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# COMPARISON OF GROWTH RATES BETWEEN DIPLOID DEBY EASTERN OYSTERS (*CRASSOSTREA VIRGINICA*, GMELIN 1791), TRIPLOID EASTERN OYSTERS, AND TRIPLOID SUMINOE OYSTERS (*C. ARIAKENSIS*, FUGITA 1913)

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***ABSTRACT*** Oyster size and morphology affect individual oyster physiology, reproductive biology, and habitat production as well as population ecological services and availability for commercial harvest. Options for oyster restoration and fishery facilitation for eastern oyster (*Crassostrea virginica*) populations in the Chesapeake Bay include the use of disease resistant diploid eastern oysters (DEBY strain), triploid eastern oysters, and triploid Suminoe oysters (*Crassostrea ariakensis*) with the objective of providing a marketable product in a reasonable time frame. Shell height-at-age, growth in shell height in relation to environmental conditions, ontogenetic changes in morphology, and changes in biomass for groups of triploid Suminoe, triploid eastern, and diploid DEBY eastern oysters held at identical grow out conditions for the first two years of their lives were evaluated.

Triploid Suminoe oysters reached shell heights of 76 mm (market size in Virginia of 3 in) at 1.1 y with triploid eastern oysters and diploid DEBY oysters attaining the same size at 1.2 y and 1.5 y, respectively. Increases in shell height were positively correlated with water temperature and salinity with the largest increases in shell height typically occurring in warmer months. Holding density significantly affected ratios of shell height (SH) to shell width (SW) and SH to shell inflation (SI) for all three oyster populations. Oysters at lower densities showed a decrease in SH:SI ratio indicative of increased cupping as well as a reduction in SH:SW indicating a trend toward more discoid or rounded form. Tissue dry weight (g) and ash free dry tissue weight (g) increased nonlinearly with size within each population and were statistically different across the three populations examined. Triploid Suminoe oysters had higher tissue weights than either triploid or diploid DEBY eastern oysters of similar ages. Both triploid eastern and Suminoe oysters had higher tissue weights than diploid DEBY oysters of similar age. Observed differences in growth rates and morphology between these groups of oysters affect both the ecological services they provide (filtration rates as well as habitat) as well as their fishery potential (time to market size).

***KEY WORDS:*** Eastern oyster, *Crassostrea*, *Crassostrea virginica*, *Crassostrea ariakensis*, DEBY strain, growth rates, height-at-age, Chesapeake Bay, triploid

## INTRODUCTION

Historically, eastern oysters (*Crassostrea virginica*) were an ecologically dominant species in Chesapeake Bay. The benthic pelagic coupling services provided by their filtration abilities combined with their ability to create and maintain three dimensional biogenic structures in the form of extensive reef habitats made these bivalves important in the Chesapeake Bay trophic structure as well as the target of an active commercial fishery. The ecological services provided by the animal including fecundity, filtration rates, and shell production as well as the fishery value increase with oyster size or shell height. Thus, declines observed in native oyster population abundance and demographics are detrimental at an ecological as well as commercial level.

Modern natural oyster populations face challenges from diseases as well as environmental and anthropogenic factors including habitat degradation and fishing pressure. In the face of increasing disease pressure, research to establish disease resistant strains of oysters began in the 1960s in an effort to increase survival and associated ecological and population effects. The Delaware Bay or DEBY strain was developed in the 1960s at Haskin Shellfish Research Laboratory as part of a selective breeding project for MSX resistance (Haskin and Ford 1979, 1987). In recent years, this strain of oysters has been used extensively in restoration and rehabilitation efforts within Chesapeake Bay because of its demonstrated resistance to MSX. Hatchery bred triploid oysters are sterile yet potentially attractive for fishery production, aquaculture, or habitat enhancement given their fast growth rates. The reduction or absence of investment in gonadal tissue by triploids facilitates the rapid growth of somatic tissue and shell. In recent years, triploid oysters have been proposed as an alternate fishery or aquaculture crop to wild diploid oysters because of the advantage they present given their rapid advancement to market size.

Unlike isodiametric shellfish such as clams or scallops, oyster morphology or shell shape is plastic (Galtshoff 1964). Oyster morphology is affected by environmental conditions as well as density (Galtshoff 1964). The shape of an oyster in turn effects the resulting shell surface area and biomass (g tissue), as well as perceived growth when only one dimension is measured. Shell surface area is a metric of available habitat in Crassostrine oysters which settle gregariously on conspecifics. Biomass serves as an indicator of both filtration rate and fecundity potential in that both of these ecological parameters scale nonlinearly with the biomass of an individual (Newell and Langdon 1996, Cox and Mann 1992). Individual oysters of the same shell height (maximum dimension umbo to growth edge in mm) may have different shell widths or shell inflation and thus present differing habitat and/or ecological value for the same shell height.

The use of triploid oysters and diploid disease resistant (DEBY strain) oysters in restoration strategies presents obvious ecological benefits. Increased disease resistance potentially increases both the number and size of reproductively capable

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diploid individuals. Triploid oysters may be advantageous in that the size of individuals will potentially increase at a more rapid rate than observed in either wild or disease resistant populations. Increases in individual size will increase the overall population demographic as well as provide immediate benefits for filtration services and an increase in habitat, i.e., the oyster shell surface area available for settlement. Use of disease resistant, triploid, or disease resistant triploid oysters in restoration activities provides a means for added shell (habitat) production or maintenance at a site (Powell and Klinck 2007).

Multiple options for oyster fishery facilitation are currently in development, being tested or under discussion. These include the use of disease resistant DEBY strain *C. virginica* as well as deployment of triploid eastern oysters and, potentially, triploid Suminoe (*C.ariakensis*) as sterile nonnatives deployed selectively for rapid production of marketable product. The ongoing Environmental Impact Statement (EIS) process focused on the Chesapeake Bay considers all three alternatives as potential options.

This study provides a side by side comparison of growth rates and morphology of triploid Suminoe, triploid eastern, and diploid DEBY eastern oysters for the first two years of their lives. These oysters were of known age and were held at the same conditions in flow through flumes maintained in the York River at Gloucester Point, VA. The objectives of this study were to describe shell height-at-age, growth in shell height in relation to environmental conditions, ontogenetic changes in morphology, and changes in biomass (dry tissue, ash free dry tissue, both in g) over time for each population of oysters and then compare values across populations.

## METHODS

All oysters were obtained from the Virginia Institute of Marine Science Aquaculture, Genetics, and Breeding Technology Center (VIMS ABC) courtesy of Dr. Standish K. Allen. The triploid Suminoe oysters were spawned in June 2005 and obtained in December 2005. The DEBY and triploid eastern oysters were spawned at VIMS ABC in May 2005 and obtained in January 2006.

All oysters were held at ambient conditions in flumes fed by unfiltered York River water. Thus all oysters were exposed to natural or wild food concentrations and types as well as seasonal trends in environmental cues. Holding densities were initially 177–193 oysters $m^{-2}$ (high, 12/8/2005 through 5/30/2006), then 116–129 $m^{-2}$ (medium, 6/1/2006 through 11/30/2006) but were changed to 39–52 $m^{-2}$ (low, 12/1/2006 through 6/20/2007) to accommodate growing oysters.

Shell height (SH, mm) the maximum dimension from the hinge to the growth edge, shell width (SW, mm) the maximum dimension perpendicular to SH, and shell inflation (SI, mm) or shell thickness, the maximum dimension across the right and left valve (Fig. 1) were measured from a minimum of 30 oysters per population monthly during growing season, less regularly during colder months.

Six oysters were collected from each population for tissue weight determination monthly during growing season, less regularly during colder months, typically at the time of morphological measurements. For each oyster, soft tissue was separated from shell after morphological measurements were made. Tissue was then dried in tared pans at 80°C for 72 h to obtain dry tissue weight (g). Dried tissue was then ashed at 450°C for 2 h to obtain ash free dry tissue weight (g).

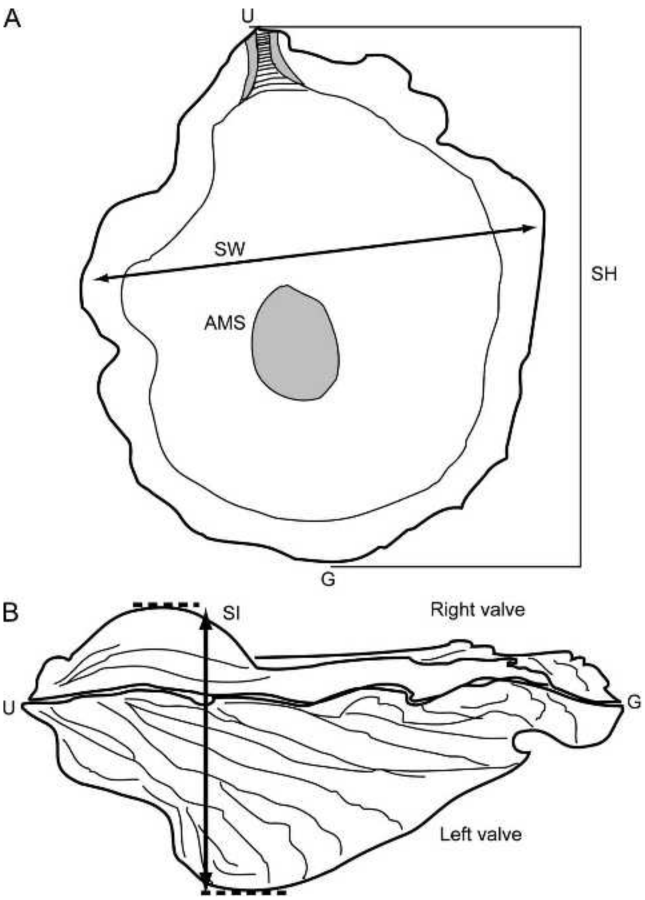

**Figure 1. Sketches of a *Crassostrea* shell with the umbo (U), growth edge (G), and adductor muscle scar (AMS) shown as reference points. Morphological measurements made for each shell are shown including shell height (A: SH, mm), shell width (A: SW), and shell inflation (B: SI).**

Water temperature (°C) and salinity (ppt) data were recorded every 10 min by YSI sondes maintained at the water intake for the seawater system that delivered water to the holding flumes. Daily averages of water temperature and salinity were calculated from the 144 measurements of each made per day.

### *Data analyses*

Alpha values for all statistical tests were established at 0.05 *a priori*.

### *Shell height-at-age relationships*

Population growth curves (age (yr), shell height (mm)) were fitted using the von Bertalanffy (VB) model (Von Bertalanffy 1938) with nonlinear least squares regression. This model describes maximum growth and does not assume rotational symmetry about an inflection point (Brown and Rothery 1993). The model equation is:

$$SH_t = SH_{max}(1 - e^{-k(t-t_0)})$$

where $SH_t$ is the shell height at time t, $SH_{max}$ is the maximum or asymptotic shell height, $t_0$ is the size at time 0, and k is a rate constant.

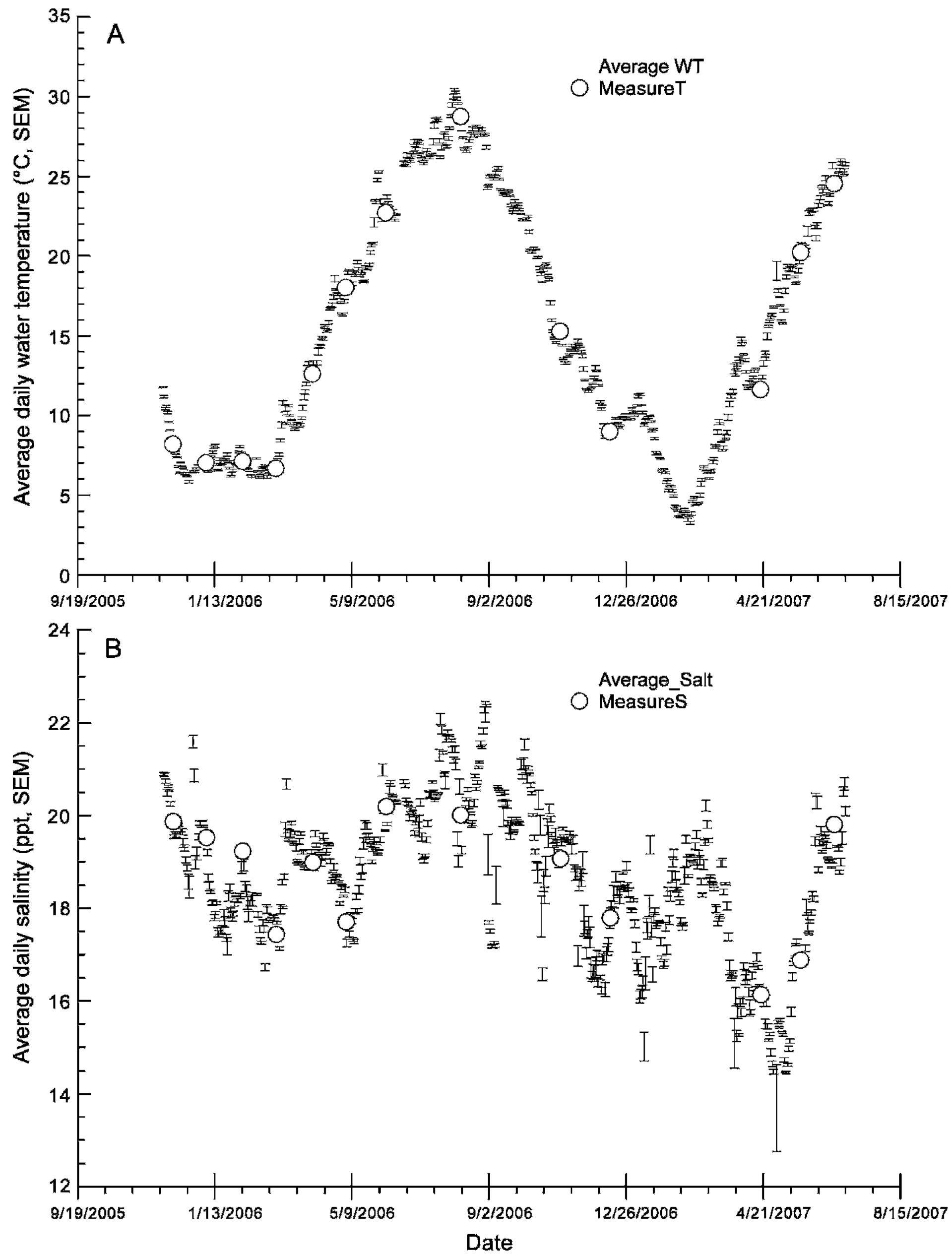

**Figure 2. Average daily water temperature (°C) and salinity (ppt) data recorded in the York River, VA at the water intake for the flow-through flumes during the experimental time frame. Error bars indicate the daily standard error of the mean for 144 measurements of each parameter.**

The fitted VB growth curves for the three populations were compared as pairs using the nonlinear coincident curve method described by Haddon (2001) based on Chen et al. (1992) and Zar (1996). This method compares two curves using the analysis of the residual sum of squares to test if two or more nonlinear curves are statistically different (Haddon 2001).

### *Increase in shell height with time*

The observed increase in shell height (mm) between measurements describes growth over time (d) and was calculated for each measurement interval using the formula below.

$$\text{Average daily increase in shell height}(\text{mm d}^{-1}) = \frac{(\text{Average shell height}_{t1} - \text{Average shell height}_{t0})}{t_1 - t_0}$$

All shell heights are in mm and both $t_0$ and $t_1$ are days. Because the actual dates for $t_0$ and $t_1$ are known, the average bottom temperatures (°C) and salinities (ppt) were also calculated for each measurement interval. Average bottom temperatures and salinities within the observed growth window were correlated with the calculated growth increment using Pearson correlations.

### TABLE 1.

**Summary of morphological measurement (mm) data for the three groups of oysters studied in relation to water temperature (°C) and salinity (ppt) on the date of measurement. Standard errors of the mean are in parentheses after the corresponding mean or average value. Abbreviations are as follows: Avg = average, WT = water temperature, S = salinity, 3Ca = triploid *C. ariakensis*, y = years, N = number of oysters measured, SH = shell height, SW = shell width, SI = shell inflation, 3Cv = triploid *C. virginica*, DB = diploid DEBY strain *C. virginica*, nm = not measured. Measurements made at 1.58 y for all groups are bold to facilitate comparisons.**

| Date Measured | Avg WT (°C) | Avg S (ppt) | 3Ca age (y) | 3Ca N | 3Ca Avg SH | 3Ca Avg SW | 3Ca Avg SI | 3Cv age (y) | 3Cv N | 3Cv Avg SH | 3Cv Avg SW | 3Cv Avg SI | DB age (y) | DB N | DB Avg SH | DB Avg SW | DB Avg SI |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 12/9/05 | 8.22 (0.9) | 19.88 (0.04) | 0.56 | 270 | 25.76 (0.24) | 18.52 (0.19) | 7.56 (0.10) | | nm | | | | | nm | | | |
| 1/6/06 | 7.05 (0.03) | 19.53 (0.02) | 0.64 | 269 | 31.29 (0.28) | 25.89 (0.25) | 9.58 (0.11) | | nm | | | | | nm | | | |
| 2/6/06 | 7.16 (0.05) | 19.24 (0.10) | 0.73 | 100 | 40.13 (0.68) | 36.86 (0.58) | 12.42 (0.20) | 0.84 | 100 | 62.38 (0.54) | 40.26 (0.36) | 20.83 (0.27) | 0.84 | 100 | 47.85 (0.64) | 31.25 (0.37) | 14.19 (0.24) |
| 3/6/06 | 6.70 (0.02) | 17.44 (0.02) | 0.80 | 99 | 44.08 (0.78) | 43.14 (0.63) | 13.36 (0.20) | 0.92 | 100 | 61.08 (0.59) | 39.20 (0.39) | 18.85 (0.25) | 0.92 | 100 | 48.76 (0.63) | 31.74 (0.39) | 13.56 (0.19) |
| 4/6/06 | 12.63 (0.09) | 19.00 (0.02) | 0.89 | 100 | 47.73 (0.77) | 50.28 (0.91) | 15.57 (0.27) | 1.01 | 100 | 66.83 (0.71) | 44.00 (0.48) | 21.09 (0.26) | 1.01 | 100 | 50.94 (0.70) | 34.08 (0.50) | 14.28 (0.23) |
| 5/4/06 | 18.04 (0.18) | 17.71 (0.05) | 0.96 | 100 | 57.77 (0.72) | 66.44 (0.95) | 18.99 (0.34) | 1.08 | 100 | 72.88 (0.64) | 54.84 (0.66) | 21.82 (0.23) | 1.08 | 100 | 56.80 (0.79) | 42.86 (0.69) | 15.17 (0.23) |
| 6/7/06 | 22.73 (0.05) | 20.21 (0.04) | 1.06 | 62 | 70.92 (1.22) | 73.67 (1.85) | 22.34 (0.49) | 1.16 | 62 | 75.39 (1.00) | 57.25 (0.86) | 23.60 (0.31) | 1.16 | 62 | 58.86 (1.20) | 47.10 (0.85) | 16.73 (0.33) |
| 8/9/06 | 28.77 (0.08) | 20.02 (0.12) | 1.23 | 63 | 100.38 (1.74) | 84.89 (1.38) | 43.70 (1.00) | 1.35 | 65 | 87.35 (1.06) | 65.29 (0.72) | 33.03 (0.51) | 1.35 | 60 | 68.12 (1.19) | 52.40 (0.90) | 23.83 (0.44) |
| 11/1/06 | 15.31 (0.01) | 19.08 (0.10) | 1.46 | 102 | 126.59 (1.70) | 101.98 (1.33) | 53.48 (0.92) | **1.58** | **50** | **95.10 (1.47)** | **69.72 (1.05)** | **37.20 (0.65)** | **1.58** | **47** | **77.32 (1.41)** | **59.02 (0.89)** | **28.49 (0.64)** |
| 12/13/06 | 9.01 (0.02) | 17.80 (0.21) | **1.58** | **116** | **136.40 (1.69)** | **111.79 (1.35)** | **58.32 (0.93)** | 1.69 | 78 | 94.36 (1.22) | 68.51 (0.77) | 36.81 (0.56) | 1.69 | 54 | 78.26 (1.52) | 58.74 (0.88) | 28.54 (0.57) |
| 4/19/07 | 11.65 (0.04) | 16.15 (0.03) | 1.92 | 76 | 139.92 (2.18) | 116.11 (1.82) | 58.46 (1.09) | 2.04 | 40 | 94.08 (1.78) | 68.85 (1.32) | 36.95 (1.21) | 2.04 | 39 | 79.77 (1.46) | 60.28 (1.08) | 28.26 (0.63) |
| 5/23/07 | 20.24 (0.15) | 16.89 (0.02) | 2.02 | 71 | 146.18 (2.35) | 126.51 (2.03) | 62.32 (1.20) | 2.13 | 36 | 96.47 (2.27) | 72.89 (1.91) | 36.47 (0.87) | 2.13 | 36 | 82.19 (1.69) | 65.92 (1.32) | 30.75 (0.72) |
| 6/20/07 | 24.53 (0.17) | 19.81 (0.09) | 2.09 | 75 | 148.33 (2.26) | 126.29 (2.02) | 66.61 (1.91) | 2.21 | 33 | 94.94 (2.14) | 70.21 (1.61) | 36.30 (0.81) | 2.21 | 38 | 84.82 (1.88) | 68.08 (1.34) | 31.08 (0.74) |

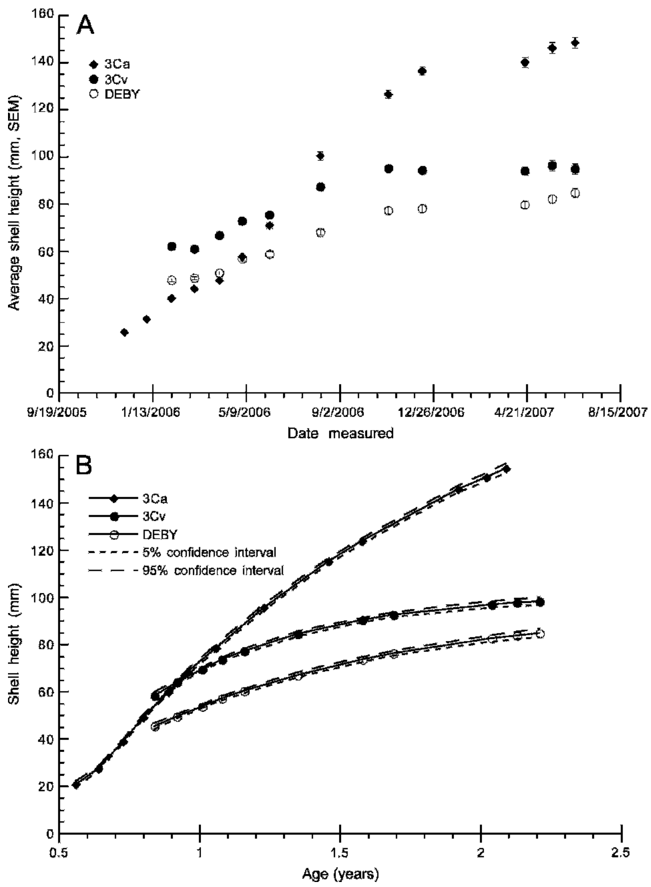

**Figure 3. Plots of average shell height (mm, with standard error of the mean [SEM]) at age (yr) for triploid Suminoe (3Ca), diploid DEBY, and triploid eastern oysters (3Cv,A) with fitted von Bertalanffy curve and 95% confidence intervals (B). Model parameters for each fitted line are presented in Table 2A. At least 30 oysters from each population were measured at each age.**

### *Ontogenetic description of shell shape*

The ratios of 1) SH to SW and 2) SH to SI were calculated for each individual as metrics to describe shell shape. SH:SW ratios near 1 indicate a disk shaped or round individual whereas SH:SW ratio values >2 are indicative of individuals that are long and narrow. SH:SI ratios provide an index of cupping or depth. SH:SI ratio values near 1 indicate an individual that is equally deep or cupped as it is long (a spherical oyster) whereas higher SH:SI values describe oysters that are longer than they are deep. Population specific Kruskal Wallis tests were used to evaluate the effect of density on SH:SW and SH:SI ratios.

### *Dry and ash free dry tissue weight in relation to shell height*

Measurements of dry tissue and ash free dry tissue weight (g) in relation to shell height present a sequential description of the relationship between shell height and tissue dry weight (g) and ash free dry weight (g). Because individual cohorts, as opposed to a range of size classes, within each population were available, each weight determination examined the range of available shell heights at that time rather than the range of potential shell heights for that population. The combined set of measurements

TABLE 2A.

**Von Bertalanffy (VB) growth model coefficients (standard error), coefficient of determination ($R^2$), and mean square of residual values for populations of triploid Suminoe (3Ca), triploid eastern (3Cv) and diploid DEBY strain eastern (DB) oysters. Residual mean square values are from the linear regression of observed *versus* predicted shell height (see text).**

| Population | $SH_{max}$ | k | $t_0$ | $R^2$ | Residual mean square |
|---|---|---|---|---|---|
| 3Ca | 250.59 (11.18) | 0.58 (0.04) | 0.41 (0.01) | 0.92 | 169.07 |
| 3Cv | 101.93 (1.65) | 1.80 (0.17) | 0.37 (0.04) | 0.69 | 55.08 |
| DB | 95.55 (3.58) | 1.12 (0.15) | 0.27 (0.06) | 0.69 | 51.98 |

provides a description of shell height in relation to tissue dry weight or ash free dry weight across the observed shell heights from April 2006 through June 2007. Linear regressions of logarithm transformed tissue dry weight (g) and ash free dry tissue weight (g) in relation to shell height (mm) were compared across populations.

## RESULTS

Water temperature and salinity data from the York River at Gloucester Point, VA during the period December 2005 through June 2007 (Fig. 2) show a seasonal cycle. Highest water temperatures (27–29°C) occur in July and August with lowest temperatures (3–5°C) observed in January and February. Highest salinities occur during July and August (22 ppt) with lowest salinities (14–16 ppt) observed during April and early May 2007 coincident with regular rainfall.

Data from morphological measurements (SH, SW, SI) on groups of oysters over time are summarized in Table 1. Water temperature and salinity data on the date of measurement are also presented (Table 1). Measurements of triploid Suminoe oysters began in December 2005 (0.56 y after spawning). Triploid eastern and DEBY oysters were not available until late January 2006. The first measurements were made for triploid eastern and DEBY oysters on Feb. 6, 2006 (Table 1).

### *Shell height-at-age relationships*

Triploid Suminoe oysters reached shell heights of 76 mm (market size in Virginia of 3 in) at 1.1 y with triploid eastern oysters attaining the same size at 1.2 y (Table 1, Figure 3). DEBY strain eastern oysters reached 76 mm at 1.5 y.

The Von Bertalanffy model was used to describe shell height-at-age data sets for all three populations (Table 2A, Figure 3).

TABLE 2B.

**Summary of statistics comparing VB models across populations per Haddon (2001). Asterisks indicate significance at the alpha = 0.05 level. Abbreviations are explained above in Table 2A.**

| Population comparison | F value | df | *p* value |
|---|---|---|---|
| 3Ca: 3Cv | 798.6 | 2261 | <0.001* |
| 3Cv:DB | 385.6 | 1494 | <0.001* |
| DB:3Ca | 6.22 | 2233 | <0.001* |

TABLE 3.

**Summary of Pearson correlations between growth rates and water temperature for populations of triploid Suminoe (3Ca), triploid eastern (3Cv) and diploid DEBY strain eastern (DB) oysters. *P* values for each comparison are given in parentheses. Growth rate describes an increase in shell height (mm $d^{-1}$). Growth rates were divided by age (months) to standardize them. Abbreviations are as follows: G = growth rate, WT = water temperature (°C), S = salinity (ppt), SG = standardized growth rate. Asterisks indicate significance at the alpha = 0.05 level.**

| Population | G: WT | G:S | SG: WT | SG: S |
|---|---|---|---|---|
| 3Ca | 0.52 (0.08) | 0.45 (0.14) | 0.13 (0.70) | 0.52 (0.09) |
| 3Cv | 0.53 (0.12) | 0.76 (0.01*) | 0.42 (0.23) | 0.74 (0.01*) |
| DB | 0.67 (0.04*) | 0.72 (0.02*) | 0.55 (0.10) | 0.73 (0.02*) |

The coefficient of determination ($R^2$) for triploid Suminoe oysters was 0.92. The $R^2$ values for triploid and DEBY strain eastern oysters were both 0.69. The absence of measurements for triploid eastern and DEBY oysters younger than 0.84 y may be reflected in the $R^2$ value as well as the coefficient estimates. The fitted Von Bertalanffy curves for each population were significantly different from each other (Table 2B).

Estimates of the asymptotic maximum height ($SH_{max}$) were greatest for triploid Suminoe oysters (250.6 mm, SE 11.18) as compared with triploid (101.9 mm, SE 1.65) or DEBY strain (95.6, SE 3.58) eastern oysters. The observed trajectories of the shell height at age data and fitted growth model for the triploid Suminoe oysters show a continued increase in shell height in June 2007 as opposed to a flatter trajectory associated with attainment of the maximum shell height range. This is in contrast with both groups of eastern oysters which are approaching maximum size in June 2007.

The k model parameter specifies the curvature of the fitted growth line (Gallucci and Quinn 1979) and is associated with the rate at which the organism approaches maximum size (Gallucci and Quinn 1979). Calculated k values for triploid eastern (1.80) and DEBY (1.12) oysters were twice as high as the triploid Suminoe k value (0.58, Table 2A). Whereas the triploid Suminoe oysters may take longer to reach maximum shell height, they attain maximum shell heights that are at least twice as large as those estimated for the other two groups (Table 2A). Observed k values in this study ranged from 0.58–1.12 and are much higher than those calculated by Kraeuter et al., 2007 (0.175–0.346) for groups of diploid *C. virginica* spanning the latitudinal range of this species. These k value estimates may also have been affected by the absence of measurements on triploid Suminoe and DEBY oysters younger than 0.84 y. The triploid Suminoe k value observed in this study was higher than that estimated by Harding and Mann 2006 (0.33) for wild diploid *C. ariakensis* from Laizhou Bay, China. The $t_0$ values observed herein are also much larger than those calculated from the literature by Kraeuter et al., 2007 (0.2 *versus*. 0.28–0.47 from this study, Table 4).

### *Increase in Shell Height Over Time*

In general, growth patterns followed the annual seasonal temperature cycle with most growth occurring during warmer months (Fig. 4). Growth patterns of young (0.5–0.6 y) triploid Suminoe oysters are an exception to this trend in that high

**TABLE 4A.**

**Summary of regression statistics used to describe oyster morphology with regard to density using a linear model where $y = m*x + b$, where m = slope and b = y intercept. All regressions had significant $P$ values ($P < 0.05$). Abbreviations are as follows: Reg = Regression identification number, $R^2$ = Coefficient of determination, n = number of individual oysters, 3Ca = triploid Suminoe, SH = shell height, h = high density, SW = shell width, m = medium density, l = low density, SI = shell inflation, 3Cv = triploid eastern, DB = diploid DEBY strain eastern.**

| Reg | X | Y | m | b | $R^2$ | n |
|---|---|---|---|---|---|---|
| 1 | 3Ca SH – h | 3Ca SW – h | 1.27 (0.02) | –12.89 (0.67) | 0.85 | 936 |
| 2 | 3Ca SH – m | 3Ca SW – m | 0.54 (0.02) | 33.35 (2.62) | 0.69 | 226 |
| 3 | 3Ca SH – l | 3Ca SW – l | 0.66 (0.03) | 25.15 (4.59) | 0.56 | 337 |
| 4 | 3Cv SH – h | 3Cv SW – h | 0.67 (0.04) | 0.45 (2.54) | 0.43 | 399 |
| 5 | 3Cv SH – m | 3Cv SW – m | 0.48 (0.04) | 22.65 (3.32) | 0.47 | 176 |
| 6 | 3Cv SH – l | 3Cv SW – l | 0.55 (0.04) | 17.25 (3.50) | 0.55 | 186 |
| 7 | DB SH – h | DB SW – h | 0.63 (0.03) | 2.71 (1.62) | 0.51 | 399 |
| 8 | DB SH – m | DB SW – m | 0.50 (0.04) | 18.82 (2.46) | 0.53 | 168 |
| 9 | DB SH – l | DB SW – l | 0.45 (0.05) | 26.05 (3.89) | 0.36 | 166 |
| 10 | 3Ca SH – h | 3Ca SI – h | 0.31 (0.01) | –0.12 (0.22) | 0.77 | 936 |
| 11 | 3Ca SH – m | 3Ca SI – m | 0.47 (0.02) | –6.64 (2.08) | 0.72 | 226 |
| 12 | 3Ca SH – l | 3Ca SI – l | 0.30 (0.03) | 18.53 (3.60) | 0.29 | 337 |
| 13 | 3Cv SH – h | 3Cv SI – h | 0.15 (0.02) | 10.97 (1.07) | 0.17 | 399 |
| 14 | 3Cv SH – m | 3Cv SI – m | 0.44 (0.03) | –6.23 (2.38) | 0.59 | 176 |
| 15 | 3Cv SH – l | 3Cv SI – l | 0.33 (0.02) | 5.10 (2.01) | 0.57 | 186 |
| 16 | DB SH – h | DB SI – h | 0.18 (0.01) | 5.30 (0.61) | 0.36 | 399 |
| 17 | DB SH – m | DB SI – m | 0.38 (0.02) | –3.10 (1.67) | 0.60 | 168 |
| 18 | DB SH – l | DB SI – l | 0.23 (0.03) | 10.75 (2.13) | 0.32 | 166 |

growth rates were observed between December 2005 and January 2006 when water temperatures were 7.66 ± 0.02°C.

Increases in shell height over time were positively correlated with average water temperature and salinity for all populations (Pearson Correlation, Table 3, Figure 4). Increase in shell height with time standardized by age (y) was also positively correlated with average water temperature and salinity. Salinity was significantly correlated with standardized growth (Table 3).

### *Ontogenetic Description of Shell Shape*

The relationships between shell height (SH) and shell width (SW) and SH and shell inflation (SI) for each population at each holding density were described with linear models (Table 4, Figure 5). The rate of SW change in relation to SH at high density was significantly higher than that observed at low density for all three groups (Table 4, Figure 5A-C). Rates of SW change with SH for both triploid Suminoe and DEBY oysters were similar at both low and medium densities (Table 4, Figure 5). Rates of SI change with regard to SH at high density were significantly lower than those observed at low density for triploid eastern and DEBY oysters and at medium density for all three groups (Table 4, Figure 5).

Oyster morphology as described by ratios of SH:SW and SH:SI changed when holding densities were decreased. Two distinct groups for each population are evident when these data are plotted (Fig. 6) with one ‘‘transition’’ point for each population. Flatter, more elongate animals were typical in all three populations at the highest densities. In general, oysters at lower densities showed a decrease in SH:SI ratio indicative of increased cupping as well as a reduction in SH:SW indicating a trend toward more discoid or rounded form (Fig. 6). The observed magnitude of these shifts was greater in triploid Suminoe than in the other two groups as indicated by the distribution of points in Figure 6 with regard to the y axis range.

Holding density significantly affected SH:SW and SH:SI ratios for all three oyster populations (population and ratio specific Kruskal Wallis tests, $P$ values < 0.001 for all tests). High densities increased ratios of SH:SW and SH:SI more than either medium or low densities (Fig. 6).

**TABLE 4B.**

**Summary of Tukey tests comparing regressions described in Table 4A. Regression identification numbers used in the Comparison column refer to the regressions described in Table 4A above. Asteriks indicate statistical significance at the alpha = 0.05 level.**

| Comparison | *p* value | Comparison | *p* value | Comparison | *p* value |
|---|---|---|---|---|---|
| 1 *versus* 2 | <0.05* | 4 *versus* 5 | <0.05* | 7 *versus* 8 | <0.05* |
| 2 *versus* 3 | <0.05* | 5 *versus* 6 | >0.05 | 8 *versus* 9 | >0.05 |
| 1 *versus* 3 | <0.05* | 4 *versus* 6 | <0.05* | 7 *versus* 9 | <0.05* |
| 10 *versus* 11 | <0.05* | 13 *versus* 14 | <0.05* | 16 versus 17 | <0.05* |
| 11 *versus* 12 | <0.05* | 14 *versus* 15 | <0.05* | 17 *versus* 18 | <0.05* |
| 10 *versus* 12 | >0.05 | 13 *versus* 15 | <0.05* | 16 *versus* 18 | <0.05* |

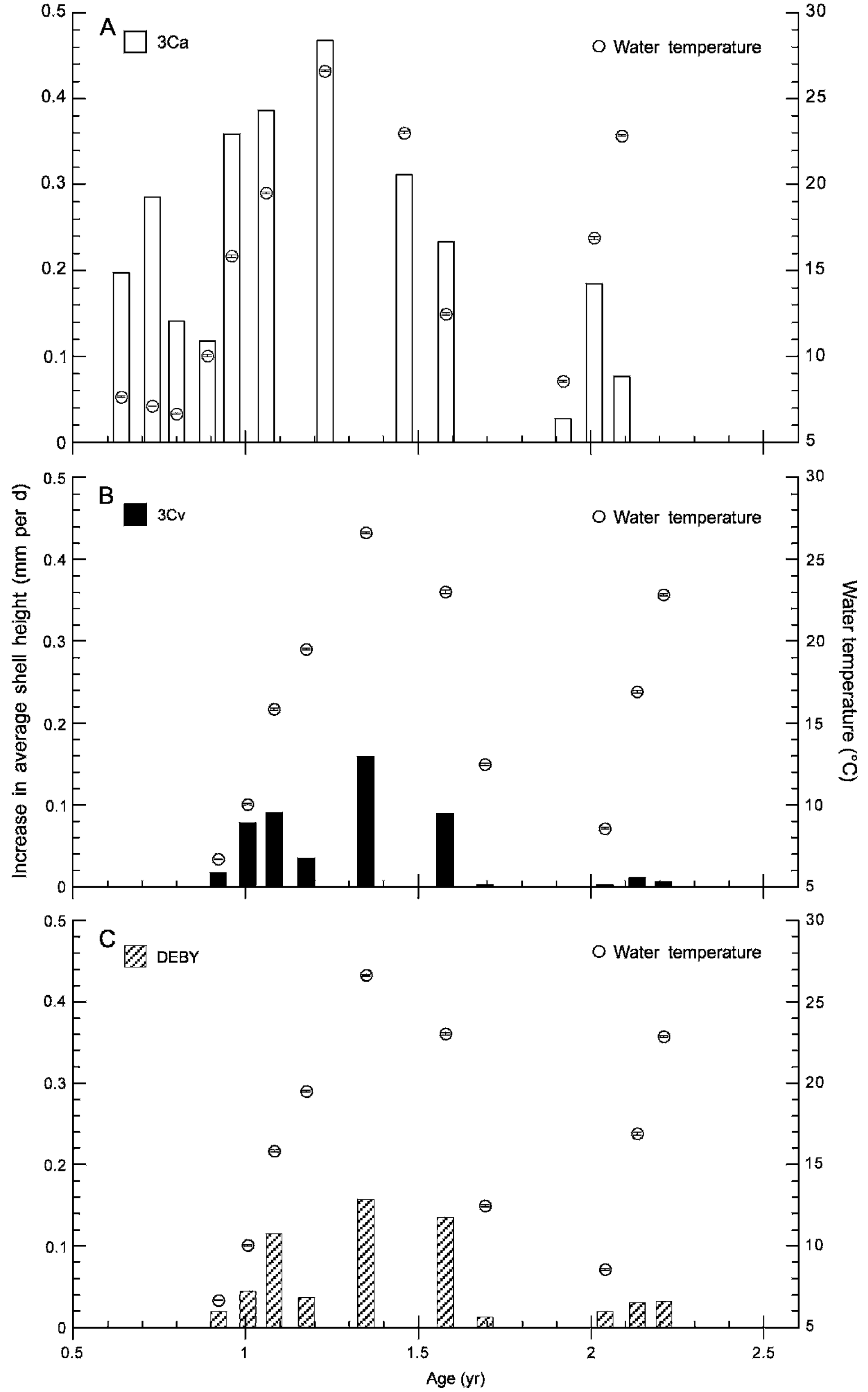

**Figure 4. Shell height growth rates in relation to age (y) and average water temperature (°C, standard error of the mean) during the growth period for triploid Suminoe (A, 3Ca), triploid eastern (B, 3Cv) and DEBY oysters (C).**

### *Dry and Ash Free Dry Tissue Weight in Relation to Shell Height*

Tissue dry weight (TDW, g) and ash free dry tissue weight (AFDW, g) in relation to shell height (SH) data for all threepopulations are summarized in Table 5. Triploid Suminoe, triploid eastern, and DEBY oysters with shell heights approximately 74–79 mm had tissue dry weights of 1.50, 1.71, and 1.88 g, respectively (Table 6). Tissue dry weight determinations for this size triploid Suminoe and eastern oysters

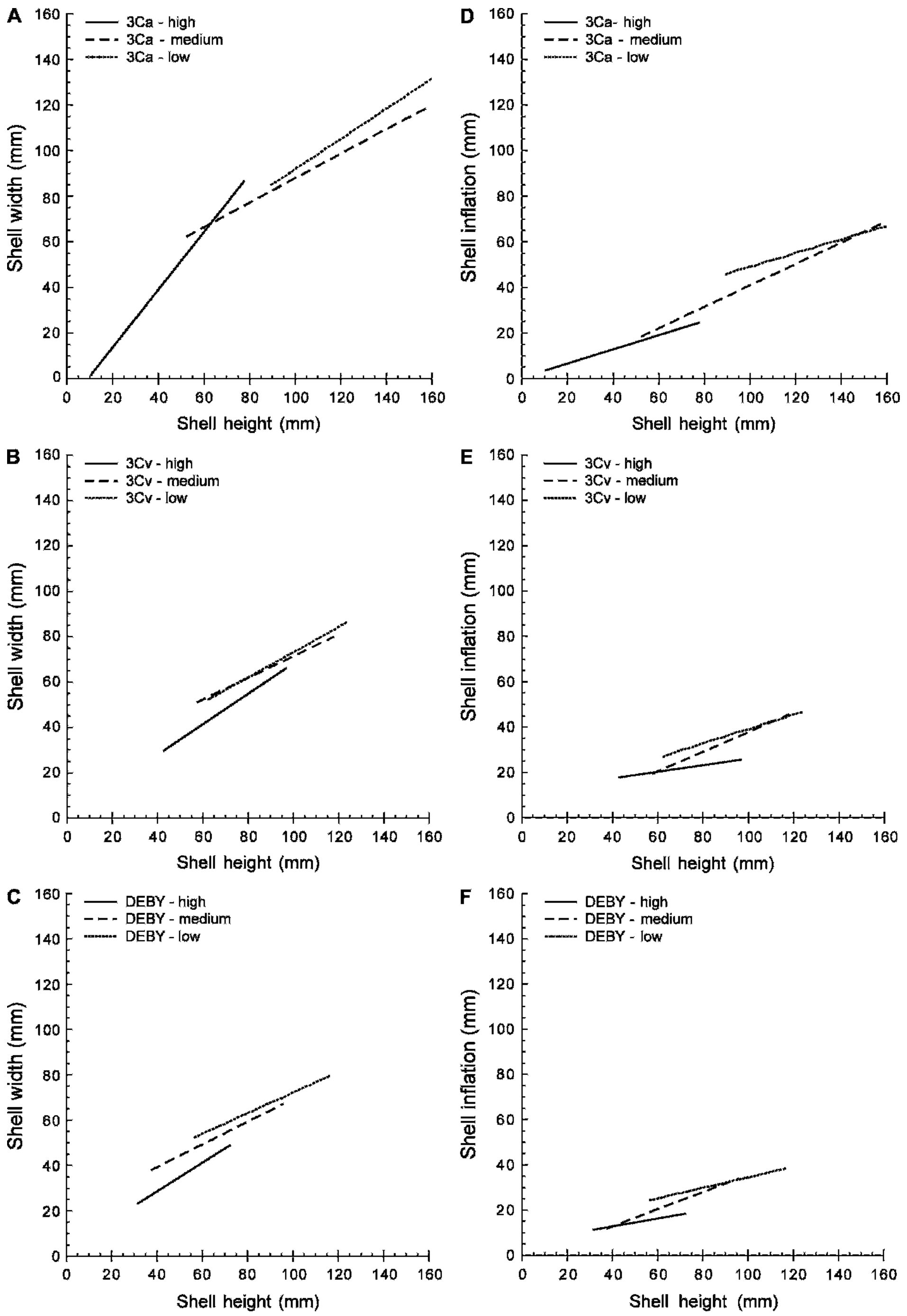

**Figure 5. Density effects on morphological ratios. Shell height versus shell width (A, B, C) and shell height versus shell inflation (D, E, F) at three different densities (high, medium, low) for each of the three oyster populations studied: triploid Suminoe (3Ca), triploid eastern (3Cv), and diploid DEBY (DEBY). Error bars represent the standard error of the mean. *n* values at for each data point are >30. Regression statistics for the fitted lines are presented in Table 5.**

were made in June 2006 whereas DEBY tissue dry weight values are from April 2007. Differences in tissue dry weight due to glycogen storage overwinter in preparation for spawning by the diploid DEBYs in relation to the triploids as well as physiological differences due to seasonal water temperature patterns (April *versus*. June, Figure 2) as well as morphological changes (SW, SI, above) may contribute to the observed differences in the TDW values observed at an absolute SH.

Population specific linear regressions of logarithm transformed TDW and AFDW data (g, y variables for two different regressions) against shell height (mm, x variable for both regressions) describe significant relationships between shell height and TDW as well as shell height and AFDW (Table 6, Fig. 7). That is, TDW and AFDW increase nonlinearly with size within each population. The population specific linear regressions for both TDW and AFDW were

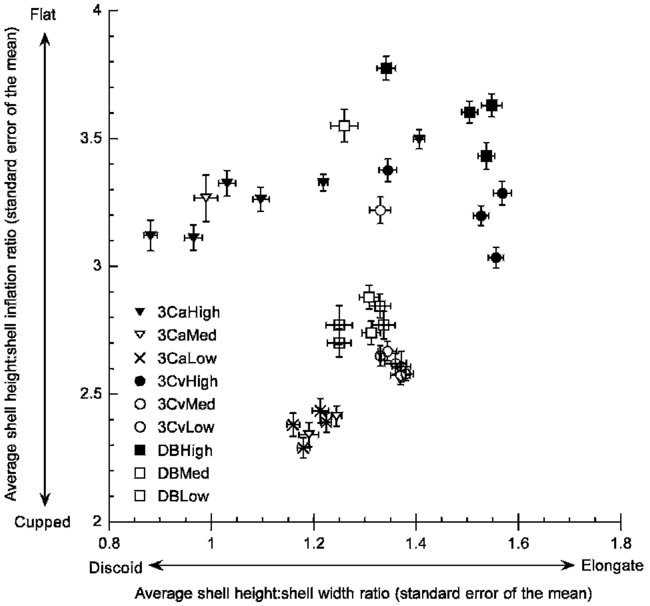

**Figure 6. Plots of the average ratios of shell height: shell width in relation to shell height: shell inflation at high, medium (Med) and low holding densities for each of three oyster populations: triploid Suminoe (3Ca), triploid eastern (3Cv), and diploid DEBY (DB). Error bars represent the standard error of the mean. *n* values for each point are >30.**

statistically different across the three populations examined (Tukey's tests, $P < 0.05$).

## DISCUSSION

Triploid Suminoe oysters reached shell heights of 76 mm (market size in Virginia of 3 in) at 1.1 y with triploid eastern oysters and diploid DEBY oysters attaining the same size at 1.2 y and 1.5 y, respectively. The maximum shell height ($SH_{max}$) for triploid Suminoe oysters predicted by the Von Bertalanffy model (250 mm, standard error = 11.18, Table 3) is within the range of predicted shell heights for diploid wild *C. ariakensis* in their native Laizhou Bay, China ($SH_{max}$ = 244.0 mm, SE = 30.41; Harding and Mann 2006). Diploid DEBY (95, Table 3) and triploid eastern (101, Table 3) maximum shell height values are smaller than all maximum shell heights calculated in Kraeuter et al., 2007 for *C. virginica* using VB models. Estimated maximum shell height values for triploid eastern and DEBY oysters in this study may have been effected by the absence of measurements on smaller oysters from these populations in that they were unavailable for measurement until 0.86 y after they were spawned.

It is important to compare populations with similar starting sizes (SH) so as to accommodate for ontogenetic growth patterns in that the most rapid growth is observed during the first two years of life (Kraeuter et al., 2007). Intraannual differences in growth rates due to latitudinal variations in seasonal temperature patterns must also be taken into account in that oyster growth slows or stops during months when water temperatures are below approximately 8°–10°C (Kirby et al., 1998, Kirby, Paynter and Dimichele 1990). When data from this study (Table 1) were used to calculate overall growth monthly growth rates as mm $month^{-1}$ following Table 2 of Kraeuter et al. (2007), the resulting rates are 6.68, 1.98, and 2.25 mm $month^{-1}$

### TABLE 5.

**Summary of dry tissue weight (g) and ash free dry tissue weight (g) determinations for each population. Unless otherwise indicated, 6 oysters from each population were used for condition index determination at each date. The standard error of the mean is given in parentheses after each value. Abbreviations are as follows: Avg = average, WT = water temperature, S = salinity, 3Ca = triploid *C. ariakensis*, y = years, TDW = tissue dry weight (g), AFDW = ash free dry tissue weight (g), 3Cv = triploid *C. virginica*, DB = diploid DEBY strain *C. virginica*. Measurements made at approximately 76 mm for all groups are bold to facilitate comparisons.**

| Date Measured | Avg WT (°C) | Avg S (ppt) | 3Ca age (y) | 3Ca Avg SH (mm) | 3Ca Avg TDW (g) | 3Ca Avg AFDW (g) | 3Cv age (y) | 3Cv SH (mm) | 3Cv Avg TDW (g) | 3Cv Avg AFDW (g) | DB age (y) | DB Avg SH (mm) | DB Avg TDW (g) | DB Avg AFDW (g) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 4/6/2006 | 12.63 (0.09) | 19.00 (0.02) | 0.89 | 52.07 (4.72) | 0.86 (0.22) | 0.76 (0.19) | 1.01 | 69.45 (4.05) | 1.64 (0.27) | 1.36 (0.24) | 1.01 | 51.5 (4.73) | 0.56 (0.11) | 0.44 (0.09) |
| 5/2/2006 | 16.33 (0.01) | 18.27 (0.02) | 0.96 | 55.25 (5.41) | 1.05 (0.14) | 0.81 (0.11) | 1.08 | 67.92 (3.98) | 1.16 (0.19) | 0.86 (0.12) | 1.08 | 58.12 (3.13) | 0.47 (0.08) | 0.36 (0.07) |
| 6/7/2006 | 22.73 (0.05) | 20.22 (0.04) | **1.06** | **74.14 (4.37)** | **1.50 (0.24)** | **1.21 (0.21)** | **1.18** | **78.85 (3.38)** | **1.71 (0.31)** | **1.39 (0.27)** | 1.18 | 58.17 (2.97) | 0.71 (0.11) | 0.56 (0.10) |
| 6/28/2006 | 26.00 (0.09) | 20.13 (0.04) | 1.16 | 84.4 (4.65) | 1.95 (0.47) | 1.30 (0.33) | 1.23 | 82.97 (3.24) | 2.12 (0.46) | 1.45 (0.36) | 1.23 | 64.73 (2.96) | 1.58 (0.34) | 1.09 (0.24) |
| 7/26/2006 | 27.51 (0.17) | 20.90 (0.04) | 1.19 | 83.98 (4.90) | 2.28 (0.61) | 1.59 (0.48) | 1.31 | 73.23 (3.23) | 1.15 (0.10) | 0.88 (0.08) | 1.31 | 61.35 (4.39) | 0.83 (0.14) | 0.62 (0.09) |
| 8/30/2006 | 27.62 (0.32) | 22.24 (1.08) | 1.29 | 94.48 (8.01) | 3.76 (0.63) | 2.63 (0.47) | 1.41 | 88.73 (2.71) | 2.65 (0.71) | 1.91 (0.58) | 1.41 | 69 (4.42) | 1.28 (0.14) | 0.94 (0.11) |
| 10/18/2006* | 19.12 (0.09) | 18.61 (0.24) | 1.42 | 116.9 (7.69) | 3.95 (1.35) | 2.62 (0.92) | 1.54 | 93.93 (6.04) | 5.27 (0.41) | 3.62 (0.27) | 1.54 | 68.93 (6.97) | 1.80 (0.83) | 1.19 (0.57) |
| 12/13/2006 | 9.01 (0.02) | 17.79 (0.21) | 1.58 | 127.1 (9.36) | 4.26 (1.01) | 2.84 (0.68) | 1.69 | 82.08 (4.27) | 2.49 (0.66) | 1.74 (0.51) | 1.69 | 72.57 (6.07) | 1.31 (0.40) | 0.92 (0.31) |
| 4/19/2007 | 11.66 (0.04) | 16.15 (0.03) | 1.92 | 130.47 (7.78) | 7.96 (1.89) | 6.00 (1.42) | 2.04 | 91.73 (5.86) | 3.07 (0.89) | 2.27 (0.67) | **2.04** | **75.37 (5.83)** | **1.88 (0.32)** | **1.43 (0.25)** |
| 5/23/2007 | 20.24 (0.72) | 16.89 (0.07) | 2.02 | 131.3 (5.61) | 9.43 (2.31) | 6.70 (1.75) | 2.13 | 100.33 (3.95) | 4.67 (1.15) | 3.47 (0.88) | 2.13 | 81.00 (4.09) | 2.66 (0.40) | 1.94 (0.29) |
| 6/14/2007 | 23.93 (0.06) | 19.36 (0.06) | 2.08 | 138.33 (3.70) | 14.97 (2.90) | 11.00 (2.15) | 2.19 | 100.90 (5.90) | 3.67 (1.04) | 2.57 (0.76) | 2.19 | 79.63 (3.20) | 2.20 (0.28) | 1.51 (0.18) |

*Three oysters (instead of 6) from each population were used for condition index on 10/18/2006.

### TABLE 6A.

**Summary of regression statistics used to describe relationships between logarithm transformed shell height (mm) and tissue dry weight (g) and ash free dry tissue weight (AFDW) for the three oyster populations. The linear regression model is Y = m*X + b. Standard errors for each coefficient are in parentheses. Abbreviations are as follows: Reg = regression number, $R^2$ = Coefficient of determination, n = number of individual oysters, Log = logarithm, 3Ca = triploid Suminoe, SH = shell height, TDW = tissue dry weight, 3Cv = triploid eastern, DB = DEBY strain eastern, AFDW = ash free dry weight.**

| Reg | X | Y | m | b | $R^2$ | n | Regression p value |
|---|---|---|---|---|---|---|---|
| 1 | Log 3Ca SH | Log 3Ca TDW | 2.69 (0.18) | −4.84 (0.36) | 0.80 | 57 | <0.01 |
| 2 | Log 3CvSH | Log 3Cv TDW | 2.41 (0.27) | −4.32 (0.51) | 0.55 | 68 | <0.01 |
| 3 | Log DBSH | Log DBTDW | 3.11 (0.23) | −5.62 (0.43) | 0.74 | 63 | <0.01 |
| 4 | Log 3Ca SH | Log 3Ca AFDW | 2.59 (0.20) | −4.79 (0.41) | 0.76 | 57 | <0.01 |
| 5 | Log 3CvSH | Log 3Cv AFDW | 2.30 (0.31) | −4.24 (0.58) | 0.46 | 68 | <0.01 |
| 6 | Log DBSH | Log DBAFDW | 3.04 (0.25) | −5.65 (0.45) | 0.71 | 63 | <0.01 |

### TABLE 6B.

**Summary of Tukey tests comparing regressions described in Table 6A. Regression identification numbers used in the Comparison column refer to the regressions described in Table 6A above. Asteriks indicate statistical significance at the alpha = 0.05 level.**

| Comparison | *p*-value | Comparison | *p*-value |
|---|---|---|---|
| 1 *versus* 2 | <0.05* | 4 *versus* 5 | <0.05* |
| 2 *versus* 3 | <0.05* | 5 *versus* 6 | <0.05* |
| 1 *versus* 3 | <0.05* | 4 *versus* 6 | <0.05* |

for triploid Suminoe, triploid eastern and DEBY, respectively (Table 7).

The observed rate for triploid Suminoe oysters is similar to growth rates from set to market observed in Texas populations of *C. virginica* (Table 7) but twice as high as those recorded for

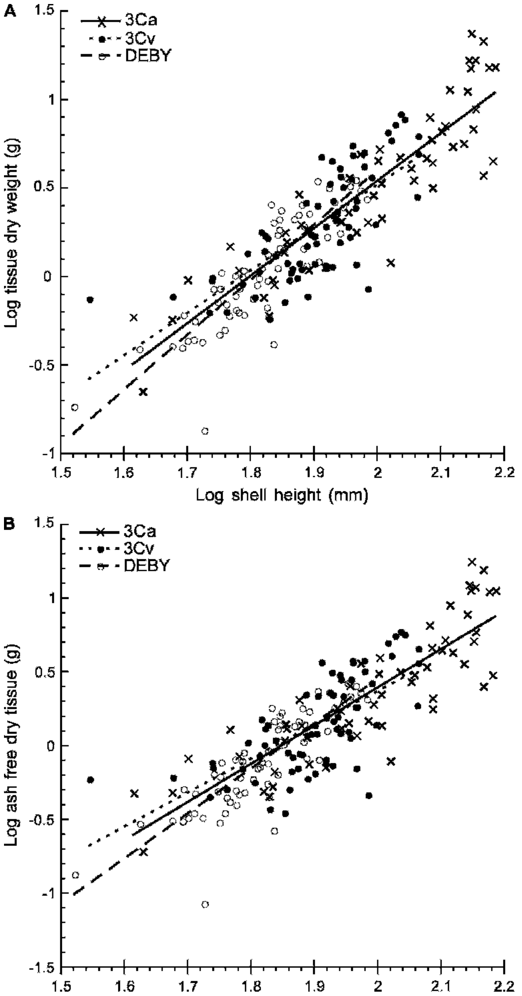

**Figure 7. Relationships between logarithm transformed shell height (mm) in relation to logarithm transformed tissue dry weight (g, A) and logarithm transformed shell height in relation to logarithm transformed ash free dry weight (g, B) for each of three oyster populations: triploid Suminoe (3Ca), triploid eastern (3Cv), and diploid DEBY (DEBY) studied. Fitted linear regressions are significantly different from each other at the alpha = 0.05 level. Regression statistics are presented in Table 6.**

**TABLE 7.**

**Comparison of these growth rates with other published values after Kraeuter et al., 2007. Abbreviations are as follows: 3Ca = triploid Suminoe, 3Cv = triploid eastern (*Crassostrea virginica*), DB = diploid DEBY strain eastern, Cv = diploid *C. virginica*.**

| Species/strain | Location | Initial size (mm) | Time deployed (months) | Total growth (mm) | Monthly growth (mm/mo) | Reference |
|---|---|---|---|---|---|---|
| 3Ca | York River, VA | 25.76 | 18.36 | 122.57 | 6.68 | This study |
| 3Cv | York River, VA | 62.38 | 16.44 | 32.56 | 1.98 | This study |
| DB | York River, VA | 47.85 | 16.44 | 36.97 | 2.25 | This study |
| Cv | Texas | set | 12 | 94 | 7.83 | Gunther 1951 |
|  | Port Aransas, TX | set | 11 | 65 | 5.91 | Menzel 1955 |
|  | Louisiana | set | 10.3 | 78.7 | 7.74 | Gunther 1951 |
|  | Chesapeake Bay, MD | 25 | 19 | 55 | 3.06 | Shaw 1966 |
|  | Terrebonne, LA | 26.8 | 20 | 63.3 | 3.17 | Menzel & Hopkins 1951 |
|  | Chincoteague Bay, MD | 28.6 | 19 | 49.3 | 2.6 | Shaw 1966 |
|  | Chesapeake Bay, MD | 46 | 60 | 46 | 0.77 | Beaven 1952 |
|  | Chesapeake Bay, MD | 46 | 24 | 39 | 1.63 | Beaven 1949 |
|  | Terrebonne, LA | 47 | 14.5 | 42 | 2.9 | Menzel & Hopkins 1955 |
|  | Terrebonne, LA | 58.9 | 12 | 19 | 1.59 | Menzel & Hopkins 1951 |
|  | Chesapeake Bay, MD | 67 | 24 | 25 | 1.04 | Beaven 1949 |
|  | Chesapeake Bay, VA | 70 | 12 | 26 | 2.17 | McHugh & Andrews 1955 |
|  | Chesapeake Bay, MD | 8 | 16.67 |  | 8.2–11.85 | Paynter & Dimichele 1990 |

*C. virginica* starting at shell heights of 25–28.6 mm in Chesapeake Bay and Terrebonne, LA (Table 7). Growth rates for triploid eastern (1.98) and DEBY (2.25) are similar to those observed in Chesapeake Bay and Terrebonne, LA (Table 7) but in general, higher than the mean monthly growth rate calculated for oysters 50–70 mm initial size (1.3 ± 0.57) by Kraeuter et al.(2007). All oysters in this study had reached 76 mm (market size in Virginia) by 18 mo postsettlement (Table 1) with triploid Suminoe and triploid eastern oysters attaining 76 mm by 1.1 and 1.2 y, respectively and diploid DEBY oysters attaining 76 mm at 1.5 y (Table 1). By comparison, wild Delaware Bay *C. virginica* took approximately 3 y to reach 70 mm (Kraeuter et al., 2007) and DEBY strain oysters 1.5 y old ranged in size 45–63 mm SH in year classes examined in culture conditions at Haskins Shellfish Research Laboratory in lower Delaware Bay by Dittman et al. (1998).

Interpretation of any changes in rates of shell growth (slope) in any dimension (SH, SW, SI) with regard to density effects should be made carefully given that oysters at higher densities were younger and in a different season (winter-spring versus. summer) than oysters at medium or low densities (Fig. 4). Thus, the effects of ontogeny and water temperature on growth in any dimension are potentially also factors because changes in holding densities corresponded with annual seasonal increases (June 2006, Figure 4) and decreases (December 2006) in water temperature purely by chance. Any future experiments should be planned with density as an actual treatment throughout the duration of the experiment and take care to begin measurements and density manipulations as soon after set as feasible. The primary focus of this experiment was to determine the optimal or maximum shell height at age. Holding densities were adjusted to encourage growth and avoid overgrowth and crowding by avoiding contact between an oyster and its neighbors.

The utility of the data set described herein is at least in part dictated by the ultimate objective of the reader. If the objective is commercial, i.e., production of a market size oyster (based on SH measurements) in the shortest possible amount of time, the comparative informative measured across species and strains at a given set of environmental conditions provides a baseline for production. If the objective is restoration of an oyster resource for ecological purposes, several other factors must be considered. From an ecological standpoint, the ontogenetic contribution of oysters in terms of habitat (Powell and Klinck 2007, Mann and Powell In review), filtration rate (Newell and Langdon 1996), and, in diploid animals, fecundity (Dame 1976, Cox and Mann 1992, Thompson et al., 1996) increases nonlinearly with size and age. Larger oysters, either diploid or triploid, provide more substrate (surface area) for recruitment. Relatively rapid shell growth by triploid oysters as compared with diploid oysters might provide accretion of shell resources at a rate potentially equal to the natural dissolution rates so as to stabilize existing reefs (Powell and Klinck 2007). Both filtration rates (Newell and Langdon 1996) and fecundity (Cox and Mann 1992) also increase nonlinearly with shell height. Thus, the contribution of large oysters to water quality, habitat, or the next generation is disproportionately larger than a 1:1 contribution when compared with smaller oysters. In ecological currency, the effective population size of an oyster population with larger (>76 mm shell height) individuals is greater than that of an oyster population whose demographic structure is smaller (<76 mm).

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## LITERATURE CITED

Beaven, G. 1949. Growth observations of oysters held on trays at Solomons Island, Maryland. *Convention Addresses National Shellfisheries Association*. 1949:43–49.

Beaven, G. 1952. Some observations on rate of growth of oysters in the Maryland area. *Convention Addresses National Shellfisheries Association*. 1952:90–98.

Brown, D. & P. Rothery. 1993. Models in biology: mathematics, statistics, and computing. John Wiley & Sons. New York, NY. 668 pp.

Chen, Y., D. A. Jackson & H. Harvey. 1992. A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. *Can. J. Fish. Aquat. Sci*. 49:1228–1235.

Cox, C. & R. Mann. 1992. Temporal and spatial changes in fecundity of eastern oysters, *Crassostrea virginica* (Gmelin, 1791) in the James River, Virginia. *J. Shellfish Res*. 11:49–54.

Dame, R. 1976. Energy flow in an intertidal oyster population. *Est. Coast. Mar. Sci*. 4:243–253.

Dittman, D., S. Ford & H. Haskin. 1998. Growth patterns in oysters, *Crassostrea virginica*, from different estuaries. *Mar. Biol*. 132:461–469.

Gallucci, V. & T. Quinn. 1979. Reparameterizing, fitting, and testing a simple growth model. *Trans. Am. Fish. Soc*. 108:14–25.

Galtshoff, P. 1964. The American Oyster, *Crassostrea virginica. U.S. Fish and Wildlife Service Fisheries Bulletin*. 64:1–180.

Gunther, G. 1951. The West Indian tree oyster on the Louisiana coast, and notes on the growth of three Gulf Coast oysters. *Science* 111:516–517.

Haddon, M. 2001. Modelling and quantitative methods in fisheries. Champman and Hall/CRC press. Boca Raton, FL. 406 p.

Harding, J. M. & R. Mann. 2006. Age and growth in wild Suminoe (*Crassostrea ariakensis*, Fugita, 1913) and Pacific (*C. gigas*, Thunberg, 1793) oysters from Laizhou Bay, China. *J. Shellfish Res*. 25(1):73–82.

Haskin, H. & S. Ford. 1979. Development of resistance to *Minchinia nelsoni* (MSX) mortality in laboratory reared and native stocks in Delaware Bay. *Marine Fisheries Review*. 41:54–63.

Haskin, H. & S. Ford. 1987. Breeding for disease resistance in molluscs. p. 431–441. In: K. Tiews (ed). Selection, hybridization, and genetic engineering in aquaculture, Volume 2. Heenemann Verlagesgellschaft MBH, Berlin.

Kirby, M., T. Soniat & H. Spero. 1998. Stable isotope sclerochronology of Pleistocene and recent oyster shells (*Crassostrea virginica*). *Palaios* 13:560–569.

Kraeuter, J., S. Ford & M. Cummings. 2007. Oyster growth analysis: a comparison of methods. *J. Shellfish Res*. 26(2):479–491.

Mann, R. & E. Powell. In review. Why oyster restoration goals in the Chesapeake Bay are not and probably cannot be achieved. *J. Shellfish Res*. 26:905–917.

McHugh, J. & J. Andrews. 1955. Computation of oyster yields in Virginia. *Proceedings of the National Shellfisheries Association*. 45:217–239.

Menzel, R. & S. Hopkins. 1951. Report on experiments to test the effects of oil well brine or ‘‘bleedwater’’ on oysters at Lake Barre oil field. Vol. 1. 1–130. Report to Texas A&M Research Foundation. Project Nine. June 26, 1951.

Menzel, R. 1955. Some phases of the biology of *Ostrea edulis* Say and a comparison with *Crassostrea virginica* (Gmelin). *Publ. Institute of Marine Science University of Texas*. 4:69–153.

Newell, R. & C. Langdon. 1996. Mechanisms and physiology of larval and adult feeding. p. 185–229. In: V. Kennedy, R. Newll, and A. Eble (eds.) The eastern oyster (*Crassostrea virginica*). Maryland Sea Grant. College Park, Maryland.

Paynter, K. & L. Dimichele. 1990. Growth of tray-cultured oysters (*Crassostrea virginica* Gmelin) in Chesapeake Bay. *Aquaculture* 87:289–297.

Powell, E. & J. Klinck. 2007. Is oyster shell a sustainable estuarine resource? *J. Shellfish Res*. 26(1):181–194.

Shaw, W. 1966. The growth and mortality of seed oysters *Crassostrea virginica* from Broad Creek, Chesapeake Bay, Maryland and in high and low salinity waters. *Proceedings of the National Shellfisheries Association*. 56:59–63.

Thompson, R., R. Newll, V. Kennedy & R. Mann. 1996. Reproductive processes and early development. p. 335–370. In: V. Kennedy, R. Newll, and A. Eble (eds.) The eastern oyster (*Crassostrea virginica*). Maryland Sea Grant. College Park, Maryland.

von Bertalanffy, L. 1938. A quantitative theory of organic growth. *Hum. Biol*. 10:181–213.

Zar, J. H. 1996. Biostatistical analysis, 3rd edition. Prentice Hall, NJ.