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## AGE AND GROWTH OF WILD SUMINOE (*CRASSOSTREA ARIAKENSIS*, FUGITA 1913) AND PACIFIC (*C. GIGAS*, THUNBERG 1793) OYSTERS FROM LAIZHOU BAY, CHINA

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**ABSTRACT** Shell height at age estimates from Suminoe (*Crassostrea ariakensis*) and Pacific (*C. gigas*) oysters from a natural oyster reef in Laizhou Bay, China were compared with shell height at age estimates from triploid *C. ariakensis* of known age from the Rappahannock River, Virginia. *C. ariakensis* and *C. gigas* reach shell heights in excess of 76 mm (3 inches) within 2 years after settlement regardless of the source location. This fast growth appears to continue through at least age 4 or age 5 in wild individuals, because the growth trajectories for both species had not reached asymptotic height in the oldest individuals collected. Estimates of the asymptotic maximum height ( $SH_{max}$ ) from fitted Von Bertalanffy (VB) growth models were greatest for Chinese *C. ariakensis* (244.0 mm, standard error of the mean [SE] 30.4) and near the maximum shell height (227.0 mm) measured at the time of collection. Maximum shell heights measured on live Chinese *C. gigas* (173.0 mm) and Rappahannock *C. ariakensis* (190.0 mm) were also within the standard error estimates for the  $SH_{max}$  estimates from the fitted VB models for Chinese *C. gigas* (158.6 mm, SE 20.3) and Rappahannock *C. ariakensis* (183 mm, SE 19.1). Fitted VB growth curves were not significantly different between species within the same habitat, within species in different habitats or between species in different habitats. The ratio of shell height to shell width and shell height to shell inflation for triploid *C. ariakensis* was significantly less than similar ratios observed in wild *C. ariakensis* and *C. gigas* oysters.

**KEY WORDS:** Suminoe oyster, *Crassostrea ariakensis*, Pacific oyster, *Crassostrea gigas*, age determination, bivalves, oysters, growth rates, resilium

### INTRODUCTION

Bivalves carry a complete record of their lives in their shells (Pannella & MacClintock 1968, Lutz & Rhoads 1980, Richardson 2001). Environmental changes as well as seasonal changes in biology and physiology are recorded in the shell structure as external rings, internal lines and growth increments or both (e.g., Pannella & MacClintock 1968, Lutz & Rhoads 1980, Ropes 1985, Richardson 2001). Using the terminology of Richardson (2001), a growth line is an internal line deposited once a year (annually), whereas the annual growth increment is the distance separating adjacent growth lines. In oysters, internal growth lines may be observed in the resilium of the hinge structure (Richardson et al. 1993a, 1993b, Kirby et al. 1998, Richardson 2001) and in the middle homogenous shell layers. The resilium is protected from damage or erosion by the valves. During periods of reduced shell growth, the ligament growth also slows producing growth lines in both shell and resilium (Richardson 2001). In temperate oysters, the annual growth cycle includes one thick, grey growth line deposited in between white growth increments (Richardson et al. 1993a). Enumerating the thick grey growth lines within a resilium or shell cross section provides an estimate of age (years) for the oyster (Richardson et al. 1993a, 1993b, Kirby et al. 1998, Richardson 2001).

Pacific (*Crassostrea gigas*, Thunberg 1793) oysters are cultured for commercial purposes around the world with initial introductions often made to supplement native oyster stocks (see reviews by Mann 1981, Mann et al. 1991, Shatkin et al. 1997). In recent years, Suminoe (*C. ariakensis*, Fugita 1913) oysters have also been proposed as candidates for commercial aquaculture and/or introductions to supplement native oyster stocks (e.g., Langdon & Robinson 1996, Hallerman et al. 2002) Whereas little is known about the population age structure of wild populations of either species in natural reef settings in their native Asian waters, some

data on growth rates in native waters are available. Zhang and Lou (1956, reported by Zhou & Allen 2003) report Chinese *C. ariakensis* reaching sizes of 100–160 mm shell height in 2–3 y, whereas Fujimori (1929, reported by Cahn 1950) describes Japanese *C. ariakensis* reaching 197-mm shell height at ages of 6 y; *C. ariakensis* from China and Japan are described as large reaching sizes in excess of 200 mm shell height (Torigoe 1981).

The observed morphology of these oysters is variable. The morphology of *C. ariakensis* has been described as discoid (Ahmed 1971) and oval or rounded with relatively flat shell layers with only the left valve concave (Wakiya 1929, Torigoe 1981). Wakiya (1929) describes shells of *C. ariakensis* from soft mud habitats as “extremely elongated” and difficult to distinguish from *C. gigas* found on mud bottoms. *C. gigas* are also described as large (reaching shell heights >400 mm, Torigoe 1981) but both valves are concave with rippled shell layers (Torigoe 1981, Langdon & Robinson 1996). Torigoe (1981) describes *C. gigas* as “oval to spatulate,” but Wakiya (1929) describes adult *C. gigas* as “extremely elongated”.

The objectives of this study are to describe shell morphology, shell height at age relationships and growth curves for wild *C. ariakensis* and *C. gigas* specimens collected concurrently from a natural population of reef oysters in Laizhou Bay, Gulf of Bohai, China and compare these data with shell morphology, shell height at age relationships, and growth curves for triploid *C. ariakensis* grown in Chesapeake Bay, USA.

### METHODS

#### Sample Collection

Oysters of both species were collected from the same natural intertidal oyster reef in Laizhou Bay, Gulf of Bohai, China (37°14'38.0, 119°03'29.9) during a quadrat survey conducted in June 2004 by Dr. Mark Luckenbach (Virginia Institute of Marine Science (VIMS), Eastern Shore Laboratory) and Dr. Christopher Richardson (University of Wales Bangor, Menai Bridge). Ambient

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salinities were 30 ppt at the time of collection. Oyster shells were separated from meats in the field at the time of collection. Shells were labeled, bagged and shipped as valve pairs corresponding to individuals. The species co-occurred on the reef and were distinguished from each other by genetic analyses (mitochondrial 16S-based molecular key, per Banks et al. 1993) of tissue samples conducted by Dr. Ryan Carnegie (VIMS, Department of Environmental and Aquatic Animal Health). A total of 11 *C. ariakensis* individuals and 186 *C. gigas* individuals were identified from this collection on the basis of genetic analyses.

Four triploid *C. ariakensis* were collected from the lower Rappahannock River, Virginia during May 2004 as the remnant of a controlled field experiment conducted with aquacultured triploid *C. ariakensis* in 2001 (Dr. J. Wesson, Virginia Marine Resources Commission). These animals were spawned at VIMS in June 2000 (Dr. S. K. Allen, VIMS Aquaculture Genetics and Breeding Technology Center, pers. comm.); thus when they were collected and again certified as triploid in May 2004 they were approximately 4 years old.

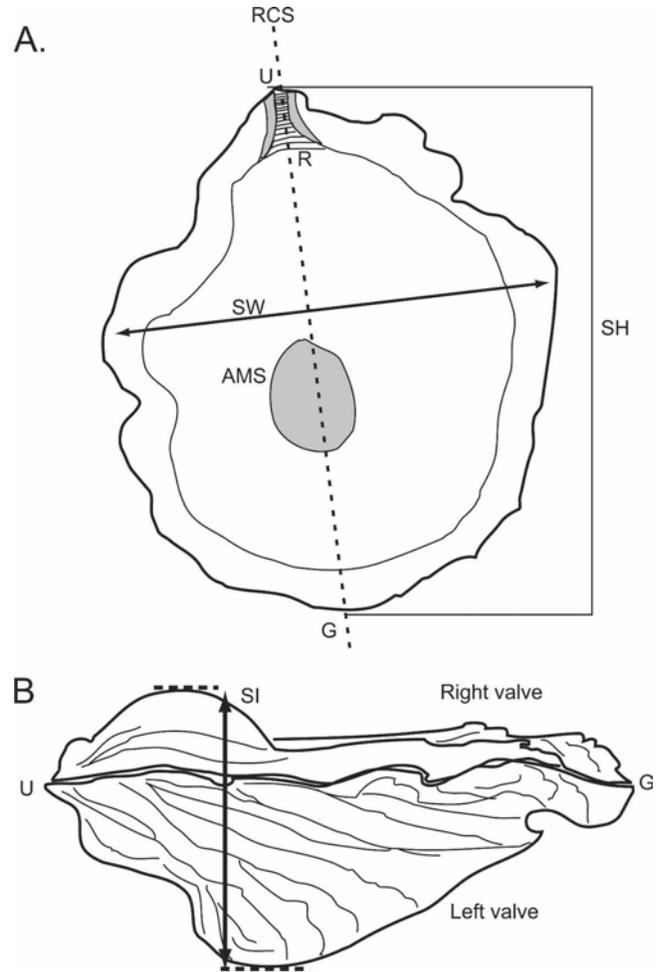
#### Laboratory Methods

The hinge structure and shell morphology of each individual oyster was examined to evaluate suitability for sectioning and age estimation. Oysters in which the resilium, adductor muscle scar and growth edge on the left valve that formed a straight line were deemed suitable for aging and were set aside. A total of nine Chinese *C. ariakensis* and 19 Chinese *C. gigas* were suitable for estimation of age and growth rates. All four of the Rappahannock triploid *C. ariakensis* were used for age estimation.

The shells for estimation of age and growth rates were gently cleaned to remove attached epifauna using a sonicator. Measurements of shell height (SH, maximum dimension from the hinge to the growth edge, mm), maximum shell width (SW, maximum dimension perpendicular to the hinge across one valve, mm) and maximum shell inflation (SI, maximum dimension perpendicular to the hinge across both valves, mm) were made for each individual (Fig. 1). 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 as deep or cupped as it is long (a spherical oyster), whereas higher SH:SI values describe oysters that are longer than they are deep. SH:SW and SH:SI ratios were compared across species within a site (Chinese *C. ariakensis* vs. Chinese *C. gigas*) and across sites within a species (Chinese vs. Rappahannock *C. ariakensis*) using 1-way ANOVAs with significance values set at  $P = 0.05$  a priori.

Shells were sectioned from hinge to the growth edge along a straight line that included the resilium and adductor muscle scar (the major axis of growth, Fig. 1 (a) using a diamond blade saw. Shell cross-sections were polished using wettable carborundum disks (240 through 600 grit) and diamond polishing suspension (Buehler Metadai, 6 and 1  $\mu\text{m}$  suspension). Shells were allowed to dry thoroughly after polishing before examination for growth signatures.

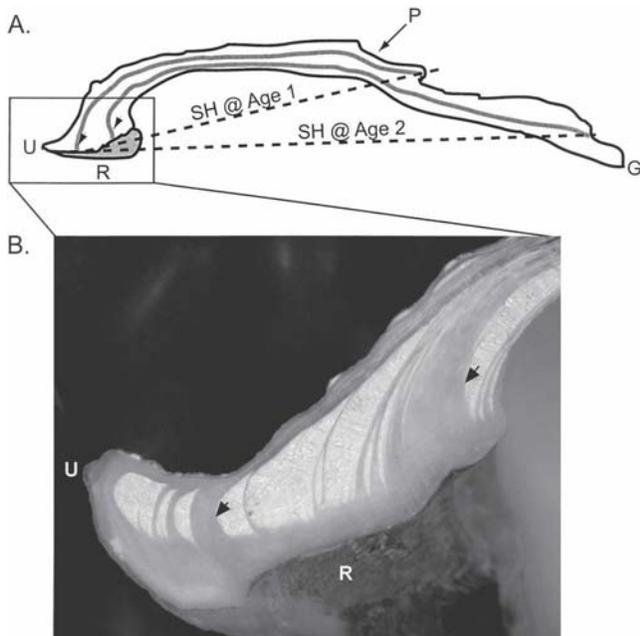
The section of the left valve containing the bulk of the adductor muscle scar was used for shell cross-section evaluation. The number of growth lines within each shell cross section were counted by following the thick grey lines that were continuous from the hinge



**Figure 1.** (A) Sketch of the left valve of a *Crassostrea* shell with the umbo (U), resilium (R), and adductor muscle scar (AMS) shown as reference points. Morphological measurements made for each shell are shown including shell height (SH, mm), shell width (SW), and shell inflation (SI). After morphological measurements were made, a radial cross section (RCS) was made for each shell following the growth trajectory through the resilium (R) and AMS to the growth edge (G). (B) Sketch of a valves of a *Crassostrea* shell in profile showing where the measurement for shell inflation (SI) was made.

to the outer shell layer throughout the valve radial cross section (Fig. 2a). Lines visible in the cross section had to also be visible in the resilium structure to be included (Fig. 2b). The position of growth lines along the radial cross section in relation to the resilium of the hinge ligament provides a growth curve for individual animals. The distance from the hinge to the emergence of a growth line in the shell exterior of the radial cross section was measured (mm) for each shell. The resilium was used to validate cross section lines given the foliation and ornamentation found in the shells of larger specimens. Shell height (mm) at age (yr) curves were plotted for populations based on the sequential measurements of growth lines (height at age) made from left valve cross sections from a size range of individuals.

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 & Rothery 1993). It has been



**Figure 2.** A. Sketch of a radial cross section of a *Crassostrea* left valve showing the annual growth lines (black arrows). Shell height at age measurements were made along axis U-G from the umbo to locations where the annual growth lines ended at the periostracum (P). B. Photograph of a representative resilium radial cross section from a 2-year-old *C. gigas* with the annual growth lines marked (black arrows).

used extensively to describe the growth of other species of shellfish (e.g., *Spisula solidissima*, Sephton & Bryan 1990; *Rangia cuneata*, Fritz et al. 1990, *Mercenaria mercenaria*, Jones et al. 1990, Devillers et al. 1998, *Ostrea edulis*, Richardson et al. 1993a and *Tiostrea (=Ostrea) lutaria*, Richardson et al. 1993b). 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.

The fitted VB growth curves for populations of Chinese *C. ariakensis*, Chinese *C. gigas*, and cultured Rappahannock *C. ariakensis* 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).

## RESULTS AND DISCUSSION

### Morphology

*C. ariakensis* from the Rappahannock River were more cupped than similarly sized individuals of either species from China as indicated by inflation measurements and SH:SI ratios (Table 1, Fig. 3, Fig. 4). The triploid Rappahannock River individuals were discoid (plate-like) when viewed from above as indicated by SH:SW ratios near 1 (Table 1, Fig. 3, 4). Ratios of SH:SW and SH:SI for Rappahannock *C. ariakensis* were significantly less than the same ratios for Chinese *C. ariakensis* (ANOVAs, DF = 1, F = 28.1 (SH:SW) and F = 8.86 (SH:SI),  $P < 0.05$ ). Ratios of SH:SW and SH:SI from Chinese *C. ariakensis* and *C. gigas* were similar (ANOVAs, DF = 1, F = 0.73 (SH:SW) and F = 0.47 (SH:SI),  $P > 0.40$ ). Ratios from all four species and site combinations satisfied assumptions of homogeneity and normality without transformation. The wild Chinese *C. ariakensis* and *C. gigas* were typically long (SH), narrow (SW), and flatter in profile (SI) with higher SH:SW and SH:SI ratios than the Rappahannock River *C. ariakensis* (Table 1, Fig. 3, 4). The descriptions and photographs of *C. ariakensis* provided by Cahn (1950) and Torigoe (1981) from Ariake Bay, Japan are similar in terms of shape (tongue-like) and SH:SW ratio to the large Chinese *C. ariakensis* and *C. gigas* examined in this study (Table 1, Fig. 3A to F,4).

### Shell Height at Age

Chinese *C. ariakensis* and *C. gigas* displayed overlap in the range of observed shell heights at age with each other and with the triploid *C. ariakensis* from the Rappahannock River, Virginia (Table 2). *C. ariakensis* and *C. gigas* reach shell heights in excess of 76 mm (3 inches) within 2 years after settlement (Table 2, Fig. 5) regardless of the source location. This fast growth appears to continue through at least Age 4 (*C. gigas*, Fig. 5) and Age 5 (*C. ariakensis*, Fig. 5) in wild individuals because the growth trajectory for both species had not begun to flatten in the oldest individuals collected (Fig. 5). The observed shell height ranges for each age class (Table 2) are within the ranges of previously published reports of shell heights at age for both species (Table 3). The triploid *C. ariakensis* in the Rappahannock River 2001 to 2004 followed a growth trajectory similar to that reported for Ariake Bay Japan by Cahn (1950, from Fujimori 1929, Fig. 5). The Rappahannock animals had not reached asymptotic shell height when they were collected in May 2004 (Fig. 5).

The observed range in shell heights at Age 1 for the Chinese oysters may be the result of differences in the timing of individual

**TABLE 1.**

Summary of morphological measurements made on individual wild diploid *C. gigas* and *C. ariakensis* from Laizhou Bay, China and cultured triploid *C. ariakensis* from the Rappahannock River, USA. Measurements were made for shell height (SH), shell width (SW), and shell thickness or inflation (SI) as shown in Figure 1 and explained in the text. Ranges for each measurement type (SH, SW, SI) are presented for each species by habitat with average ratio and standard error of the mean (SE) values.

Site	Species	n	SH Range (mm)	SW Range (mm)	SI Range (mm)	Average SH:SW Ratio (SE)	Average SH:SI Ratio (SE)
Laizhou Bay, China	<i>C. ariakensis</i>	9	113–227	60–135	26.3–72.0	1.79 (0.07)	4.01 (0.30)
	<i>C. gigas</i>	19	38–173	35–107	25.0–50.0	1.92 (0.09)	3.74 (0.23)
Rappahannock River, US	<i>C. ariakensis</i>	4	170–190	145–157	55.1–79.6	1.19 (0.03)	2.57 (0.23)

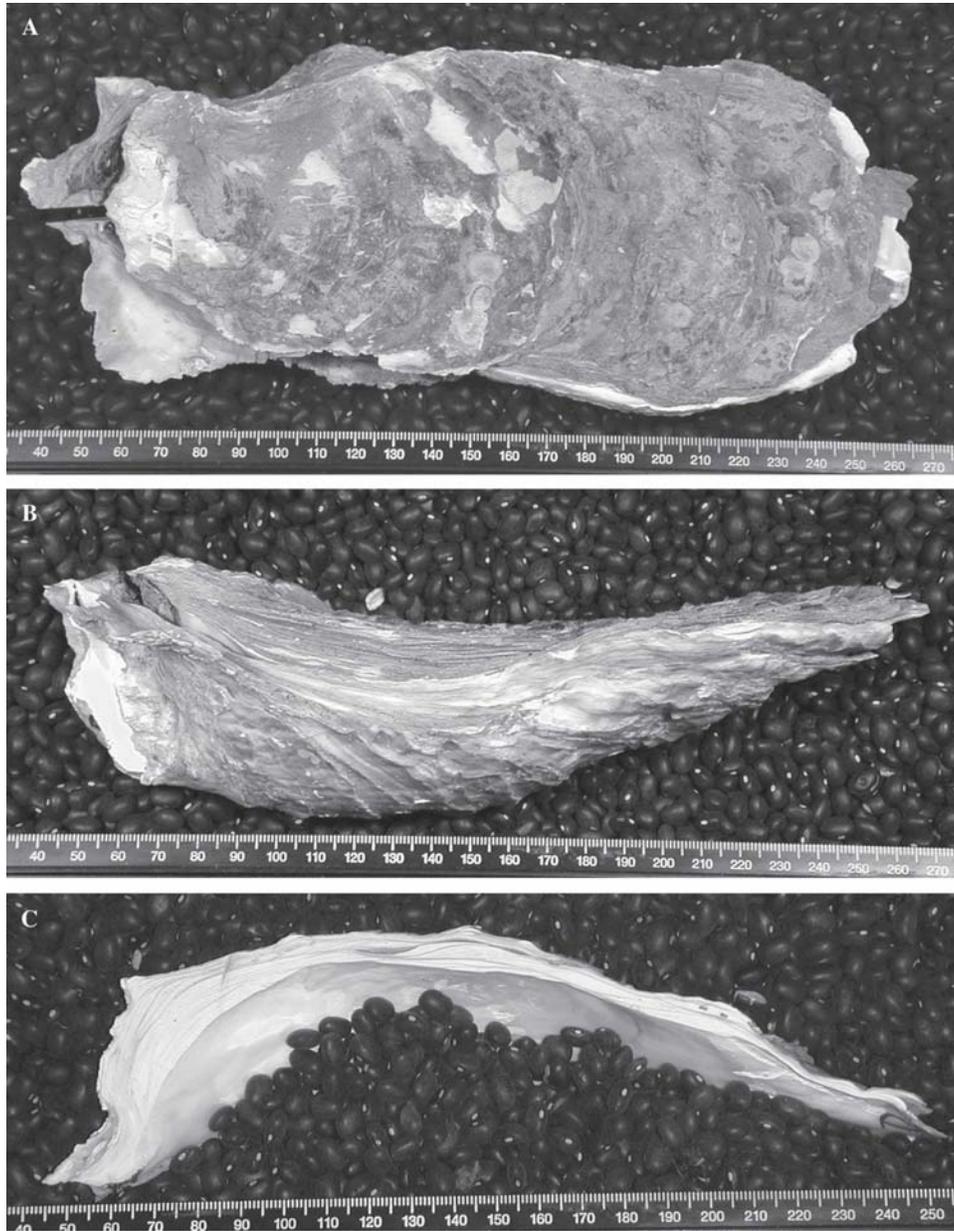


Figure 3. Photographs of representative specimens from China and the Rappahannock River, Virginia. A to C, Chinese *C. ariakensis*, SH = 227 mm.

recruitment. Potential differences in the timing of spawning (Perdue & Erickson 1984, Langdon & Robinson 1996) and recruitment between species may be offset by differences in the growth rates of each species at temperatures less than 25°C. Whereas recruits of both species grow faster at 25°C than at 15°C, *C. gigas* spat growth is less at 20°C than at 25°C and *C. ariakensis* spat grow as fast at 20°C as they do at 25°C (Langdon & Robinson 1996). *C. gigas* that settle early in the season may stop growing earlier than conspecific *C. ariakensis* because of differences in thermal physiology. Although *C. ariakensis* may recruit later, they are able to grow at lower temperatures than *C. gigas* and the relatively extended growing window probably offsets differences in the timing of recruitment resulting in the observed overlap in size range (*C. gigas*: 27–55 mm SH, *C. ariakensis*: 27–57 mm SH) when the first growth line (Age 1) was deposited.

#### VB Growth Model Coefficients and Model Fitting

Fitted VB growth curves (Fig. 6) were not significantly different between species within the same habitat (Chinese *C. gigas* vs. *C. ariakensis*,  $F = 2.2$ ,  $P = 0.10$ , degrees of freedom = 71), within species in different habitats (Chinese *C. ariakensis* vs. Rappahannock *C. ariakensis*,  $F = 1.13$ ,  $P = 0.35$ ,  $df = 45$ ) or between species in different habitats (Chinese *C. gigas* vs. Rappahannock *C. ariakensis*,  $F = 0.93$ ,  $P = 0.43$ ,  $df = 55$ ).

Estimates of the asymptotic maximum height ( $SH_{max}$ ) were greatest for Chinese *C. ariakensis* (244.0 mm, SE 30.41) and near the maximum shell height (227.0 mm) measured at the time of collection (Fig. 6, Table 4). Maximum shell heights measured on live Chinese *C. gigas* (173.0 mm) and Rappahannock *C. ariakensis* (190.0 mm) were also within the standard error estimates for the

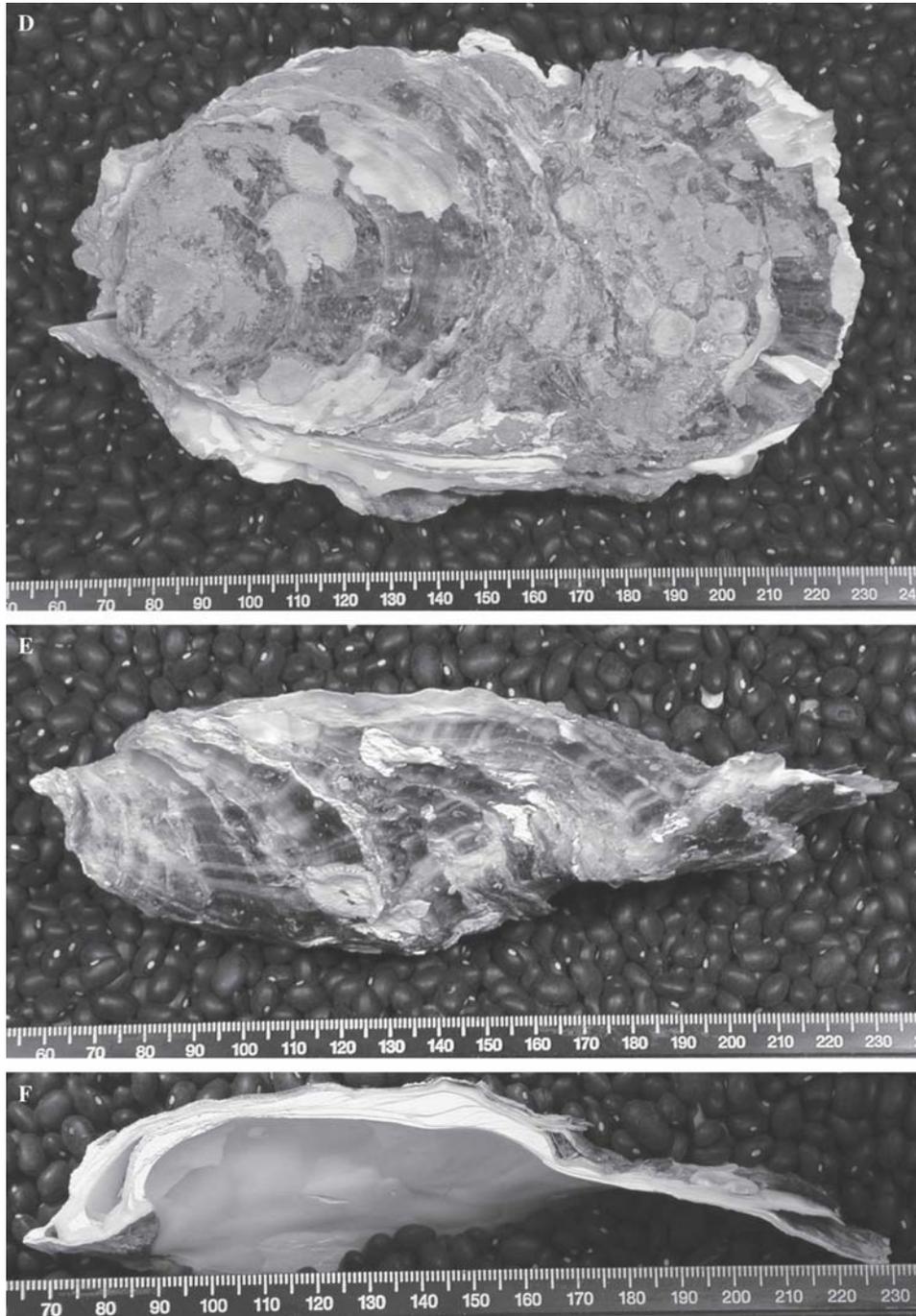


Figure 3. D to F, Chinese *C. gigas*, SH = 165 mm.

$SH_{max}$  estimates from the fitted VB models for Chinese *C. gigas* (158.6 mm, SE 20.25) and Rappahannock *C. ariakensis* (183 mm, SE 19.14; Table 4). The reported  $SH_{max}$  estimates for *C. ariakensis* (Table 4) are within the range of shell heights reported for *C. ariakensis* from Ariake Bay, Japan (Cahn 1950: 240 mm; Torigoe 1981: 200 mm). The  $SH_{max}$  estimates for *C. gigas* (Table 4) are smaller than the reported maximum size range for Japan (Cahn 1950: Tokoro, 400 mm; Torigoe 1981: Ariake Bay, 448 mm). The lack of representation of older age classes in the wild population and the fact that 13 out of the 19 *C. gigas* examined were 2 years old or less with only one 4 year old available resulted in dispro-

portionate representation of younger individuals and uneven sample sizes across the age distribution, which may have skewed the estimate of asymptotic height towards the smaller individuals (Fig. 5 and 6, Tables 2 and 4).

The  $k$  model parameter specifies the curvature of the fitted growth line (Gallucci & Quinn 1979) and is associated with the rate at which the organism approaches maximum size (Gallucci & Quinn 1979). Observed  $k$  values (Table 4) for *C. ariakensis* were 0.33 (Chinese, diploid) and 0.55 (Rappahannock triploid), respectively with a  $k$  value of 0.68 observed for the *C. gigas*. Coefficients of determination ( $R^2$ ) for the Chinese and Rappahannock *C. ari-*

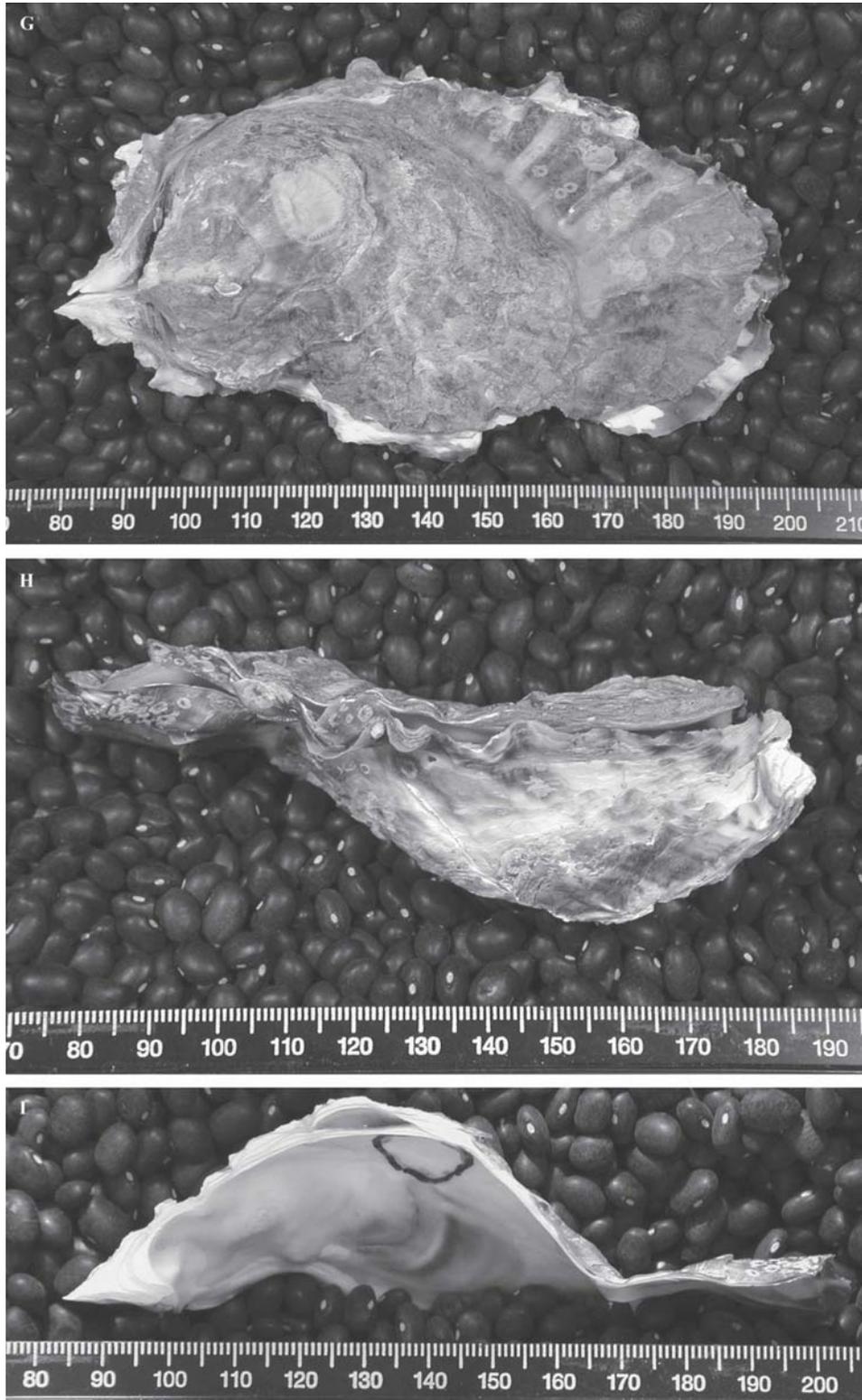


Figure 3. G to I, Chinese *C. gigas*, SH = 126 mm.

*akensis* were greater than or equal to 0.94 (Table 4). The *C. gigas* coefficient of determination was 0.89 and this may be reflective of the fact that most of the specimens examined (17/19) were less than 3 y old (Fig. 5, Tables 2 and 4). The relative under representation or absence of older *C. gigas* at or near asymptotic height is

reflected in the high  $k$  value (0.68) and lower coefficient of determination (0.89) relative to the *C. ariakensis* populations both of which had more balanced distribution of individuals across age classes (Fig. 5, Tables 2 and 4).

Salinities in Laizhou Bay (30 ppt) are higher than those typi-

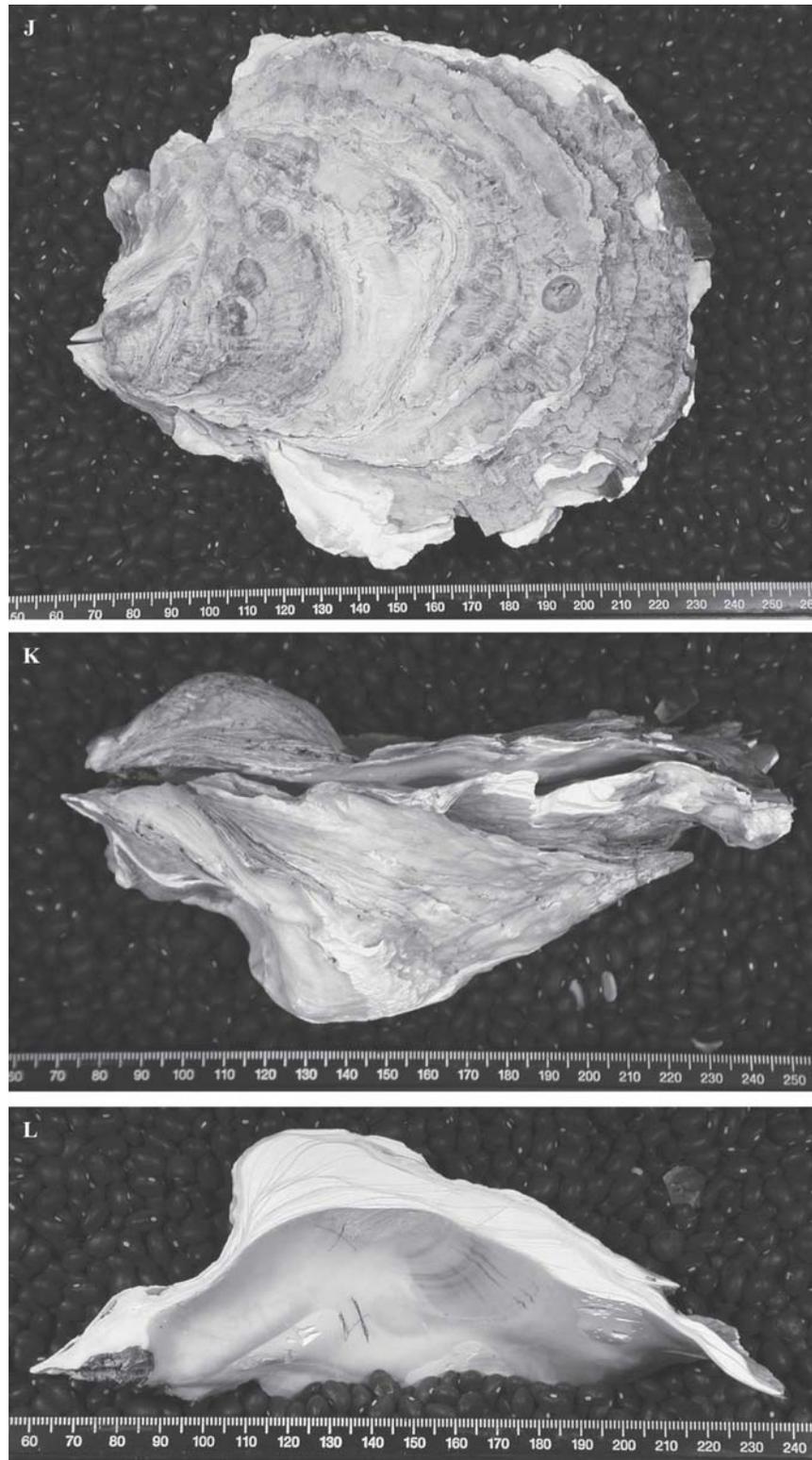
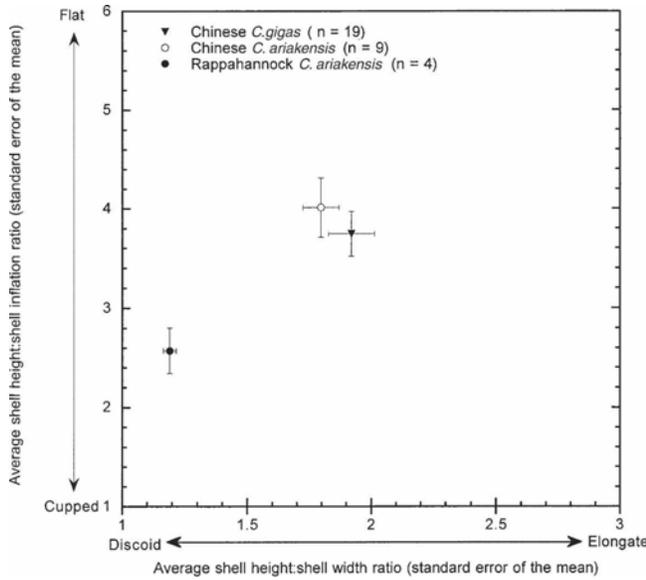


Figure 3. J to L, Rappahannock *C. ariakensis*, SH = 180 mm.

cally observed in the lower Rappahannock River (12–15 ppt, Stroup & Lynn 1963), but both sites have salinities within the documented salinity tolerance of both species (e.g., Robinson 1992, Langdon & Robinson 1996, Almeida et al. 1997, Calvo et al. 1999, 2001, Grabowski et al. 2004). Seasonally water temperatures

in the Rappahannock River range from 4°C to 28°C (Stroup & Lynn 1963). Laizhou Bay probably experiences a similar annual water temperature range based on documented annual water temperature profiles from adjacent habitats (Yellow Sea, Chung et al. 1993; South Korean coastal habitats, Kang et al. 2000).



**Figure 4.** Average shell height (SH): shell width (SW) ratios (with standard error of the mean) in relation to average shell height: shell inflation (SI) ratios (with standard error of the mean) for wild Chinese *C. ariakensis* and *C. gigas* and triploid Rappahannock *C. ariakensis*. Ratios of SH:SW and SH:SI for Rappahannock *C. ariakensis* are significantly less than these ratios for Chinese *C. ariakensis* (ANOVAs,  $P < 0.05$ ). Ratios of SH:SW and SH:SI are similar for both Chinese species (ANOVAs,  $P > 0.05$ ).

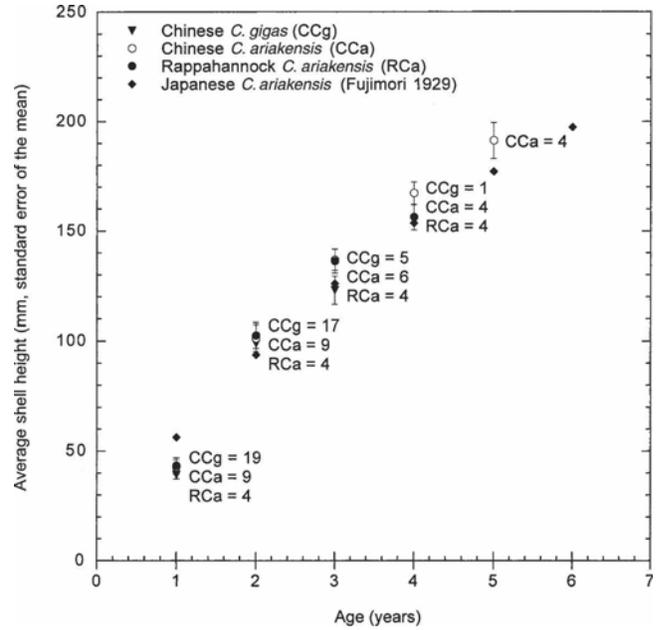
Oysters have the potential to live in excess of 10 y in the absence of disease pressure, environmental degradation or human fishing pressure (Richardson et al. 1993a, 1993b). Evolutionarily life history has evolved to ensure success of the species over the course of its lifetime; that is, each individual only has to reproduce successfully once to maintain the population. Recruitment in wild populations should not necessarily be expected every year given

**TABLE 2.**

Observed average shell height (SH) at age (standard error of the mean) and the observed range of shell heights at age for populations of Chinese *C. gigas* (CHCg), Chinese *C. ariakensis* (CHCa), and Rappahannock *C. ariakensis* (RACa) examined in this study. Measurements were made from internal growth lines within the left valve of each individual. SE = standard error of the mean.

Population	Age	n	Average SH (mm, SE) at Age	Range of Observed SH at Age (mm)
CHCg	1	19	39.31 (2.12)	27–55
	2	17	99.0 (3.78)	68–130
	3	5	123.0 (6.44)	105–145
	4	1	155 (NA)	NA
CHCa	1	9	42.7 (3.3)	27–57
	2	9	101.42 (6.05)	75–134
	3	6	136.83 (4.74)	120–152
	4	4	167.25 (5.23)	155–179
RACa	5	4	191.25 (8.14)	170–204
	1	4	43.38 (3.54)	35–50
	2	4	102.37 (5.85)	95–120
	3	4	136.48 (5.54)	125–150
	4	4	156.20 (5.91)	140–165

NA = Not applicable.



**Figure 5.** Average shell height (mm, standard error of the mean) at age for wild Chinese *Crassostrea ariakensis* and *C. gigas* and triploid *C. ariakensis* from the Rappahannock River, Virginia, United States in relation to reported shell-height at age for *C. ariakensis* in Ariake Bay, Japan (Fujimori 1929 reported by Cahn 1950). *n* values for each species at age are presented to the right of each data point for Chinese and Rappahannock River animals.

the potential for interannual variability in recruitment to estuarine and marine benthic habitats (Loosanoff 1966, Powell & Cummins 1985). The observed age distribution within wild collections (11 2-y-old *C. gigas* out of 19 total, four 5-y-old *C. ariakensis* out of 9 total) indicates that we are seeing cohorts. Size variation within

**TABLE 3.**

Summary of published shell-heights at age for *C. ariakensis* and *C. gigas*.

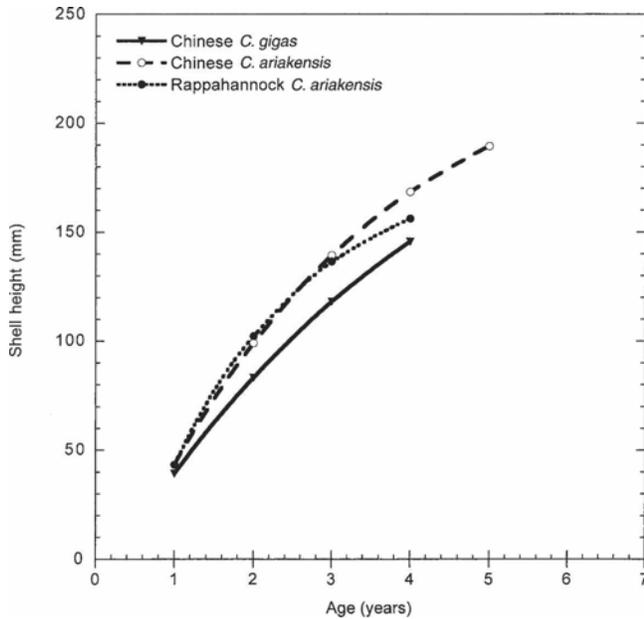
<i>C. ariakensis</i>			<i>C. gigas</i>		
Age	SH (mm)	Location	Age	SH (mm)	Location
1	55	Japan <sup>1</sup>	1	20.1	Portugal <sup>3</sup>
				(SD 6.1)	
	45	Washington, US <sup>2</sup>		24.4	Mexico <sup>4</sup>
	45–50	Oregon, US <sup>2</sup>		30	Washington, US <sup>2</sup>
	30–60	California, US <sup>2</sup>		40–100	Oregon, US <sup>2</sup>
2	97	Japan <sup>1</sup>		50	California, US <sup>2</sup>
	100	Washington, US <sup>2</sup>	2	60–70	Portugal <sup>3</sup>
	65–90	Oregon, US <sup>2</sup>		65.6	Mexico <sup>4</sup>
	110	California, US <sup>2</sup>		110	Washington, US <sup>2</sup>
3	124	Japan <sup>1</sup>		70–90	Oregon, US <sup>2</sup>
4	152	Japan <sup>1</sup>		145	California, US <sup>2</sup>
5	179	Japan <sup>1</sup>			
6	197	Japan <sup>1</sup>			

<sup>1</sup> Ariake Bay, Japan. Fujimori 1929 from Cahn 1950.

<sup>2</sup> Puget Sound, Washington, US; Yasquina and Coos Bay, Oregon, US; Tomales Bay, California, US. Langdon and Robinson 1996.

<sup>3</sup> Rio de Averno and Mondego River estuary, Portugal. Almeida et al. 1997.

<sup>4</sup> Bahia de La Paz, Mexico. Arizpe 1996.



**Figure 6.** Fitted Von Bertalanffy growth curves for wild Chinese *Crassostrea ariakensis* and *C. gigas* and triploid *C. ariakensis* from the Rappahannock River, Virginia, United States.

a cohort may reflect time of settlement (early vs. late, see earlier), position in reef structure, or local conditions in the microhabitat in which the animal settled.

Comparisons of shell height at age and fitted growth curves present one element of comparison between oyster species within and across sites but these comparisons do not address the difference in inflation rates/cupping observed between the Rappahannock triploid *C. ariakensis* and the wild oysters of both species. The discoid, cupped Rappahannock oysters were larger in all dimensions than the Chinese oysters. When the four triploid Rappahannock *C. ariakensis* were shucked in May 2004, the meat fully filled the shell cavity with an average meat wet weight of 117.5 g (standard error of the mean, SE = 7.43 g) and average dry weight of 27.01 g (SE = 2.24 g), J. Harding, unpublished data). This effective increase in shell volume has a direct correlation to the biomass of the animal and, in diploid individuals, fecundity. In the absence of tissue weights (wet or dry) for the diploid Chinese oysters, direct comparisons of biomass within a species (triploid vs. diploid), site (*C. ariakensis* versus *C. gigas*) or within species across sites are impossible, although it is probable that biomass trends for sites and species follow the observed trends in external morphology. In the absence of detailed habitat or ecological in-

**TABLE 4.**

Von Bertalanffy growth model coefficients (standard error), coefficient of determination ( $R^2$ ), and mean square of residual values for populations of Chinese *C. ariakensis* (CHCa), Chinese *C. gigas* (CHCg), and Rappahannock *C. ariakensis* (RACa). Residual mean square values are from the linear regression of observed versus predicted shell height (see text).

Population	Age/n	SHmax	k	$t_0$	$R^2$	Residual Mean Square
CHCg	1/19, 2/17, 3/5, 4/1	158.6 (20.25)	0.68 (0.20)	0.58 (0.08)	0.89	383.22
CHCa	1/9, 2/9, 3/6, 4/4, 5/4	244.0 (30.41)	0.33 (0.08)	0.40 (0.13)	0.94	125.33
RACa	1–4/4	183.0 (19.14)	0.55 (0.15)	0.51 (0.51)	0.96	92.19

formation for either collection site (e.g., annual temperature and salinity profiles, sediment characterization, population density) it is impossible to attribute observed differences in morphology to genetic (triploid vs. diploid), habitat, or ecological factors including competition for space or resources. Application of these growth trajectories to other oyster populations and habitats must include consideration of genetics and individual morphology (biomass) as well as ambient seasonal salinity and water temperature profiles for the habitats of interest.

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