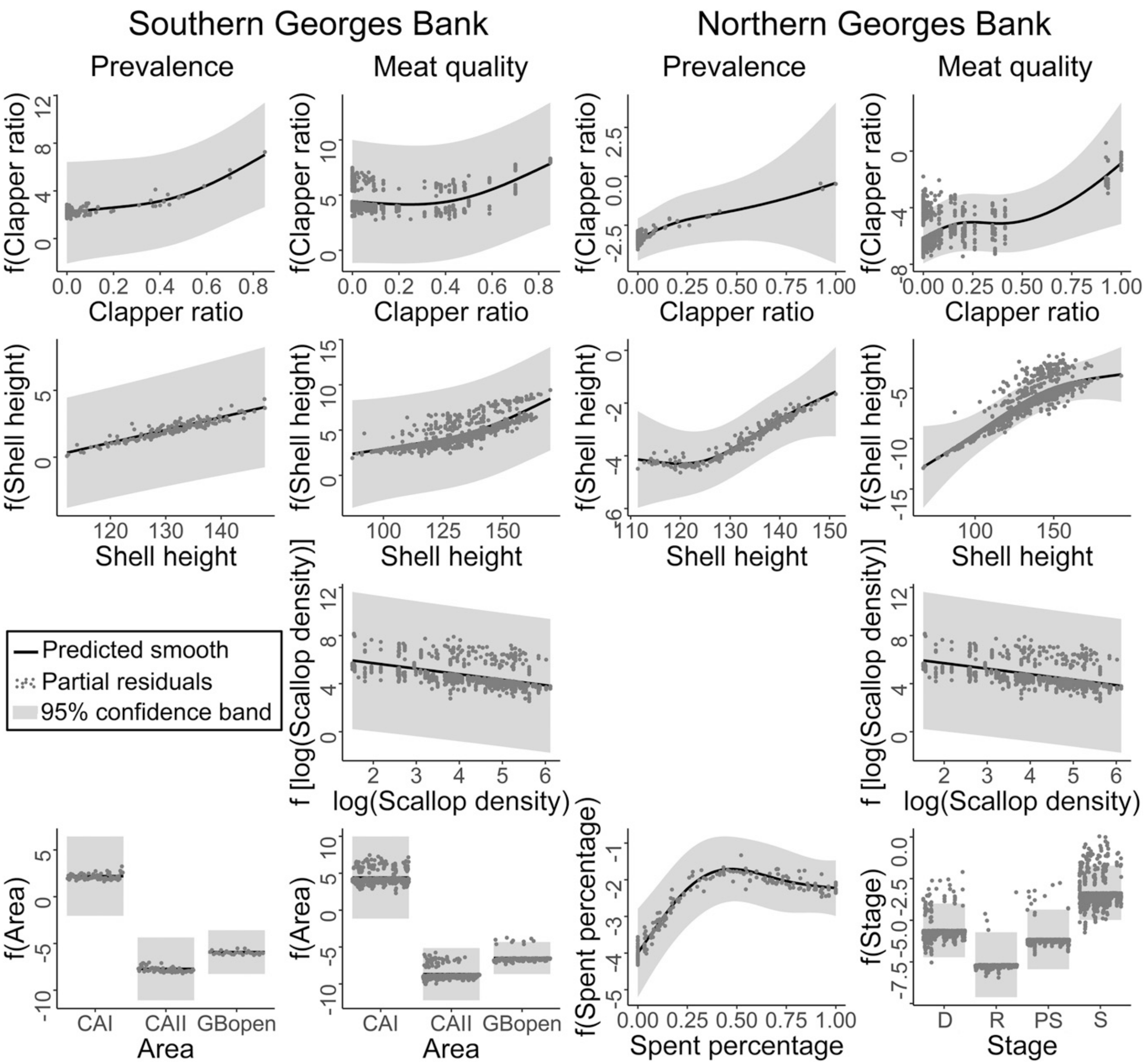

Figure 4. Predicted smooth terms for each final model with 95% confidence bands and partial residuals. Clapper ratio was a station-level variable in all models. Shell height was the average shell height per station in the prevalence models and the shell height of individual scallops in the meat quality models. Reproductive stage was included as spent percent at each station, a continuous variable, in the prevalence models and as reproductive stage, a categorical variable, in the meat quality models. Area was a categorical variable in all models. Scallop density was not in the final models for gray meat prevalence.

This study demonstrates the value of using a mixed-model approach to assess the relative contributions of potential predictors when multiple patterns seem to exist. Stations with extremely high gray meat prevalence were clustered in CAI, an area that was reopened to fishing after a prolonged closure just before the start of this sampling program (Levesque et al. 2016), and area was a significant predictor for gray meat prevalence in the southern Georges Bank stations. Seemingly similar clusters of gray meat scallops were observed near the habitat closure at the northern tip of CAII, an area closed to mobile bottom-tending gear since 1994 (NEFMC 1998). Yet, area and downstream distance from a closed area were not retained in the model for the northern stations, suggesting that the CAII HAPC was not acting as a disease reservoir during this sampling period. Conversely, even though a high proportion of gray meat scallops were in spent condition in the southern stations, reproductive stage was not retained as a predictor in the final model for southern Georges Bank. Taken together, these results indicate that gray meats were caused by different processes in the southern and northern stations during this study.

The clapper ratio was included in each model as an indicator of natural scallop mortality at each station. This ratio was positively correlated with gray meat prevalence and gray meat color of individual scallops, suggesting that regardless of the cause, scallops with gray meats experience high mortality rates relative to the population as a whole. Gray meats linked to

TABLE 5.

Significance of the fixed effect terms in the final models for gray meat prevalence at each station during each trip, assessed using a type III ANOVA.

Fixed effect terms	Edf	Ref. df	df	*F*	*P* Value
Southern Georges Bank					
Location	4.870	5.898	–	2.044	0.063
Clapper ratio	2.225	2.539	–	7.735	<0.001
Average shell height	2.136	1.001	–	13.882	<0.001
Area	–	–	2	4.895	0.009
Northern Georges Bank					
Clapper ratio	1.976	2.291	–	3.541	0.02
Average shell height	2.504	2.829	–	8.943	<0.001
Spent percent	2.758	2.942	–	8.695	<0.001

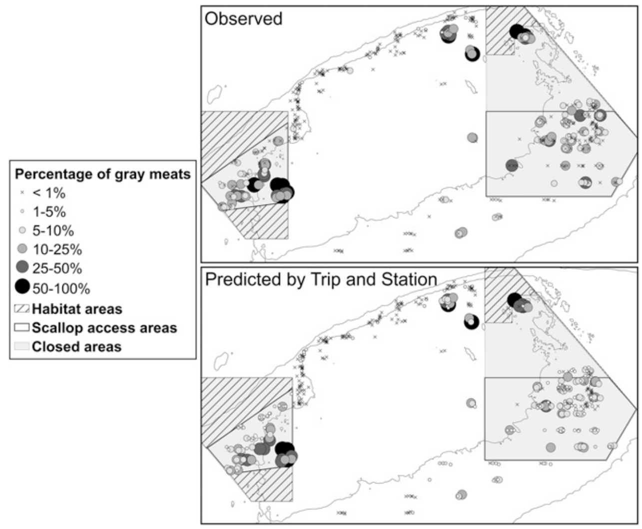

Figure 6. Maps showing observed gray meat prevalence averaged over each station during each trip and predicted gray meat prevalence at each station during each trip on Georges Bank. The map of observed gray meat prevalence includes data from the southern 2013–2014 and northern 2015–2017 surveys. The map of predicted gray meat prevalence combines predicted gray meat prevalence from models for the southern and northern surveys.

disease caused by apicomplexan or bacterial infections have been associated with mass mortality events (Gulka et al. 1983, Stokesbury et al. 2007, Kristmundsson et al. 2015). Moreover, even though scallop meat quality can be reduced following spawning if adductor muscle is catabolized (Barber & Blake 2016), this could be coupled with weakened immune systems and reduced stress response capacities (Chu et al. 1996, Xiao et al. 2005, Li et al. 2007, Brokordt et al. 2015). Consequently, spent scallops could be more susceptible to the infections, complicating efforts to determine a single cause for gray meats.

All of these models also indicated a strong relationship between scallop shell height and gray meats, with larger scallops more likely to have discolored meats. Fishermen have reported that low-quality discolored meats are common in old scallops, but previous research did not find a correlation between sea scallop shell height and meat color (Inglis et al. 2016). Kristmundsson et al. (2015) found that gray meats were most common in their largest size class of Iceland scallops. Apicomplexan infection was observed in all size classes, but the highest grades of infection and macroscopic changes that affected meat quality were seen in larger and mature Iceland scallops. They speculated that the high rates of infection in older scallops was related to physiological changes or altered immune responses, yet the highest infection rates and lowest meat qualities were observed in the spring before spawning, contrasting with the results of this study (Kristmundsson et al. 2015).

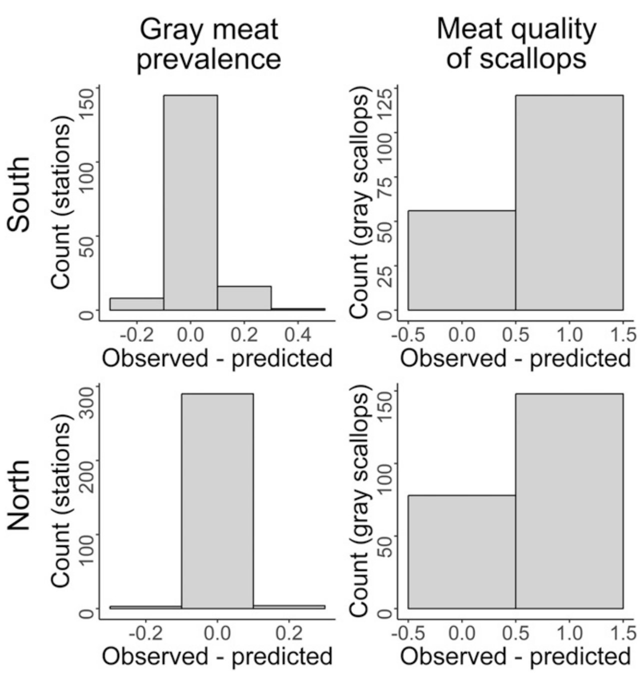

Figure 5. Histograms showing the differences between the observed and predicted gray meat prevalence (left) and the observed and predicted meat color of gray scallops (right) for the southern and northern stations.

Disease transmission is typically density dependent, with infection spreading more readily where there are high densities of animals (McCallum et al. 2001, Lloyd-Smith et al. 2005, Bidegain et al. 2016). Surprisingly, although scallop density was a significant factor for predicting meat color in individual scallops from southern Georges Bank and retained in the model for the northern stations, the probability of scallops having gray meats decreased with increasing density. This counterintuitive result might be related to habitat quality, with poor scallop habitat found in low-density areas. Food limitation and other stressors could to lead to lower quality meats following gametogenesis or to reduced scallop resistance to infections (Barber & Blake 1983, Chu et al. 1996, Luna-González et al. 2000, Xiao et al. 2005, Li et al. 2007, Brokordt et al. 2015). Alternatively, this result might be explained by recent research on apicomplexan parasites in whelks. Kristmundsson and Freeman (2018) have theorized that *Merocystis kathae*, the apicomplexan that infects scallops, may require two hosts during its life cycle, passing through the gastrointestinal tract of the common whelk and a pectinid bivalve. In this scenario, a high density of scallops or whelks could increase the incidence of gray meats caused by the parasite. Consequently, future

TABLE 6.

Summary of the binomial generalized additive mixed-model analysis for the meat color of individual scallops based on gray meat presence (gray or brown meat) or absence (white meat).

Meat color of individual scallops (binomial)			
Full model: GM ~ f(Location) + f(Bottom depth) + f(Scallop density) + f(Clapper ratio) + f(Bottom temperature) + f(Shell height) + Stage + downstream distance + Area + f(Station) + f(Trip)			
Model fixed effects	**Edf**	**AIC**	**Δ_{AIC}**
Southern Georges Bank			
f(L) + f(SCD) + f(CR) + f(SH) + Area	38.55	835.05	–
f(L) + f(D) + f(SCD) + f(CR) + f(SH) + Stage + Area + DownD	45.04	836.92	1.87
f(L) + f(BT) + f(D) + f(SCD) + f(CR) + f(SH) +Stage + DownD	46.98	839.52	4.48
f(L) + f(BT) + f(D) + f(SCD) + f(CR) +f(SH) + Area + DownD	45.22	840.02	4.98
f(L) + f(BT) + f(D) + f(SCD) + f(CR) + f(SH) + Stage + Area	46.39	840.77	5.72
f(L) +f(BT) + f(D) + f(SCD) + f(CR) + f(SH) + Stage + Area + DownD	48.07	841.59	6.55
f(L) + f(BT) + f(D) + f(SCD) + f(SH) + Stage + Area + DownD	42.33	844.72	9.68
f(BT) + f(D) + f(SCD) + f(CR) + f(SH) + Stage + Area + DownD	49.16	849.49	14.45
f(L) + f(BT) + f(SCD) + f(CR) + f(SH) + Stage + Area + DownD	49.20	849.90	14.85
f(L) + f(BT) + f(D) + f(CR) + f(SH) + Stage + Area + DownD	46.67	851.17	16.13
f(L) + f(BT) + f(D) + f(SCD) + f(CR) + Stage + Area + DownD	48.37	929.51	94.46
Northern Georges bank			
f(SCD) + f(CR) + f(SH) + Stage	45.99	1,113.29	–
f(L) + f(BT) + f(SCD) + f(CR) + f(SH) + Stage + Area + DownD	48.57	1,113.33	0.04
f(L) + f(BT) + f(D) + f(SCD) + f(SH) + Stage + Area + DownD	48.91	1,113.35	0.06
f(L) + f(D) + f(SCD) + f(CR) + f(SH) + Stage + Area + DownD	48.98	1,113.37	0.09
f(BT) + f(D) + f(SCD) + f(CR) + f(SH) + Stage + Area + DownD	46.95	1,115.48	2.19
f(L) + f(BT) + f(D) + f(SCD) + f(CR) + f(SH) +Stage + DownD	47.98	1,115.86	2.58
f(L) + f(BT) + f(D) + f(CR) + f(SH) + Stage + Area + DownD	47.64	1,117.55	4.26
f(L) + f(BT) + f(D) + f(SCD) + f(CR) + f(SH) + Stage + Area + DownD	54.67	1,120.08	6.79
f(L) + f(BT)+f(D)+f(SCD)+f(CR)+f(SH)+Stage + Area	51.36	1,120.58	7.30
f(L) + f(BT) + f(D) + f(SCD) + f(CR) + f(SH) + Area + DownD	47.35	1,235.30	122.02
f(L) + f(BT) + f(D) + f(SCD) + f(CR) + Stage + Area + DownD	46.95	1,256.05	142.76

BT, bottom temperature; GM, gray meat presence or absence; CR, clapper ratio; D, bottom depth; DownD, downstream distance; Edf, estimated degrees of freedom; L, location; SCD, scallop density; SH, shell height; Stage, reproductive stage. The full model, final model, and the models with each effect dropped from the full model are shown. Trip and station were included as random effects.

research on gray meats in scallops should include documentation of whelk densities.

It must be noted that the surveys in the southern and northern parts of Georges Bank took place during different years. Gray meat outbreaks caused by apicomplexan infections have been described as episodic (Kristmundsson et al. 2015), and if the high gray meat incidence documented in CAI was caused by this parasite, the conditions that resulted in the outbreak may have passed. The proportions of gray and brown meats observed during research surveys in the CAII HAPC dropped by more than 50% between 2012 and 2013, with stock quality in the area described as good during the latter survey, further suggesting that changes may have been occurring on Georges Bank (Rudders et al. 2013, 2014). Therefore, the shift

TABLE 7.

Significance of the fixed effect terms in the final models for meat color of individual scallops, assessed using a type III ANOVA.

Fixed effect terms	Edf	Ref. df	df	Chi sq.	*P*-Value
Southern Georges Bank					
Location	8.597	10.525	–	30.681	<0.001
Scallop density	1.000	1.000	–	8.057	0.004
Clapper ratio	2.285	2.598	–	12.217	0.003
Shell height	2.253	2.625	–	86.455	<0.001
Area	–	–	2	11.460	0.003
Northern Georges Bank					
Scallop density	2.112	2.505	–	5.726	0.116
Clapper ratio	2.587	2.818	–	14.132	0.004
Shell height	2.192	2.575	–	103.674	<0.001
Stage	–	–	3	93.450	<0.001

in likely causes for gray meats between the southern and northern Georges Bank stations may have been temporal rather than spatial, and gray meats observed across Georges Bank since 2015 may be due to normal muscle catabolism during reproduction or responses to unidentified environmental stressors.

Examination of research on toxoplasmosis, caused by a heavily researched apicomplexan parasite, may provide a basis for better understanding gray meats in scallops. The parasite that causes toxoplasmosis in mammals and birds, *Toxoplasmosis gondii*, is found in healthy and symptomatic individuals (Dubey et al. 1998). Healthy individuals show no signs of infection, whereas immunocompromised individuals develop nonspecific symptoms such as fever and malaise (Dubey et al. 1998). Expanded data collection and improved screening have been recommended to combat toxoplasmosis (Tenter et al. 2000). Similarly, continued monitoring of scallop health through targeted disease surveys and the development of rapid screening tests could provide the information needed to develop measures to minimize the impacts of gray meats on the fishery and scallop stocks.

ACKNOWLEDGMENTS

We would like to thank our many colleagues at CFF for their participation in the bycatch study over the years. We would also like to thank our collaborators at the UMass Dartmouth School of Marine Science and Technology, who participated in our early collections of gray meat scallops, and at Roger Williams University Aquatic Diagnostic Laboratory, who have done the histological and molecular analyses of our samples. We are grateful to the vessel owners, operators, and crew members who made this project possible. This study was funded by the NOAA Sea Scallop Research Set-Aside grants NA13NMF4540011, NA15NMF4540059, and NA16NMF4540034. The funders had no role in study design. Coonamessett Farm Foundation, Inc., is a nonprofit scientific research foundation.

LITERATURE CITED

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. In: Petrov, B. N. & F. Csaki, editors. Second international symposium on information theory. Budapest, Hungary: Akademiai Kiado. pp. 267–281.

Barber, B. J. & N. J. Blake. 1983. Growth and reproduction of the bay scallop, *Argopecten irradians* (Lamarck) at its southern distributional limit. *J. Exp. Mar. Biol. Ecol.* 66:247–256.

Barber, B. J. & N. J. Blake. 2016. Reproductive physiology. In: Shumway, S. E. & G. J. Parsons, editors. Scallops: biology, ecology, aquaculture & fisheries, 3rd edition. Amsterdam, The Netherlands: Elsevier Publishing. pp. 253–300.

Bidegain, G., E. N. Powell, J. N. Klinck, T. Ben-Horin & E. E. Hofmann. 2016. Marine infectious disease dynamics and outbreak thresholds: contact transmission, pandemic infection & the potential role of filter feeders. *Ecosphere* 7:e01286.

Bivand, R., T. Keitt & B. Rowlingson. 2015. Rgdal: bindings for the geospatial data abstraction library. R package version 1.1-3. Available at: https://CRAN.R-project.org/package=rgdal.

Bolker, B. 2017. Bbmle: tools for general maximum likelihood estimation. R package version 1.0.20. Available at: https://CRAN.R-project.org/package=bbmle.

Breheny, P. & W. Burchett. 2017. Visualization of regression models using visreg. *R J.* 9:56–71.

Brokordt, K., H. Pérez, C. Herrera & A. Gallardo. 2015. Reproduction reduces HSP70 expression capacity in *Argopecten purpuratus* scallops subject to hypoxia and heat stress. *Aquat. Biol.* 23:265–274.

Chu, F. E., E. M. Burreson, F. Zhang & K. K. Chew. 1996. An unidentified haplosporidian parasite of bay scallop *Argopecten irradians* cultured in the Shandong and Liaoning provinces of China. *Dis. Aquat. Org.* 25:155–158.

Dubey, J. P., D. S. Lindsey & C. A. Speer. 1998. Structures of *Toxoplasma gondii* tachyzoites, bradyzoites, and sporozoites and biology and development of tissue cysts. *Clin. Microbiol. Rev.* 11:267–299.

Fisher, R. A. 2000. Biology of certain commercial species: scallops. In: Martin, R. E, E. P. Carter, G. J. Flick & L. M. Davis, editors. Marine and freshwater products handbook. Boca Raton, FL: CRC Press. pp. 83–110.

Garcia, L., L. Siemann, R. Smolowitz, D. Rudders & R. Smolowitz. 2018. Optimizing the Georges Bank scallop fishery by maximizing meat yield and minimizing bycatch. Final report for the 2017 NOAA sea scallop research set-aside program. Available at: https://www.nefsc.noaa.gov/coopresearch/pdfs/FR17-0030.pdf.

Gould, E., D. Rusanowsky & D. A. Luedke. 1988. Note on muscle glycogen as an indicator of spawning potential in the sea scallop, *Placopecten magellanicus*. *Fish Bull.* 86:597–601.

Gulka, G., P. W. Change & K. A. Marti. 1983. Prokaryotic infection associated with a mass mortality of the sea scallop, *Placopecten magellanicus*. *J. Fish Dis.* 6:355–364.

Inglis, S., Á. Kristmundsson, M. A. Freeman, M. Levesque & K. Stokesbury. 2016. Gray meat in the Atlantic sea scallop, *Placopecten magellanicus* & the identification of a known pathogenic scallop apicomplexan. *J. Invertebr. Pathol.* 141:66–75.

Kristmundsson, Á., Á. Erlingsdóttir & M. A. Freeman. 2015. Is an apicomplexan parasite responsible for the collapse of the Iceland scallop (*Chlamys islandica*) stock? *PLoS One* 10:e0144685.

Kristmundsson, Á. & M. A. Freeman. 2018. Harmless sea snail parasite causes mass mortalities in numerous commercial scallop populations in the northern hemisphere. *Sci. Rep.* 8:7865.

Kristmundsson, Á., S. Helgason, S. H. Bambir, M. Eydal & M. A. Freeman. 2011. Previously unknown apicomplexan species infecting Iceland scallop, *Chlamys islandica* (Müller, 1776), queen scallop, *Aequipecten opercularis* L. & king scallop, *Pecten maximus* L. *J. Invert. Pathol.* 108:147–155.

Levesque, M. M., S. D. Inglis, S. E. Shumway & K. D. E. Stokesbury. 2016. Mortality assessment of Atlantic sea scallop (*Placopecten magellanicus*) from gray-meat disease. *J. Shellfish Res.* 35:295–305.

Li, Y., J. C. Qin, C. A. Abbott, X. Li & K. Benkendorff. 2007. Synergistic impacts of heat shock and spawning on the physiology and immune health of *Crassostrea gigas*: an explanation for summer mortality in Pacific oysters. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 293:R2353–R2362.

Lloyd-Smith, J. O., P. C. Cross, C. J. Briggs, M. Daugherty, W. M. Getz, J. Latto, M. S. Sanchez, A. B. Smith & A. Swei. 2005. Should we expect population thresholds for wildlife disease? *Trends Ecol. Evol.* 20:511–519.

Luna-González, A., C. Cáceres-Martínez, C. Zúñiga-Pacheco, S. López-López & B. P. Ceballo-Vázquez. 2000. Reproductive cycle of *Argopecten ventricosus* (Sowerby 1842) (Bivalvia: Pectinidae) in the Rada del Puerto de Pichilingue, B.C.S., Mexico and its relation to temperature, salinity & food. *J. Shellfish Res.* 19:107–112.

McCallum, H., N. Barlow & J. Hone. 2001. How should pathogen transmission be modeled? *Trends Ecol. Evol.* 16:295–300.

Medcof, J. C. 1949. Dark-meat and the shell disease of scallops. *Prog. Rep. Atlantic Coast Stations* 45:3–6.

Merrill, A. S. & J. A. Posgay. 1964. Estimating the natural mortality rate of sea scallop (*Placopecten magellanicus*). *Int. Comm. NW Atl. Fish. Res. Bull.* 1:88–106.

Naidu, K. S. 1970. Reproduction and breeding cycle of the giant scallop *Placopecten magellanicus* (Gmelin) in Port au Port Bay, Newfoundland. *Can. J. Zool.* 48:1003–1012.

National Marine Fisheries Service (NMFS). 2017. Fisheries of the United States 2016. NOAA Current Fishery Statistics No 2016. US Department of Commerce. Available at: https://www.st.nmfs.noaa.gov/commercial-fisheries/fus/fus16/index.

New England Fisheries Management Council (NEFMC). 1998. Final amendment #11 to the northeast multispecies fishery management plan, amendment #9 to the Atlantic Sea scallop fishery management plan, amendment #1 to the monkfish fishery management plan, amendment #1 to the Atlantic salmon fishery management plan, components of the proposed Atlantic herring fishery management plan for essential fish habitat incorporating the environmental assessment. Available at: https://s3.amazonaws.com/nefmc.org/OriginalOminibusAmendment.pdf.

Northeast Fisheries Science Center (NEFSC). 2018. 65th northeast regional stock assessment workshop assessment report. NEFSC Ref Doc 18-11. US Department of Commerce. Available at: https://www.nefsc.noaa.gov/publications/crd/crd1811/crd1811.pdf.

Patten, R. 1935. The life history of *Merocystis kathae* in the whelk, *Buccinum undatum*. *Parasitology* 27:399–430.

R Core Team. 2017. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available at: http://www.R-project.org/.

Robinson, W. E., W. E. Wheling, M. P. Morse & G. C. McLeod. 1981. Seasonal changes in soft-body component indices and energy reserves in the Atlantic deep-sea scallop, *Placopecten magellanicus*. *Fish. Bull.* 79:449–458.

Robusto, C. C. 1957. The cosine-Haversine formula. *Am. Math. Mon.* 64:38–40.

Rudders, D. B., W. B. DuPaul & J. Bergeron. 2013. An inventory of the sea scallop resource in the Georges Bank closed area II and surrounds. Final report for the 2012 NOAA sea scallop research set-aside program. Available at: https://www.nefsc.noaa.gov/coopresearch/pdfs/FR12-0031_VIMS_SCA_ResourceGB.pdf.

Rudders, D. B., W. B. DuPaul & J. M. Hudson. 2014. An assessment of sea scallop abundance and distribution in the northeast Georges Bank area. Final report for the 2013 NOAA sea scallop research set-aside program. Available at: https://www.nefsc.noaa.gov/coopresearch/pdfs/FR13-0020_VIMS_SCA_GB.pdf.

Shadish, W. R., A. F. Zuur & K. J. Sullivan. 2014. Using generalized additive (mixed) models to analyze single case designs. *J. Sch. Psychol.* 52:149–178.

Stevenson, J. A. 1936. The Canadian scallop: its fishery, life-history and some environmental relationships. MS thesis, University of Western Ontario, London, Ontario.

Stokesbury, K. D. E., B. P. Harris, M. C. Marino, II & J. J. Nogueira. 2007. Sea scallop mass mortality in a marine protected area. *Mar. Ecol. Prog. Ser.* 349:151–158.

Tenter, A. M., A. R. Heckeroth & L. M. Weiss. 2000. *Toxoplasma gondii*: from animals to humans. *Int. J. Parasitol.* 30:1217–1258.

Wickham, H. 2016. Ggplot2: elegant graphics for data analysis. New York, NY: Springer-Verlag.

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc. Ser. B Stat. Methodol.* 73:3–36.

Xiao, J., S. E. Ford, H. Yang, G. Zhang, F. Zhang & X. Guo. 2005. Studies on mass summer mortality of cultured Zhikong scallops (*Chlamys farreri* Jones et Preston) in China. *Aquaculture* 250:602–615.