Shell growth of sea scallops (*Placopecten magellanicus*)
in the southern and northern Great South Channel, USA

Bradley P. Harris and Kevin D. E. Stokesbury


Shell growth of sea scallops in two commercially productive regions of the Great South Channel (GSC) (41°4′N 69°16′W) was studied using tag—recapture experiments. Commercial fishers captured and returned 9.7% of the 11,704 sea scallops tagged in the southern GSC study area, and 7.9% of the 18,274 sea scallops tagged in the northern GSC study area. Scallop density and shell height distribution were sampled with underwater video in the two study areas. In the southern GSC tagged scallops grew faster, reached larger asymptotic size, and had higher growth performance (φ) than in the northern GSC study area. Mean sea scallop density in the southern GSC was 0.117 scallops m⁻² (s.e. = 0.01) and 2.601 scallops m⁻² (s.e. = 0.28) in the northern GSC. Environmental factors, fishing pressure, and sea scallop density all influence shell growth on a fine geographic scale (1–100 km²) and should be considered in area-specific management strategies, such as that currently used in the USA sea scallop fishery.

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B. P. Harris and K. D. E. Stokesbury: School for Marine Science and Technology, University of Massachusetts Dartmouth, 706 South Rodney French Boulevard, New Bedford, MA 02744, USA. Correspondence to B. P. Harris: tel: +1 508 910 6359; fax: +1 508 999 8197; e-mail: bharris@umassd.edu.

Introduction

The shell growth of the sea scallop, *Placopecten magellanicus*, in USA waters varies both temporally and spatially and is affected by water depth, temperature, food availability, flow velocity, and fishing pressure (MacDonald and Thompson, 1985a, b; Wildish et al., 1987; Schick et al., 1988; Thouzeau et al., 1991; Wildish and Saulnier, 1992; Shumway et al., 1987). In the Georges Bank stock area (≈35,000 km²), the temporal and spatial variabilities of sea scallop shell growth are poorly understood (Figure 1). Therefore, a single, stock-wide, von Bertalanffy growth function (VBGF) is used to estimate shell growth and to predict shell height at age of sea scallops (von Bertalanffy, 1938; Beverton and Holt, 1957; SAW, 2004).

In 2004, the USA commercial sea scallop fishery shifted from a stock-wide to an area-specific rotational management strategy. Currently, fishing effort is directed to or restricted from zones within the stock area, including limited access to two large marine protected areas (MPA) on Georges Bank and one in the southern Great South Channel (GSC; Figure 1; Murawski et al., 2000; 50 CFR Part 648, 2004; SAW, 2004; Munro and Pauly, 1983). This study represents the first tag—recapture comparison of the shell growth of sea scallops within the Georges Bank stock area.

We examined sea scallop shell growth in two commercially productive areas of the GSC (41°4′N 69°16′W) by conducting tag—recapture experiments, and compared VBGF parameters fit to our tag—recapture data with those previously estimated for Georges Bank using an index of growth performance (Merrill et al., 1966; Serchuk et al., 1979; Pauly and Munro, 1984; Moreau et al., 1986; Thouzeau et al., 1991). Further, we examined the density and shell height distribution of sea scallops in the two study areas using underwater video (Stokesbury, 2002; Stokesbury et al., 2004a). Our tag—recapture growth data cover temporal and spatial scales of 1–2 years and <5 km², respectively.

Material and methods

Study areas

Sea scallops were tagged in two areas of the GSC where sea scallop densities support commercial harvests, but where
shell height distributions differ (Figure 1). Video surveys, commercial landings, and anecdotal evidence indicate that sea scallops >120 mm shell height are common in the southern GSC near the Nantucket Lightship Area, in contrast to the northern GSC where sea scallops >120 mm are rare (SAW, 2001; Stokesbury et al., 2004b). We tagged 11,704 sea scallops in GSC study area 1 (GSC1) on four cruises during 12–13 May, 19–20 May, 24–25 May, and 8–9 June 2001, and 18,274 sea scallops in GSC study area 2 (GSC2), 74 km north-northwest of GSC1, during one cruise from 9 to 12 September 2002 (Figure 1).

Tagging

Sea scallops were collected with a New Bedford-style scallop dredge and tagged aboard commercial scallop vessels (Bourne, 1964; Caddy, 1989). Few sea scallops smaller than 90 mm were caught owing to the selectivity of the dredge collection bag, which is constructed of 88.9-mm diameter steel rings.

We attached a plastic Peterson disc tag to the left (upper) shell of each sea scallop with stainless steel wire (Figure 2). During the tagging procedure, individual sea scallops remained aboard the vessel for 4–5 h, and were kept alive in tubs (41 cm wide × 67 cm long × 29 cm deep) with flow-through seawater. Shell heights were measured with a measuring board (±1 mm) (Figure 2). Tagged sea scallops were released at locations within or adjacent to the capture areas.

Commercial fishers returning tagged shells, along with the date and location of capture, were rewarded with a cap. The tag number, shell height, recapture date, and location of each returned shell were recorded.

Video survey of sea scallop density and shell height distribution

We deployed the SMAST video survey pyramid from the vessel prior to capturing sea scallops for tagging (Figure 3). A DeepSea multi-SeaCam 2050© underwater camera mounted vertically on the pyramid 1575 mm above the pyramid’s base provided a 2.841-m² quadrat of the sea floor (Figure 4). All sea scallops in the view area were counted, including those along the edge of the quadrat image that were only partially visible. To correct for this edge effect, 56 mm, based on the average shell height of the sea scallops observed, was added to each edge of the quadrat image, increasing the quadrat size to 3.235 m² (Stokesbury, 2002).

Owing to the small size of the growth study areas (<5 km²) we did not use predetermined video sampling stations, but instead randomly chose a starting station where the tide and wind would cause the survey vessel to drift through the GSC growth study area. At the first station, the pyramid was lowered to the sea floor. Footage of the station was recorded, then the pyramid was raised so that the sea floor was no longer visible. The vessel drifted
approximately 50 m, and the pyramid was lowered to the sea floor again to obtain a second station, and so on. When the vessel reached the edge of the growth study area, the pyramid was hauled to the surface and the vessel repositioned for another drift until coverage of the area was obtained.

Video footage of the sea floor was recorded on S-VHS tapes. Time, depth, number of live and dead sea scallops, substrate, latitude and longitude at each station were noted. After each survey, the videotapes were reviewed in the laboratory; the field data were verified, and the shell height (mm) of each sea scallop visible was measured using Image Pro Plus® software (Tagged Image File Format; Figure 4).

Data analysis

The growth increment (mm) for each recaptured sea scallop shell was determined by subtracting the shell height at tagging ($H_{t1}$) from that at recapture ($H_{t2}$) (Figure 2). The number of days between release and recapture are days at liberty ($\Delta t$).

The instantaneous growth rate $G$, where $G = ([\ln(H_{t2}) - \ln(H_{t1})]\/(\Delta t))\times100$, was calculated for each recaptured shell in each study area (Ricker, 1975; Weatherly and Gill, 1987). Mean $G$ for each 10-mm size class, based on the shell height of the sea scallop at tagging (i.e. 65 mm size $\equiv H_{t1} = 60-69$ mm), in each study area was calculated. We tested these data for heterogeneity of variance and normality with Levene’s test and the Kolmogorov–Smirnov goodness-of-fit (K–S) test, respectively, and data failing these tests were log$_{10}$ transformed and retested (Levene, 1960; Chakravarti et al., 1967).
Welch's approximate t formation, then equality in the mean was tested with the non-parametric Wilcoxon Signed Ranks test (Zar, 1999; Hollander and Wolfe, 1999).

We performed a linear regression of the observed daily growth increment on each tagged sea scallop's average shell height between tagging and recapture, \( GI = a + \frac{b}{2}H_{t} \), where \( a \) is the regression constant and \( b \) is the slope, the VBGF parameter \( H_{\infty} = -\frac{a}{b} \), and \( k = -b \) (Gulland and Holt, 1959).

Finally, we estimated the VBGF parameter \( k \), where \( k = [\ln(H_{\infty} - H_{t})] - [\ln(H_{\infty} - H_{t})/(\Delta t)] \), using trial values of \( H_{\infty} \) (Munro, 1982). The trial \( H_{\infty} \) producing the lowest coefficient of variation (CV), the ratio of the standard deviation to the mean, for \( k \) was the best fit. This technique is referred to as the CV method.

Previous Georges Bank sea scallop shell growth studies estimated VBGF parameters using different methods (counting shell rings and tagging), different VBGF fitting methods, and covered much larger temporal and spatial scales than this study (Merrill et al., 1966; Serchuk et al., 1979; Thouzeau et al., 1991). Therefore, the definitions of the VBGF parameters \( H_{\infty} \) and \( k \) differ between studies (Francis, 1988). To compare VBGF growth models between our study areas and previous studies we calculated a growth performance index, \( \phi' \), where \( \phi' = \log(k) + 2\log(H_{\infty}) \) (Pauly and Munro, 1984; Moreau et al., 1986). This index has been used to compare growth estimates of the Patagonian scallop, Zygochlamys patagonica (Defeo and Gutierrez, 2003).

Mean sea scallop densities and shell height distributions were calculated for GSC1 and GSC2. Mean sea scallop density was the total number of sea scallops observed divided by the total number of stations, multiplied by the average density for each group (Francis, 1988). To compare VBGF growth models between our study areas and previous studies we calculated a growth performance index, \( \phi' \), where \( \phi' = \log(k) + 2\log(H_{\infty}) \) (Pauly and Munro, 1984; Moreau et al., 1986). This index has been used to compare growth estimates of the Patagonian scallop, Zygochlamys patagonica (Defeo and Gutierrez, 2003).

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Results

Tagging

In total, 25 commercial scallop vessels returned 1144 tagged sea scallops from GSC1 after 60–900 days at liberty, and 1450 were returned from GSC2 after 140–360 days at liberty (Figure 6). Owing to shell breakage and pre-recapture mortality (indicated by encrusting organisms growing on the underside of the shell), respectively, 251 and 153 shells from GSC1 and 716 and 158 shells from GSC2 were removed from the growth analysis. Therefore, shell growth was estimated using 740 and 576 tag
recaptures from GSC1 and GSC2, respectively. Shell material was frequently observed covering the wire tag anchors (Figure 2). Posgay (1963) reported similarly and suggested that tagging did not negatively affect sea scallop shell growth.

Instantaneous growth ($G$)

Sea scallop shell growth data were non-normally distributed (K-S: GSC1 = 0.075, $p < 0.001$; GSC2 = 0.207, $p < 0.001$), and had unequal variance (Levene’s test; $F = 35.133$, $p < 0.001$) in both study areas. Logarithmic transformation did not normalize the distributions nor correct for unequal variance. The data divided into 10-mm size classes also failed these tests in all cases except the comparison of 55-mm and 65-mm sea scallops from GSC1, each of which had a small sample size ($n = 9$).

In GSC1, sea scallops of each 10-mm size class had significantly lower mean and median $G$ than the preceding size class, with the exception of 55 mm vs. 65 mm and 125 mm vs. 135 mm. 

Figure 5. Histograms and summary statistics of tagged sea scallop, Placopecten magellanicus, shell heights in the Great South Channel study areas. The asterisks and crosses indicate the minimum and maximum shell heights tagged in GSC1 and GSC2, respectively, and $n$ is the number of sea scallops tagged.

Figure 6. Days at liberty ($\Delta t$) for sea scallops, Placopecten magellanicus, tagged in the GSC1 and GSC2 study areas. Day 0 equals the tagging date for each sea scallop.
In GSC2, sea scallops of each 10-mm size class had significantly lower mean and median $G$ than the preceding size class, with the exception of 105 mm vs. 115 mm (Figure 8, Table 1). The results of Welch’s approximate $t$-test and the non-parametric Wilcoxon Rank Sum test are consistent, indicating that both mean and median $G$ differed between successive size classes within study areas, and between equal size classes across study areas.

Table 1. Comparison of difference in mean (Welch’s approximate $t$-test) and median (Wilcoxon $W$) instantaneous growth rate ($G$) followed by the probability ($p$) at $\alpha = 0.05$ of sea scallop, Placopecten magellanicus, by size class in the GSC1 and GSC2 areas.

<table>
<thead>
<tr>
<th>Area</th>
<th>Size class comparison</th>
<th>$\Delta G$</th>
<th>$t$</th>
<th>$p$</th>
<th>Wilcoxon $W$</th>
<th>$p$</th>
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</thead>
<tbody>
<tr>
<td>GSC1</td>
<td>55 vs. 65</td>
<td>0.0111</td>
<td>1.614</td>
<td>0.107</td>
<td>106</td>
<td>0.077</td>
</tr>
<tr>
<td></td>
<td>65 vs. 85</td>
<td>0.0483</td>
<td>8.759</td>
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<td>333</td>
<td>&lt;0.001</td>
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<td>85 vs. 95</td>
<td>0.0136</td>
<td>5.019</td>
<td>&lt;0.001</td>
<td>7383</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>95 vs. 105</td>
<td>0.0067</td>
<td>5.432</td>
<td>&lt;0.001</td>
<td>55832</td>
<td>&lt;0.001</td>
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<tr>
<td></td>
<td>105 vs. 115</td>
<td>0.0174</td>
<td>10.273</td>
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<td>7920</td>
<td>&lt;0.001</td>
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<tr>
<td></td>
<td>115 vs. 125</td>
<td>0.0062</td>
<td>2.644</td>
<td>0.008</td>
<td>2879</td>
<td>&lt;0.001</td>
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<tr>
<td></td>
<td>125 vs. 135</td>
<td>0.0029</td>
<td>0.667</td>
<td>0.505</td>
<td>302</td>
<td>0.154</td>
</tr>
<tr>
<td>GSC2</td>
<td>85 vs. 95</td>
<td>0.0104</td>
<td>3.027</td>
<td>0.003</td>
<td>4791</td>
<td>0.005</td>
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<tr>
<td></td>
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<td>&lt;0.001</td>
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<td>0.577</td>
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<td>0.429</td>
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<tr>
<td>GSC1 vs. GSC2</td>
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<td>0.0258</td>
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<td>&lt;0.001</td>
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<td>95 vs. 95</td>
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<td>92139</td>
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<td></td>
<td>115 vs. 115</td>
<td>0.0079</td>
<td>1.771</td>
<td>0.077</td>
<td>323</td>
<td>&lt;0.001</td>
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</table>

$t$ = Welch’s approximate $t$. $\Delta G$ = Difference in mean $G$ for size classes compared.
Each size class of sea scallops in GSC1 had a significantly higher $G$ than the same size class in GSC2 (Table 1). In both study areas, instantaneous growth rates approached zero with increasing size class, indicating asymptotic shell growth (Figures 7, 8). In GSC1, mean $G (0.0375, \text{s.e.} = 0.0007)$ was significantly higher than in GSC2 ($0.0160, \text{s.e.} = 0.0007; t = 21.1, \text{d.f.} = 1309.8$, two-tailed $p < 0.001$). Median $G$ in GSC1 ($0.0375, 25\% = 0.0236, 75\% = 0.0473$) was significantly higher than in GSC2 ($0.0112, 25\% = 0.00597, 75\% = 0.0190; \text{Wilcoxon } W = 235484.50$, two-tailed $p < 0.001$ corrected for ties).

Von Bertalanffy growth function and the growth performance index

The three fitting methods resulted in distinct VBGF parameters, but similar $\phi'$ for GSC1. Maximum and minimum $\phi'$ values for this study were estimated using the 95% confidence intervals of $H_\infty$ and $k$. Only mean $\phi'$ was determined for the CV method, because estimates of variance for $H_\infty$ cannot be calculated as it is a fixed value (Figure 9, Table 2).

In GSC2 19.2% of tagged sea scallops grew <2 mm compared with 4.8% in GSC1 for the same number of days at liberty. Therefore, neither the linear nor the CV methods converged on a VBGF solution for the GSC2 data. For GSC2, the non-linear method resulted in mean $\phi' = 3.592$, with range equal to mean $\phi' \pm 0.17$ (Figure 9).

All three $\phi'$ for GSC1 were higher than $\phi'$ for GSC2 (Figure 9). Merrill et al. (1966) estimated Walford (1964) linear regressions equal to VBGF parameters $H_\infty = 144.21 \text{ mm}$ and $k = 0.34 \text{ y}^{-1}$ for shell features, and $H_\infty = 139.9 \text{ mm}$ and $k = 0.41 \text{ y}^{-1}$ for tag-recapture data from the Canadian Georges Bank. Thouzeau et al. (1991) fitted the VBGF parameters $H_\infty = 144.87 \text{ mm}$ and $k = 0.28 \text{ y}^{-1}$ using shell ring counts from sea scallops also collected on the Canadian Georges Bank. Serchuk et al. (1979) used National Marine Fisheries Service data from many locations on Georges Bank to fit VBGF $H_\infty = 152.46 \text{ mm}$ and $k = 0.34 \text{ y}^{-1}$, values currently used as the stock-wide Georges Bank growth parameters (SAW, 2001).

The maximum and minimum estimates of $\phi'$ in GSC1 encompassed $\phi'$ calculated from Serchuk et al. (1979) and the two estimates calculated from Merrill et al. (1966), but were higher than $\phi'$ calculated using the VBGF of Thouzeau et al. (1991) (Figure 9). The $\phi'$ estimated for GSC2 was lower than in previous Georges Bank studies (Figure 9).
Sea scallop shell growth rates and performance differed between the two study areas. Overall, sea scallops grew faster in GSC1 than in GSC2. Instantaneous growth rates were higher for all size classes in GSC1, compared with GSC2, indicating faster growth for sea scallops of equal shell height. Sea scallops grew towards a larger asymptotic shell height, $H_\infty$, and had higher $\phi'$ in GSC1 than GSC2. Further, separating sea scallops into 10-mm size classes for analysis increased the precision of the growth comparison between GSC1 and GSC2, because growth differed between the size classes within each area.

The differences in instantaneous shell growth rate evident from this tagging study correspond with shell height frequency distributions sampled with commercial dredges during the tagging experiment and underwater video surveys (Figures 5, 10). In both study areas, $H_\infty$ estimated from tagging data approximates the 99th percentile of size frequencies observed in the dredge samples, and the 95th percentile observed in the video survey samples. This difference in percentiles may be due to the dredge having lower selectivity for very large sea scallops, which form depressions in the sea floor (Caddy, 1989).

The southern and northern Great South Channel study areas (GSC1 and GSC2) are 74 km apart; both are dominated by granule–pebble substrata, but have differing water depths and flow velocities (Stokesbury et al., 2004b). Increasing water depth is correlated with decreasing shell growth and smaller $H_\infty$ (Schick et al., 1988; Naidu, 1991). However, GSC1 was an average 18 m deeper than GSC2, but had faster growth rates and larger $H_\infty$, suggesting that within the depth range of this study (50–80 m), depth did not inhibit shell growth.

The differences in GSC1 and GSC2 shell growth may be due to greater flow velocities in GSC2 limiting sea scallop feeding. Sea scallops are filter-feeders, and food availability may be constrained directly by low seston abundance or indirectly by high flow velocities impeding filtration. Flow velocities $>10$ cm s$^{-1}$ may inhibit sea scallop feeding (Wildish et al., 1987; Wildish and Saulnier, 1992, 1993). Near-bottom current speeds appear twice as high in GSC2

![Figure 9. The growth performance index ($\phi' = \log_{10}(k) + 2\log_{10}(H_\infty)$) for sea scallop, Placopecten magellanicus, in GSC1 and GSC2, compared with the results of previous Georges Bank studies.](https://academic.oup.com/icesjms/article-abstract/63/5/811/661668)
than in GSC1 (Brown and Moody, 1987; Butman, 1987; Butman and Beardsley, 1987).

Encounters with fishing gear may inhibit growth by physically damaging the shell margin or burying the sea scallop (Caddy, 1973). If the rate of tag recapture (percentage of tagged sea scallops recaptured/\(D_t\)) is used as a proxy for fishing pressure, then GSC2 experienced 2.2 more fishing pressure than GSC1. The high rate of shell breakage in GSC2 (49.3%) compared with GSC1 (24.0%) also suggests higher rates of encounter with fishing gear. Therefore, the potentially negative impacts of fishing pressure on shell growth should be considered when determining area-specific fishing intensity.

Video surveys indicated that sea scallop density was >20× higher in GSC2 than in GSC1. Therefore, growth rate and growth performance in GSC2 may be density-dependent. Parsons and Dadswell (1992) found that shell growth of juvenile sea scallops (5–29-mm shell height) in suspended culture was also inversely related to stocking density.

The VBGF parameters of Serchuk et al. (1979) and Merrill et al. (1966) result in estimates of \(\phi_t\) that agree with GSC1, suggesting that GSC1 shell growth is similar to the historical Georges Bank average growth. Thouzeau et al. (1991) suspected that their samples were affected by Lee’s phenomenon (Lee, 1912), which may explain why \(\phi_t\) based on their VBGF parameters differ from GSC1 and other Georges Bank studies (Schick et al., 1988; Caddy, 1989).

Sea scallop shell growth rates differed between our study areas, suggesting that a single stock-wide growth model may over- or underestimate growth when applied to spatially specific management areas. Additionally, the VBGF parameters we estimated for GSC1 and GSC2 varied with different fitting methods while \(\phi_t\) remained similar. Therefore, using VBGF parameters \(k\) and \(H_\phi\) to compare sea scallop shell growth directly between areas and with previous studies may be misleading. However, the index of growth performance (\(\phi_t\)) was consistent with instantaneous growth estimates. Our research suggests that environmental factors (e.g. flow velocity), fishing pressure, and sea scallop density may influence shell growth on a fine geographic scale (1–100 km\(^2\)), and should be considered in spatially specific management strategies.

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