Shell Height-To-Weight Relationships for Atlantic Sea Scallops (*Placopecten magellanicus*) in Offshore U.S. Waters

SHELL HEIGHT-TO-WEIGHT RELATIONSHIPS FOR ATLANTIC SEA SCALLOPS (*PLACOPECTEN MAGELLANICUS*) IN OFFSHORE U.S. WATERS

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ABSTRACT Generalized linear mixed models were developed for allometric relationships in Atlantic sea scallops (*Placopecten magellanicus*). These models used environmental covariates such as depth, latitude, geographic area, fishing pressure, population density, and season. This study makes several technical improvements to existing allometric models. We found depth, latitude, and geographic area to be important covariates in models for scallops on Georges Bank, whereas depth and fishing pressure were important for mid-Atlantic scallops. Our allometric relationships have important implications for stock assessment and fisheries management.

KEY WORDS: *Placopecten magellanicus*, scallop, allometric relationships, meat weight, commercial fisheries

INTRODUCTION

Allometric relationships between shell height and weight (meat weight, gonad weight, whole weight) for sea scallops are useful for several purposes. Shell height/weight relationships allow the conversion of shell height data into biomass, which is important because shell height data are easier and less time-consuming to obtain than weights, particularly of soft tissues. Allometric relationships, therefore, allow for efficient collection of biomass data, because large quantities of shell height data can be collected on research surveys or by at-sea observers. When combined with estimates of growth, allometric relationships can be used to estimate production-to-biomass ratios and the fraction of production dedicated to somatic and reproductive output.

Scallop meat and gonad weight at a given shell height can vary with season and location. In particular, these weights decrease considerably after spawning and tend to be less in deeper water (Haynes 1966, Robinson et al. 1981, MacDonald & Thompson 1985a, MacDonald & Thompson 1985b, Worms & Davidson 1986, MacDonald & Bourne 1987, Barber et al. 1988, Serchuk & Smolowitz 1989, Schmitzer et al. 1991, Almeida et al. 1994, Dibacco et al. 1995, Lai & Helser 2004, Rothschild et al. 2009, Sarro & Stokesbury 2009). This article represents the most extensive study of shell height/weight relationships for the Atlantic sea scallop *Placopecten magellanicus* in U.S. waters. We estimated mean regional and subregional relationships, and also conducted a systematic investigation of putative predictors of meat, gonad, and whole weights, including the potential influence of depth, latitude, fishery closures, population density, seasonal variation, and fine- and broad-scale effects of spatial location. We estimated these effects using generalized linear mixed-effects models (GLMMs) (Venables & Dichmont 2004), a more accurate statistical approach than used in previous scallop work.

We demonstrate that differences in estimated allometric relationships can be important by relating our findings to some typical fisheries assessment metrics, such as yield per recruit. Last, we discuss the implications of our findings in terms of resource partitioning between tissue types.

METHODS

Data Collection

Shell heights and meat weights from individual sea scallops were sampled from 2001 to 2010 during the annual Northeast Fisheries Science Center (NEFSC) sea scallop survey. Gonad and whole weights were also collected beginning in 2003. The surveys were conducted on 2 different research vessels (*R/V Albatross IV* from 2001 to 2007 and *R/V Hugh Sharp* from 2008 to 2010) using a 2.44-m modified New Bedford scallop dredge with 51-mm rings and a 38-mm plastic liner. The dredge was deployed at 3.8 knots for 15 min bottom time at each depth-stratified random station. At about half of the stations, ~6 scallops per station were selected randomly for dissection. The scallop shells were cleaned with wire brushes, measured to the nearest millimeter, and then weighed whole to the nearest gram. The adductor muscle and gonad were removed carefully, the sex was noted, and both organs were weighed to the nearest gram after excess water was eliminated (only meats were weighed during 2001 and 2002). Other information also collected routinely included the depth, the location, and the total number of scallops caught at each station. Partial data loss occurred in 2003, and data from that year were not used. Data were divided into 2 broad regions that were analyzed separately: the Mid-Atlantic Bight (MAB), from Long Island to Virginia, and Georges Bank (GBK), including the neighboring areas of the Great South Channel and Nantucket Shoals (Fig. 2). Data in the 2009 and 2010 surveys were collected about 6 wk earlier than during the 2001 to 2008 surveys (mid May to late June compared with early July to mid August) and were generally excluded from analyses, although these data were used for comparative purposes. During the 2001 to 2002 and 2004 to 2008 surveys, 4,181 individual scallops were sampled from 717 stations in the MAB and 6,145 individual scallops were sampled from 812 stations on GBK.

Meat weight data were also collected on commercial scallop vessels by at-sea observers to evaluate temporal trends in meat weights and the weights of commercially shucked scallops. During 1 tow per observer watch, roughly 100 scallops retained for sale were shucked by a commercial fisherman and sampled. Shell heights of these scallops were measured to the nearest 5 mm, the meats were packed in aggregate into a graduated cylinder, and their volume was recorded. The volume was converted
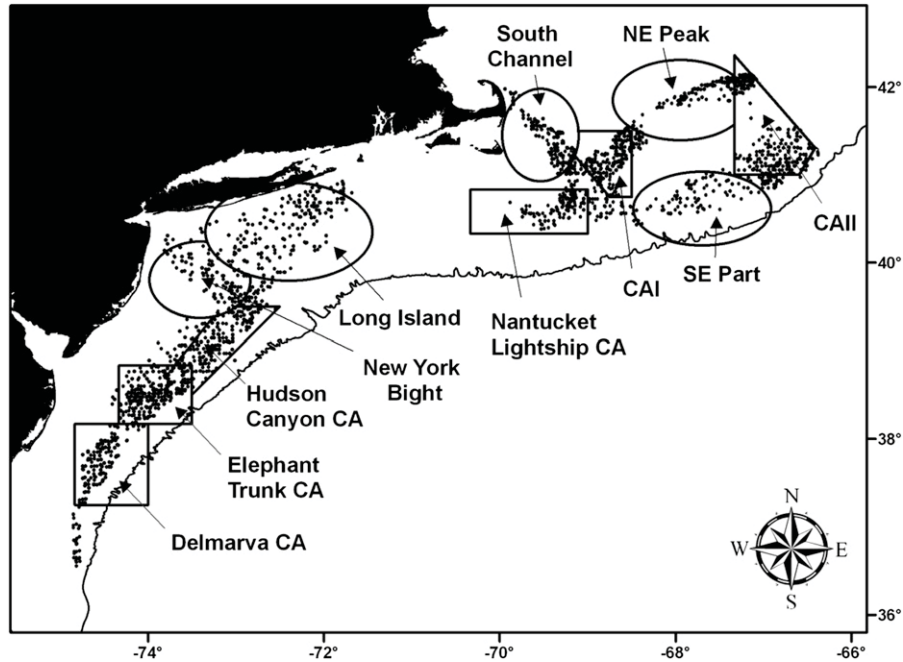
Figure 1. Location of meat weight samples collected and approximate locations of subregions in the U.S. exclusive economic zone of the northwest Atlantic Ocean. CA, closed area. NE Peak, Northern Edge and Peak; SE Part, Southeast Part.

to weight using a density estimate of 1.05 g/mL^3 (Caddy & Radley-Walters 1972, Smolowitz et al. 1989). Also recorded were the date, time, location, and depth of the tows where the scallops were collected. For this portion of our study, we used observer data collected between 2001 and 2009.

Data Preprocessing and Analysis

Some data preprocessing was necessary. Preliminary meat weight/shell height models using survey data indicated a residual pattern for scallops smaller than 70 mm in shell height, probably because of the low meat weights (1–3 g) of these animals and because meat weight could only be measured to the nearest gram. For these reasons, the analysis was restricted to scallops 70 mm

and larger in shell height. Implausible outliers likely resulting from data entry errors were removed according to the following rules: meat weight and gonad weight should not be greater than half the whole weight, gonad weight should not be greater than twice the meat weight, and meat weight or gonad weight should not exceed 250 g. Shell height, depth, density, and longitude were log$_e$ transformed and centered (i.e., the overall mean was subtracted from each observation (Pinheiro & Bates 2000)). The intercept and other parameter estimates were adjusted back to the original (not centered) scale after model fitting.

GLMMs (Venables & Dichmont 2004) were used to predict scallop weight components, using equations of the form
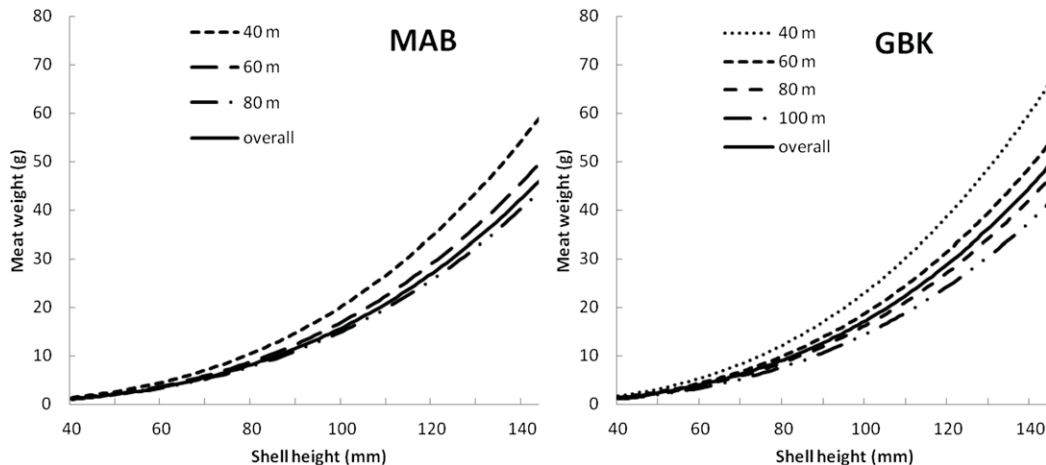

Figure 2. Shell height/meat weight relationships at relationships depth, and overall in the Mid-Atlantic Bight ($W = \exp[\alpha + a(St) + \beta \ln(L) + \gamma \ln(D)]$) and at Georges Bank ($W = \exp[\alpha + a(St) + \beta \ln(L) + \gamma \ln(D) + b(L_{St})]$). GBK, Georges Bank; MAB, Mid-Atlantic Bight.

TABLE 1.

Coefficients and SEs for several models.

Formula	α	β	γ	δ	ρ	ω	β × γ	AIC	BIC
Georges Bank									
Height + (Height/Year_Sta)	–10.20 (0.007)	2.84 (0.024)						7,038	7,072
Height + Depth + (Height/Year_Sta)	–8.05 (0.006)	2.84 (0.023)	–0.507 (0.029)					6,784	6,824
Height + Depth + [Area] + (Height/Year_Sta)	–7.94 (0.014)	2.81 (0.023)	–0.489 (0.03)		a			6,692	6,766
Height + Depth + Latitude + [Area] + (Height/Year_Sta)	**14.38 (0.014)**	**2.83 (0.023)**	**–0.529 (0.029)**	**–5.98 (0.737)**	**b**			**6,634**	**6,714**
Area effects	a	b							
Closed Area 2	–0.001 (0.018)	0.04 (0.018)							
North East Peak	–0.137 (0.02)	–0.049 (0.022)							
Nantucket Lightship	0.04 (0.023)	–0.05 (0.024)							
South Channel	–0.109 (0.021)	–0.114 (0.02)							
South East Part	–0.027 (0.026)	–0.08 (0.026)							
Mid-Atlantic Bight									
Height + (Year_Sta)	–10.8 (0.007)	2.97 (0.026)						3,846	3,865
Height + Depth + (Year_Sta)	–8.82 (0.006)	2.93 (0.026)	–0.45 (0.029)					3,633	3,659
Height + Depth + Height × Depth + (Year_Sta)	–16.89 (0.006)	4.64 (0.026)	1.57 (0.029)				–0.43 (0.131)	3,624	3,656
Height + Depth + [Clop] + Height × Depth + (Year_Sta)	–17.1 (0.009)	4.66 (0.026)	1.62 (0.031)		0.03 (0.012)		–0.43 (0.131)	3,622	3,660
Height + Depth + Latitude + [Clop] + [Area] + (Year_Sta)	**–8.15 (0.041)**	**2.94 (0.026)**	**–0.45 (0.034)**	**–0.02 (0.021)**	**0.09 (0.024)**			**3,623**	**3,687**

The response in each case was meat weight. The models with minimum Akaike's information criterion (AIC) values are in bold type. Bayesian information criterion (BIC) are listed for comparison. Random effects are shown as the parameters inside parentheses. All random effects were grouped by year_station, and each model included a random intercept, indicated by Year_Sta. Some models also included a random effect for height. Categorical variables, either subarea or clop (closed versus open) are in square brackets. Interaction terms are represented as factor 1×factor 2. Subarea effects for the third (a) and fourth (b) GBK models are listed in columns by subarea. Based on 6,145 scallops at 812 stations (Georges Bank) and 4,181 scallops from 717 stations (Mid-Atlantic Bight).

$$W = \exp(a + b_0\ln(H) + b_1\ln(c_1) + b_2\ln(c_2) + \cdots + b_n\ln(c_n)), \quad (1)$$

where W is weight (either meat weight, gonad weight, or whole weight), H is shell height, $c_{1 \ldots} c_n$ were covariate predictors (e.g., depth, scallop density; in the basic model these are absent), and a and the b_i were parameters to be estimated. Examination of the variance of the weights as a function of shell height indicated that variance (weight) increased approximately linearly with shell height, implying that the Poisson family was appropriate for the distributions of meat weights (McCullagh & Nelder 1989). The GLMMs in all analyses therefore used the Poisson family with a log "link" (the inverse of the exp function in Eq (1)). Because shell height/weight relationships for scallops at the same station are likely to be more similar than those at other stations, we considered the sampling station as a grouping factor (random effect) in the analysis.

To test the appropriateness of our distributional assumptions, we simulated meat weight data using a relationship to shell height with known parameter values. We added multiplicative process error, additive measurement error in shell height, and random effects in both shell height and the intercept to each simulated data point. We then fit or attempted to fit models from some common distributional families available in the lme4 R statistical package (R Development Core Team 2008), including Gaussian, Poisson, gamma, and inverse Gaussian. These models were compared based on their relative ability to estimate the underlying parameter values and the magnitude of the random effects in the simulated data.

Potential fixed-effect predictors of weight included shell height, depth, density, latitude, subarea (finer scale regional divisions important for area management within each of the broader geographic regions; Fig. 1), and management status (closed or open to fishing). Shell height, depth, density, and latitude were continuous variables, whereas subarea and management status were factors indicating whether a scallop occurred inside or outside a particular subarea, or whether the scallop occurred in an area that was currently closed or open to fishing. Year was examined separately. Random effects were considered either for the intercept alone (constant term a in Eq (1)) or for both the intercept and the shell height coefficient. We used Akaike's information criterion (AIC (Burnham & Anderson 2002)) to select models.

Somewhat simplified versions of the best model were used to explore the effects of year, subarea, and fishery management (closed vs. open fishing areas). A simple linear mixed model with an intercept fixed at 0 was used to determine a conversion factor for calculating meat weight or gonad weight from whole weight.

The at-sea observer meat weights were compared with those predicted from the observed shell heights using the best model obtained from the research vessel data. For each month,

TABLE 2.

Shell height/gonad weight best model results.

Formula	α	β	γ	δ	ρ	ω	β × γ	AIC	BIC
Georges Bank									
Height + (Height/Year_Sta)	−10.55 (0.017)	2.8 (0.056)						11,112	11,145
Height + Depth + (Height/Year_Sta)	−6.38 (0.015)	2.79 (0.055)	−0.97 (0.063)					10,911	10,951
Height + Depth + [Area] + (Height/Year_Sta)	−5.9 (0.029)	2.77 (0.054)	−1.02 (0.064)		a			10,854	10,926
Height + Depth + [Area] + Height × Depth + (Height/Year_Sta)	**−20.1 (0.029)**	**−9.13 (0.055)**	**4.09 (0.068)**		**b**		**0.7 (0.253)**	**10,848**	**10,927**
Area effects	a	b							
Closed Area 2	−0.15 (0.039)	−0.14 (0.039)							
North East Peak	−0.2 (0.042)	−0.19 (0.042)							
Nantucket Lightship	−0.28 (0.046)	−0.27 (0.046)							
South Channel	−0.22 (0.043)	−0.21 (0.042)							
South East Part	−0.41 (0.058)	−0.4 (0.057)							
Mid-Atlantic Bight									
Height + (Height/Year_Sta)	−14.11 (0.017)	3.41 (0.066)						4,684	4,715
Height + Depth + (Height/Year_Sta)	−9.88 (0.016)	3.34 (0.065)	−0.98 (0.075)					4,534	4,570
Height + Depth + Latitude + (Height/Year_Sta)	−12.4 (0.015)	3.34 (0.065)	−0.9 (0.078)	0.06 (0.016)				4,524	4,567
Height + Depth + Latitude + [Clop] + [Area] + (Height/Year_Sta)	**−10.47 (0.111)**	**3.36 (0.066)**	**−0.88 (0.086)**	**−0.008 (0.057)**	**0.37 (0.072)**			**4,506**	**4,579**

The parameters estimated are the intercept (α), the shell height coefficient (β), the depth coefficient (γ), the latitude coefficient (δ), the subarea or closed-versus-open coefficient (ρ), the shell height-by-depth interaction β × γ. The models with minimum Akaike's information criterion (AIC) values are in bold type. Bayesian information criterion (BIC) are listed for comparison. Random effects are shown as the parameters inside parentheses. All random effects were grouped by year_station, and each model included a random intercept, indicated by Year_Sta. Some models also included a random effect for height. Categorical variables, either subarea or clop (closed versus open) are in square brackets. Interaction terms are represented as factor 1 × factor 2. Subarea effects for the third (a) and fourth (b) GBK models are listed in columns by subarea. Based on 4,980 scallops from 670 stations (Georges Bank) and 3,256 scallops from 594 stations (Mid-Atlantic Bight).

the median predicted meat weights from these equations were compared with the monthly median volumetric meat weights by

$$\text{Monthly meat weight anomaly}$$
$$= (\text{Predicted} - \text{Observed})/\text{Predicted} \qquad (2)$$

Eq (2) gives the monthly median fractional difference between the weights predicted by the research vessel data (collected during the July to August period by scientists) and the commercially shucked meat weights. The data produced by Eq (2) were fit with a second-degree Loess smoother using a 25% span.

In combination with the growth parameters estimated in Hart and Chute (2009) and the dredge selectivities estimated in the 2010 scallop assessment (Northeast Fisheries Science Center 2010), we used the shell height-to-meat weight conversion equations estimated here to generate yield-per-recruit curves for both GBK and MAB sea scallops (see Hart (2003) for a description of the methods). We included depth effects, and estimated separate curves for the open and closed areas on GBK. The overall point estimates were weighted averages (by recruitment proportion) across the distribution of depths at which sea scallops occur in each region (Northeast Fisheries Science Center 2010).

We compared the partitioning of resources, by tissue type, in each region. The analysis was based on comparing ratios of gonad to whole weight, and meat to whole weight. All data analyses were conducted using the R statistical program (v2.9.2).

RESULTS

Simulation Results

Simulations testing the appropriateness of the various available error structures indicated that the Poisson family was the best choice. The gamma family GLMM failed to converge. The Gaussian family GLMM estimated the true underlying parameters adequately, but overestimated the magnitude of the random effects and produced a poor fit as reflected by the AIC. The inverse Gaussian GLMM produced a very tight fit to the data, but underestimated the magnitude of the random effects. The Poisson family GLMM reproduced the true parameter values reasonably well and came closest to estimating the magnitude of the simulated random effects.

Research Vessel Shell Height/Weight Relationships

The best model (i.e., the model with the lowest AIC, Table 1) for predicting meat weight of MAB sea scallops included the following as predictors: shell height (H), covariates for depth (D) in both the intercept and the shell height terms, a covariate for the closed-versus-open condition (u), as well as a random effects term for the intercept only:

$$E(M) = \exp(\alpha + \gamma \ln D + \rho u + [\beta + \rho \ln D] \ln H + r),$$

where $E(M)$ is the predicted meat weight in grams and r is the grouping/random effect. For gonad and whole weight, the

TABLE 3.

Shell height/whole weight best model results.

Formula	α	β	γ	δ	ρ	ω	β × γ	AIC	BIC
Georges Bank									
Height + (Height/Year_Sta)	−8.89 (0.005)	3 (0.021)						16,932	16,965
Height + Depth + (Height/Year_Sta)	−7.92 (0.004)	3 (0.021)	−0.23 (0.02)					16,813	16,852
Height + Depth + [Area] + (Height/Year_Sta)	−7.83 (0.01)	3 (0.021)	−0.25 (0.02)		a			16,794	16,866
Height + Depth + Latitude + [Area] + (Height/Year_Sta)	**−17.64 (0.009)**	**3 (0.021)**	**−0.23 (0.02)**	**2.62 (0.542)**	**b**			**16,773**	**16,851**
Area effects	a	b							
Closed Area 2	−0.06 (0.013)	−0.07 (0.013)							
North East Peak	0.001 (0.014)	−0.04 (0.016)							
Nantucket Lightship	−0.02 (0.015)	0.01 (0.017)							
South Channel	−0.02 (0.014)	−0.01 (0.014)							
South East Part	0.006 (0.018)	0.03 (0.018)							
Mid-Atlantic Bight									
Height + (Height/Year_Sta)	−9.7 (0.005)	3.15 (0.026)						8,981	9,012
Height + [Clop] + (Height/Year_Sta)	−9.73 (0.006)	3.15 (0.026)			0.07 (0.008)			8,908	8,945
Height + Depth + [Area] + (Height/Year_Sta)	−9.39 (0.009)	3.14 (0.026)	−0.06 (0.022)		a			8,896	8,957
Height + Depth + Latitude + [Area] + (Height/Year_Sta)	**−11.3 (0.023)**	**3.14 (0.026)**	**−0.03 (0.024)**	**0.05 (0.016)**	**b**			**8,889**	**8,956**
Area Effects	a	b							
Elephant Trunk	−0.06 (0.012)	−0.1 (0.017)							
Hudson Canyon	−0.07 (0.013)	−0.14 (0.026)							
Long Island	−0.009 (0.013)	−0.13 (0.041)							
New York Bight	0.02 (0.014)	−0.07 (0.032)							

The parameters estimated are the intercept (α), the shell height coefficient (β), the depth coefficient (γ), the latitude coefficient (δ), the subarea or closed-versus-open coefficient (ρ), the shell height-by-depth interaction β × γ. The models with minimum Akaike's information criterion (AIC) values are in bold type. Bayesian information criterion (BIC) are listed for comparison. Random effects are shown as the parameters inside parentheses. All random effects were grouped by year_station, and each model included a random intercept, indicated by Year_Sta. Some models also included a random effect for height. Categorical variables, either subarea or clop (closed versus open) are in square brackets. Interaction terms are represented as factor 1 × factor 2. Subarea effects for the third (a) and fourth (b) models for each region are listed in columns by subarea. Based on 4,980 scallops at 670 stations (Georges Bank) and 3,256 scallops at 594 stations (Mid-Atlantic Bight).

best models included random/grouping effects r_1 and r_2 for both the intercept and slope (ln H), and used depth and latitude (L) as covariates for the intercept only. The whole-weight model also included subarea (s) as a predictor of the intercept (Tables 2 and 3):

$$E(G) = \exp(\alpha + \gamma \ln D + \delta \ln L + \beta \ln H + r_1 + r_2 \ln H)$$

$$E(W) = \exp(\alpha + \gamma \ln D + \delta \ln L + \theta s + \beta \ln H + r_1 + r_2 \ln H),$$

where $E(G)$ and $E(W)$ denote predicted gonad and whole weight (in grams), respectively.

For GBK sea scallops, the best model (Table 1) for predicting meat weights of scallops included as predictors shell height (H), depth (D), latitude (L), and subarea (u). All covariates affected the intercept, but random effects (r_1 and r_2) affected the slope as well (Table 1):

$$E(M) = \exp(\alpha + \gamma \ln D + \delta \ln L + \theta u + \beta \ln H + r_1 + r_2 \ln H).$$

The best model for gonad weight for GBK scallops included covariates for depth on both the intercept and the slope (ln$H$ term), plus a subarea effect on the intercept only and random effects (r_1 and r_2) on the intercept and slope (Table 2):

$$E(G) = \exp(\alpha + \gamma \ln D + \theta u + (\beta + \rho \ln D) \ln H + r_1 + r_2 \ln H).$$

The best whole-weight model for GBK scallops included covariates for depth, latitude, and subarea, with random effects on the intercept only (Table 3):

$$E(W) = \exp(\alpha + \gamma \ln D + \delta \ln L + \theta u + \beta \ln H + r_1).$$

In all cases, depth was the most important predictor of meat, gonad, and whole weight after shell height. AIC values for models that included depth were always less than comparable models without depth. Sea scallop weights tended to be greater at shallower depths (Fig. 2).

Meat weights by subarea were variable. The New York Bight and Delmarva areas produced heavier meats across all depths, although this effect was not apparent at 50 m (Fig. 3). The Southeast Part and Closed Area 1 subareas had larger meats at depth. Meats were smallest in the South Channel and Northern Edge and Peak regions (Fig. 3). The effect of subarea may be somewhat confounded with depth because the median depth of the subareas varies (Fig. 3). Closed areas on GBK tended to have larger meats at all shell heights (Fig. 4).

Meat weights at shell height in the MAB area varied somewhat by year. The heaviest meats occurred in 2004 (Fig. 5), and
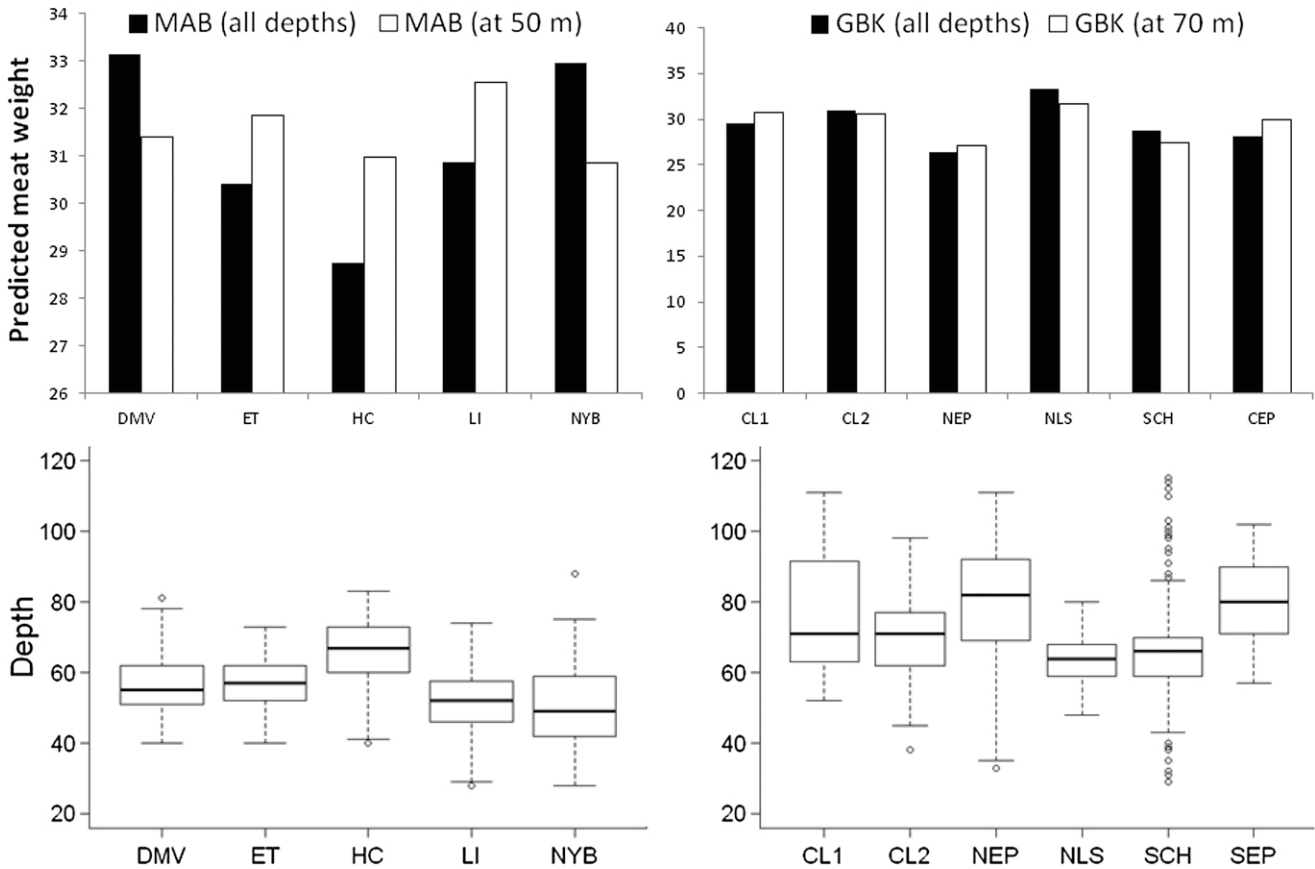
Figure 3. Predicted meat weight for a 120-mm scallop in each subarea in the Mid-Atlantic Bight (MAB) and Georges Bank (GBK). The boxplots indicate the depth of each observation by subarea. The thick lines are median depth and the height of the boxes indicates interquartile range. CL1, closed area 1; CL2, closed area 2; DMV, Delmarva; ET, Elephant Trunk; HC, Hudson Canyon; LI, Long Island; NEP, Northern Edge and Peak; NLS, Northern Light Ships; NYB, New York Bight; SEP, Southeast Part; SCH, South Channel.

meats were slightly heavier after 2008, when the annual survey was conducted earlier in the year. By contrast, meat weights were more consistent across years on GBK, except in 2007, when larger meats were found (Fig. 5). The seasonally earlier surveys in 2009 and 2010 did not produce meats that differed substantially from meats in other years.

Estimates from reduced models (i.e., models that use shell height as the only predictor) were fairly similar to most previous estimates (Table 4). Our estimates predict slightly heavier meats at small shell heights, but lighter meats at very large shell heights than other estimates, with the exception of that of Lai and Helser (2004) (Fig. 6).

Meat and Gonad Weight as a Function of Whole Weight

We fit a linear mixed model to characterize the relationship between whole weight and meat weight, and between whole weight and gonad weight, with the fit forced through the origin, and random effects for the intercept:

$$E(M) = \beta W + a(St) + r \qquad (3)$$

Meat weights and gonad weights since 2009 were slightly smaller (as a function of whole weight) in the MAB and slightly larger on GBK (Table 5).

Seasonal Effects on Meat Weight

Meat weights in the MAB were influenced by season. Weights were highest between April and August, and lowest during November to January (Fig. 7). On GBK, a bimodal pattern is evident, with peaks in December and June, and valleys in April and October.
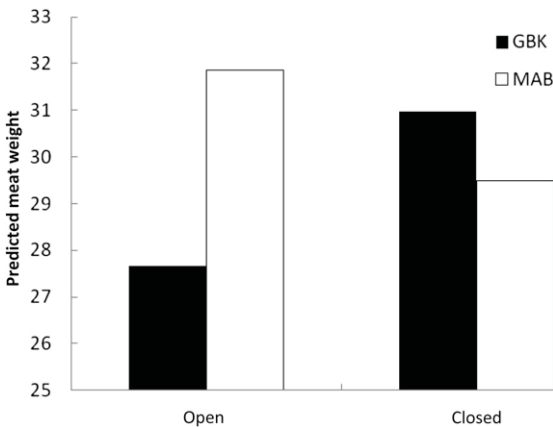

Figure 4. Predicted meat weight (measured in grams) by management strategy for a 120-mm scallop in the Mid-Atlantic Bight ($W = \exp[\alpha + a(St) + \beta \ln(L)]$) and Georges Bank ($W = \exp[\alpha + a(St) + \beta \ln(L) + b(L_{St})]$). GBK, Georges Bank; MAB, Mid-Atlantic Bight.
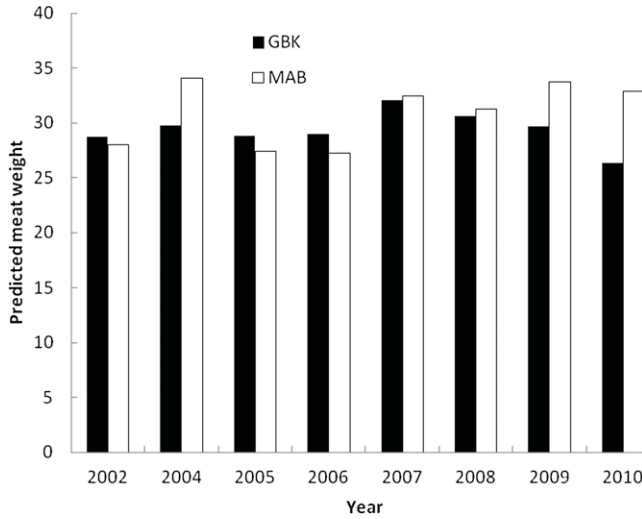
Figure 5. Predicted meat weight (measured in grams) by year for a 120-mm scallop in the Mid-Atlantic Bight ($W = \exp[\alpha + a(St) + \beta \ln(L)]$) and Georges Bank ($W = \exp[\alpha + a(St) + \beta \ln(L) + b(L_{St})]$). GBK, Georges Bank; MAB, Mid-Atlantic Bight.

TABLE 4.

Current shell height/meat weight parameters compared with those from other studies.

	α	β	γ
Mid-Atlantic Bight			
Haynes (1966)	−11.09	3.04	
Serchuk and Rak (1983)	−12.16	3.25	
Lai and Helser (2004)	−12.34	3.28	
This study	−10.80	2.97	
This study with depth effect	−8.94	2.94	−0.43
Georges Bank			
Haynes (1966)	−10.84	2.95	
Serchuk and Rak (1983)	−11.77	3.17	
Lai and Helser (2004)	−11.44	3.07	
This study	−10.25	2.85	
This study with depth effect	−8.05	2.84	−0.51

The parameters estimated are the intercept (α), the shell height coefficient (β), the depth coefficient (γ), in the Mid-Atlantic Bight and Georges Bank.

Yield-per-Recruit Analysis

Yield per recruit in both regions was highest in shallow water (Fig. 8). Estimates of F_{max} (the annual fishing rate that achieves maximum yield per recruit) were slightly lower in shallower depths. The biomass per recruit at F_{max} (B_{max}) was higher at shallow depths and in closed areas (Table 6). The MAB had variable estimates of F_{max} and B_{max} at depth, although they are mitigated somewhat by the fairly consistent depth profile of the region (Fig. 3).

Partitioning of Resources

Meat weight as a proportion of whole weight decreased in both regions. The scallops in the MAB apportioned resources to gonad weight increasingly as their size increased, but this was not observed in GBK scallops (Fig. 9). Some of the difference between regions was probably a result of differences in the residual weight—the mass remaining when gonad and meat weight are subtracted from whole weight, which can be used as a proxy for shell weight. GBK scallops had substantially heavier residual weights (Fig. 10).

DISCUSSION

Although there have been a number of previous studies relating sea scallop meat or gonad weight to shell height, several aspects of our study make it distinctive. Previous studies of offshore sea scallop populations either froze soft tissue samples or brought live scallops to land, where the animals were weighed. Both procedures potentially distort results because tissues can gain or lose mass during transport or freezing. Scallops from our study were weighed at sea immediately after capture, and were more diverse geographically than those in previous experiments. The large number of sampling locations in our study allowed for precise estimation of weights at shell height, with or without covariates such as depth.

We also used an advanced modeling approach (GLMM), which has several advantages over the methods used in previous shell height/meat weight studies. Our use of a generalized linear model with a log link function avoids log-transforming the response variable (weight), which can induce bias in back-transformation (Beauchamp & Olson 1973, Venables & Dichmont 2004). An approximate bias correction can be estimated (Beauchamp & Olson 1973), but does not appear to have been applied in previous studies.

We used random effects to group scallops from the same station. Random effects improved the model fit (i.e., decreased the AIC) in all analyses, demonstrating that individuals at the same sampling site are more similar to each other than to the general population. Studies that collected multiple samples (scallops) per site but that did not include random effects typically overstate the precision of their estimates. This occurs because the analysis assumes that within-site observations are independent when, in fact, they often are highly correlated. For example, Sarro and Stokesbury (2009) report an overall sample size of 14,168 scallops, and their analysis treated observations from each scallop as independent (i.e., their model did not use random effects). However, these scallops were collected in batches of 150–200 scallops from the same site, and, in agreement with our study, scallops within each site were more similar than those at different sites (Rothschild et al. 2009). Thus, the within-site observations were effectively pseudo-replicates, and treating them as independent induced an overestimate of the true precision.

The GLMM approach also allows specification of the appropriate variance structure of the response variable, whereas a log-transformed regression assumes implicitly that variance increases with the square of the mean—an assumption that is rarely checked and appears incorrect for scallop weights. *A priori* simulations demonstrated that a Poisson family GLMM performed better than any other candidate family we tested. In fact, the Poisson family error structure was superior in (1) reproducing the true underlying parameter values, (2) quantifying the magnitude of random effects, and (3) delineating the
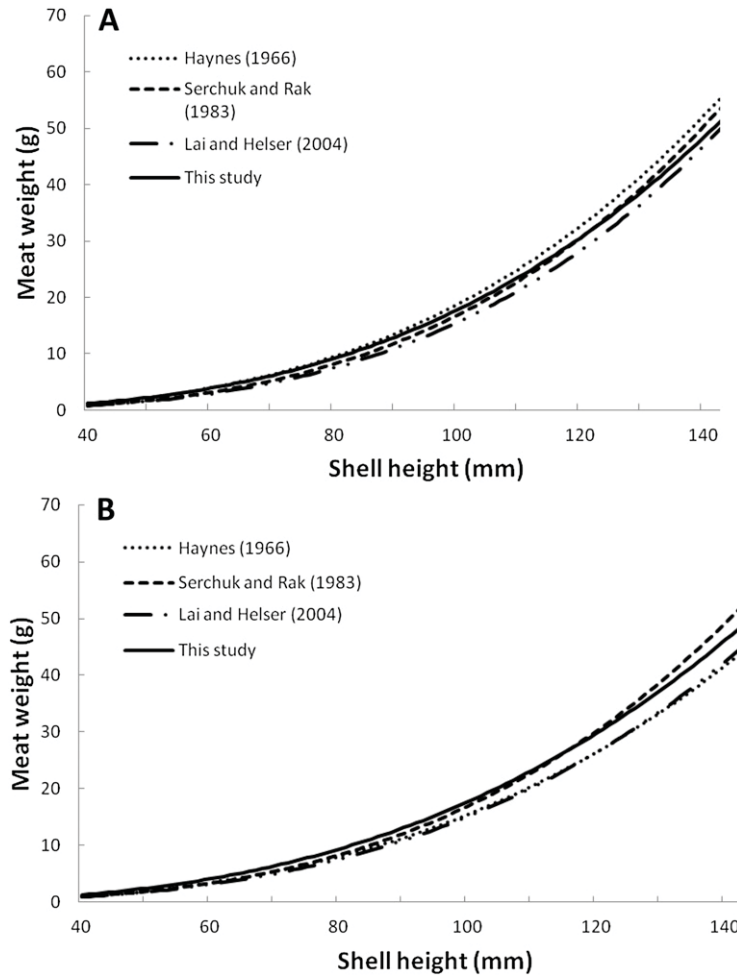
Figure 6. (A, B) Comparison of shell height/meat weight parameter estimates in the Mid-Atlantic Bight (A) and Georges Bank (B). Directly comparable models only; $W = \exp[\alpha + a(St) + \beta \ln(L)]$.

appropriate precision of the estimates based on the magnitude of the simulated error.

In our models that predicted meat, gonad, and whole weight, depth was consistently the strongest predictor after shell height. This agrees with several other studies and is likely related to greater food availability at shallow depths (MacDonald &

Thompson 1985a, MacDonald & Thompson 1985b, MacDonald & Bourne 1987, Barber et al. 1988, Lai & Helser 2004).

Closed areas also had an effect on all 3 tissue weights, with heavier weights inside closures than outside. This agrees

TABLE 5.

Mixed-effects model fits using whole weight to predict meat weight and gonad weight.

	β
Mid-Atlantic Bight	
Meat weight × β = Whole weight (<2009)	6.94 (0.001)
Meat weight × β = Whole weight (>2008)	6.49 (0.001)
Gonad weight × β = Whole weight (<2009)	22.22 (0.001)
Gonad weight × β = Whole weight (>2008)	17.86 (0.001)
Georges Bank	
Meat weight × β = Whole weight (<2009)	7.94 (0.001)
Meat weight × β = Whole weight (>2008)	8.55 (0.002)
Gonad weight × β = Whole weight (<2009)	13.70 (0.001)
Gonad weight × β = Whole weight (>2008)	18.87 (0.001)

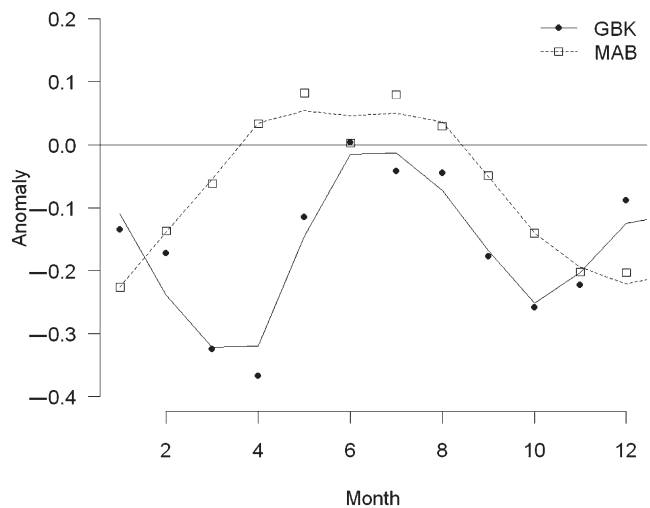The model was forced through the origin to be used as a conversion factor.

Figure 7. Seasonal anomalies in meat weight. The points were fit by a second-degree Loess smooth with a 25% span. GBK, Georges Bank; MAB, Mid-Atlantic Bight.
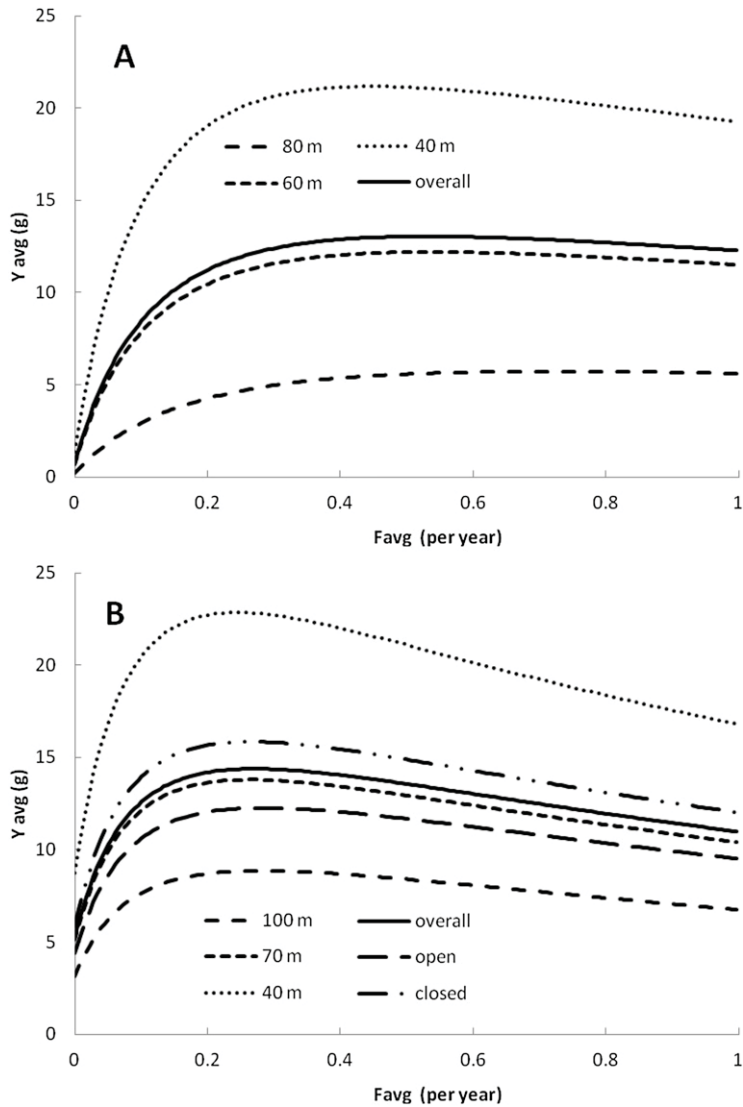
Figure 8. (A, B) Yield-per-recruit curves for the Mid-Atlantic Bight (A) and Georges Bank (B).

TABLE 6.

Yield-per-recruit estimates with depth effects and open versus closed areas.

Area	F_{max}	Y_{max} (g)	B_{max} (g)
Mid-Atlantic Bight			
Overall	0.53	13.04	52.75
40 m	0.45	21.17	74.83
60 m	0.53	12.20	50.16
80 m	0.72	5.72	37.75
Georges Bank			
Overall	0.32	14.38	72.75
40 m	0.29	22.85	112.12
70 m	0.31	13.79	69.89
100 m	0.33	8.86	49.63
Open, 60 m	0.34	12.27	61.43
Closed, 60 m	0.31	15.85	80.19

F_{max} is the annual fishing rate at peak yield per recruit (Y_{max}), and B_{max} is the average biomass per recruit at F_{max}.

with the results of Kaiser et al. (2007), who studied populations of the great scallop *Pecten maximus* in the English Channel and suggested that reduced weights in fished areas may reflect sublethal damage from contact with scallop gear. Hart and Chute (2009) found that sea scallops within closed areas had faster growth than those outside. However, sublethal damage was not the cause of slower growth in the fished areas because the open and closed growth curves only diverged when the scallops were large enough to be fished commercially. Hart and Chute (2009) instead proposed that scallopers tend to fish harder in areas where scallops grow faster, thus leaving fished areas with scallops that, on average, grow slower than those in closed areas. We suggest that a similar process is occurring with meat weights, so that areas with heavier meats are fished harder. Growth, meat, and gonad weights are all likely positively correlated with food supply, so that scallops in areas with greater food supplies may be fished especially hard because these animals exhibit both faster growth and larger meats.
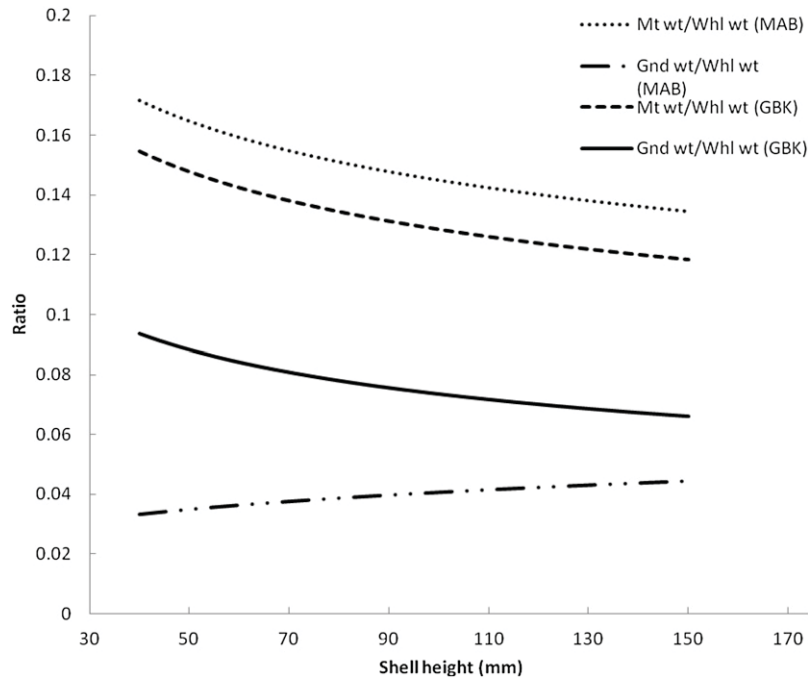
Figure 9. Investment of energy resources in tissue type as a proportion of whole weight by size. GBK, Georges Bank; Gnd wt, gonad weight; MAB, Mid-Atlantic Bight; Mt wt, meat weight; Whl wt, whole weight.

In addition to the growth advantages just mentioned, shallow areas are often closer to shore and thus less costly to fish. As a result, the shallow subareas (and shallow parts of subareas) are generally fished first, with deeper areas fished only when the catch per unit effort in the shallow areas drops off. Because many scallop subareas are managed rotationally, and because fishing effort is increased gradually over time after an area opens, the timing of the survey relative to closure status may be important. If an area is surveyed early during a rotational open period when the fishing effort is restricted to allow a gradual increase in fishing pressure, there may still be a substantial portion of the shallow-water population available to survey. It is also probable that closed areas tend to produce heavier meats because the shallow regions within these subareas will have relatively dense populations. In open areas, biomass tends to be concentrated in deeper areas that produce smaller meats. For example, the closed areas on GBK tend to have larger meats at all shell heights than the open areas (Fig. 4).

None of our models indicated that scallop density affects meat, gonad, or whole weights negatively. This is because sea scallops—even at very high natural densities—filter only a small portion of the available water column in a day, and thus are unlikely to deplete their food supply (Hart & Chute 2009). We did find a weak positive relationship between density and meat weight for MAB sea scallops, in accord with Lai and Helser (2004). This is likely not a direct effect, but may indicate that more favorable locations have greater densities of scallops as well as larger meat weights.

Gonad weights were larger on GBK than the MAB at the same shell height and depth. This likely reflects spawning cycle differences in the 2 regions. MAB scallops often have a major spawning event during spring whereas the principal spawning season of GBK scallops is in the early autumn, with only minor reproductive activity occurring during spring (Schmitzer et al. 1991, Almeida et al. 1994,

Dibacco et al. 1995). Research vessel data collection occurred after the spring spawning events, but before the late summer/early autumn spawning activity. Scallops in the MAB were likely rebuilding their gonad mass during our sampling period, whereas the gonads were approaching their prespawn peak on GBK.

The allocation of resources to different somatic tissues also differs by region. In the MAB, allocation to gonad weight as a function of whole weight increased gradually with shell height, whereas meat weight allocation decreased. On GBK, allocations to both meat and gonad weights, as a function of whole weight, decreased with increasing shell height (Fig. 9). Some of the differences in resource allocation between the regions can be explained by differing allocation to the building of the shell. Residual weights were higher on GBK than in the MAB at all lengths (Fig. 10), reflecting heavier shell weights on GBK. This may be induced by the stronger currents on GBK, which could cause the scallops to form thicker shells as a protective measure. The heaviest residual weights were found in the Northern Edge and Peak, where water currents are the strongest. Interpretation of these results require some caveats, however, because the gonads in each region are in different developmental phases at the time they are sampled in the surveys.

Relationships between whole and meat weights allow for conversions between these 2 units to set catch quotas or trip limits for both scallopers that land whole scallops and those that land only the meats. The traditional ratio between whole and meat weight is 8.33. This agrees well with our estimate for GBK scallops, but is higher than our estimate for the MAB, again possibly as a result of the thinner shells there (Table 5). Our estimates were made from scallops with shells that had been scrubbed clean. Whole scallops caught commercially often have attached epifauna on their shells and thus may have a somewhat higher whole weight-to-meat weight ratio.
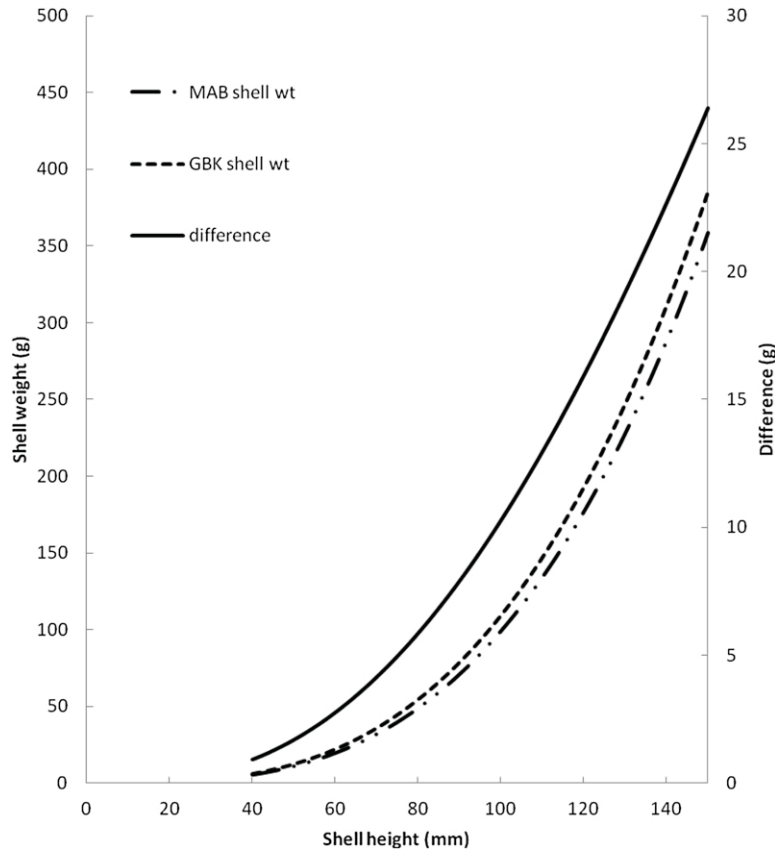
Figure 10.   Residual weight [Whole weight – (Meat weight + Gonad weight)] of scallops in the Mid-Atlantic Bight (MAB) and Georges Bank (GBK). The difference between regions in absolute weight is plotted on the secondary *y*-axis.

Seasonal variation in meat weights, including a pronounced decrease in meat weight after the late summer or early autumn spawn, has been noted previously (Haynes 1966, Serchuk & Smolowitz 1989, Rothschild et al. 2009, Sarro & Stokesbury 2009). Several of these studies constructed separate shell height/meat weight relationships for different seasons or months. This approach can confound depth or area effects with true seasonal variation, especially if the scallops from different months are sampled from different locations, as was the case in all the studies noted here. Our approach avoids this problem by estimating meat weight as a function of shell height and other covariates in a consistent time of year, and then computing seasonal anomalies in this relationship separately.

Seasonal patterns in meat weight are driven by ecological and life history factors. Meat weights increase in the spring because of increased food intake during the spring bloom. A pronounced decrease in meat weights occurs during September and October in both regions, coinciding with the fall spawn. Meat weights increase somewhat in December and January on GBK, but decrease again before increasing during summer. The winter increase in meat weight on GBK is best explained by what Friedland et al. (2008) call the "fall dump," a phenomenon in which a large bloom of phytoplankton that is produced usually in October is consumed incompletely by the zooplankton at that time of year. The remaining phytoplankton eventually die and settle to the sea floor. This fall dump provides a nutritional boost to the benthos and explains the increase in winter sea scallop meat weights on GBK. The benefits of the fall dump tend to disappear as its constituent phytoplankton is eaten by demersal organisms, leading to the decrease in meat weights observed in February and March. The subsequent spring bloom likely produces additional phytoplankton dumps and the spring increase in meat weight on GBK. The fall dump is not typical in the MAB region.

Understanding the seasonal meat weight patterns is useful for fishery management if measures can be developed to direct more fishery effort to the months when the meat weights are high. For example, in some years, managers imposed a September to October closure in rotational fishery areas in the MAB both to improve meat yields in the fishery and to avoid interactions between the scallop fishery and loggerhead turtles that migrate south during that time (Murray 2011).

A more complete understanding of allometric relationships can provide important tools to fisheries managers. Yield-per-recruit analysis indicates that scallops in shallow water have higher yields per recruit, and the maximum yield per recruit for these animals occurs at a lower fishing mortality than those from deeper waters. A similar pattern was found for Bay of Fundy sea scallops (Smith et al. 2001, Smith & Rago 2004). Because there is a natural tendency for scallops in shallower areas to be fished harder, it is likely that yield per recruit cannot be optimized for both shallow and deep waters at the same time unless specific area management is imposed that controls fishing effort by depth.

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