

GROWTH AND SURVIVORSHIP OF NON-NATIVE (*CRASSOSTREA GIGAS* AND *CRASSOSTREA ARIAKENSIS*) VERSUS NATIVE EASTERN OYSTERS (*CRASSOSTREA VIRGINICA*)

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ABSTRACT The decline of wild populations of the eastern oyster *Crassostrea virginica* from fishing impacts and disease combined with limited success in its culture has stimulated discussion among coastal managers about the risks and benefits of introducing non-native oysters in Maryland, Virginia, and North Carolina. Field experiments in 1999 to 2000 and 2001 to 2002 comparing growth, survivorship, and prevalence of disease in 2 non-native oysters, *C. gigas* and *C. ariakensis*, versus *C. virginica* in North Carolina estuaries demonstrated that in high-salinity (>25‰) waters, performance of *C. gigas* in culture greatly surpassed that of both of the other oysters (with growth 162.4% higher than *C. virginica* and 54.1% higher than *C. ariakensis* and survivorship 33.1% higher than *C. virginica* and 22.3% higher than *C. ariakensis*). *C. ariakensis* survivorship at these high salinity sites was highly variable and unpredictable even when using environmental covariates, and at salinities below ~10‰ this species did not grow, rendering its culture nonviable at low salinity. However, in waters of intermediate salinity (15‰ to 25‰), *C. ariakensis* outgrew both of the other 2 oysters (35.9% higher than *C. gigas* and 24.5% higher than *C. virginica*) and exhibited 42.1% higher survivorship than *C. gigas*. Although survivorship of *C. virginica* and *C. ariakensis* did not differ significantly at intermediate salinities, only *C. virginica* failed to achieve legally harvestable sizes and, based on its increasingly high susceptibility to death from disease with age, is likely to have experienced much greater mortality by the time of complete grow-out. Experimental elevation above the bottom augmented growth and survivorship of *C. ariakensis* most strongly, whereas *C. gigas* was not influenced by rack height. Before large-scale introduction of any non-native oyster occurs, the quantitative biologic results should first be incorporated into economic evaluations that weigh expected profitability and ecosystem benefits against the potential ecologic risks of introduction (both for wild release and for aquaculture of triploids).

KEY WORDS: *Crassostrea ariakensis*, *Crassostrea gigas*, *Crassostrea virginica*, economic feasibility, triploid, oyster disease, oyster growth, oyster survivorship

INTRODUCTION

Previous introductions of non-native species have often had severe consequences for ecologic communities, including reduction of the diversity, abundance and distribution of native fauna and flora (Carlton 1992, Ruiz et al. 2000). Consequently, prior to intentionally introducing any exotic fisheries species, managers should carefully weigh potential negative against positive ecological effects and evaluate under what conditions (aquaculture of nonreproductives versus wild release), if any, introduction may be economically and ecologically justifiable. A key component of this evaluation process is defining the rationale or need for introduction (Carriker 1992). Specifically, there must be clearly identified and scientifically defensible reasons why the native species is inadequate (Courtney & Robins 1989) and the introduced species is expected to have a high potential for success (Mann 1979, Rosenfield & Kern 1979, Mann et al. 1991).

Frustration with the slow pace of restoration efforts targeting wild populations of the eastern oyster *Crassostrea virginica* (Gmelin 1791) coupled with high mortality rates associated with culture of this species over the past several decades have resulted in advocacy by the shellfish industry to introduce non-native oysters in Maryland, Virginia, and North Carolina (Mann et al. 1991, Byrne 1996, Shatkin et al. 1997). Two species, the Pacific oyster, *C. gigas* (Thunberg 1793), and the Suminoe oyster, *C. ariakensis* (Fujita 1913), have been proposed as candidates for triploid aquaculture and even wild introductions. Native to Japan and the Korean peninsula (Mann et al. 1991), *C. gigas* has been successfully introduced to France, Oregon, Washington, western Canada, Australia, and New Zealand (Shatkin et al. 1997) and currently ac-

counts for over 80% of the world's fishery production of oysters (Ayers 1991). Despite some taxonomic confusion with *C. rivularis*, the native distribution of *C. ariakensis* is believed to range from Pakistan through China to Japan, where it extends well into lower-salinity (i.e., <25‰) portions of estuaries (Breese & Malouf 1977, Langdon & Robinson 1996).

Resource managers currently face one of the most ecologically critical decisions in the history of environmental and fisheries management in the United States, whether *C. gigas* or *C. ariakensis* should be either intentionally released to propagate in the wild or cultured as nonreproductives in controlled aquaculture settings (National Research Council 2003). Some past studies provide information on and discussions of potential ecologic risks and perceived ecosystem (e.g., enhanced bio-filtration rates) and fisheries benefits of the 2 types of introduction (Mann 1979, Andrews 1980, Mann et al. 1991, Gaffney & Allen 1992, Lipton et al. 1992, Byrne 1996, Gottlieb & Schweighofer 1996, Shatkin et al. 1997). Several scientists have emphasized that significant risks to local and regional ecosystems exist and have yet to be fully addressed. For instance, introduction of reproductively viable non-native oysters could lead to eventual invasion of other estuaries in neighboring states or regions of the United States. Because information on the biology of these 2 species is sparse, the NRC Committee on Non-native Oysters in the Chesapeake Bay recently recommended that further research be conducted on the performance of native versus non-native oyster species (National Research Council 2003).

Realization of the potential fisheries benefits of introducing non-native oysters depends on their biology within the estuaries of the eastern United States, their marketability (see Grabowski et al. 2003 for relevant comparative information on marketability), and the integrated bioeconomics. Previous studies performed in Ches-

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peake Bay comparing the biology of *C. virginica* to either *C. ariakensis* or to *C. gigas* (Barber & Mann 1994, Calvo et al. 1999, Calvo et al. 2001) have documented higher resistance to *Perkinsus marinus* and *Haplosporidium nelsoni* and faster individual growth rates of both non-native species compared with *C. virginica* (Langdon & Robinson 1996, Calvo et al. 1999, Calvo et al. 2001), although the growth advantage seems to vary with salinity for *C. gigas*. However, direct comparison of the two non-native oyster species has yet to be conducted within the eastern United States and neither non-native species has been experimentally cultured in North Carolina. Here we present results of field trials covering the full range of potentially viable salinity regimes in coastal North Carolina. These trials were designed to assess the growth, survivorship, and disease prevalence and severity of the two non-native species under consideration for introduction and contrast these results to those obtained simultaneously for *C. virginica*. In addition, we tested if elevating oysters off the bottom differentially affects survival and growth of native versus non-native oysters.

MATERIALS AND METHODS

A series of experiments was conducted to compare growth, survivorship, and disease (dermo, *P. marinus*) prevalence and severity among native *C. virginica* (eastern oyster) and 2 non-native species, *C. gigas* (Pacific oyster) and *C. ariakensis* (Suminoe oyster), in North Carolina from 1999 to 2002. For each experiment, triploid seed *C. gigas* and *C. ariakensis* were obtained from the quarantine hatchery at the Virginia Institute of Marine Sciences (VIMS) and compared with diploid *C. virginica* obtained from Leslie Lee, Sloop Point Seafood, Hampstead, North Carolina. Triploid non-native oysters were raised at VIMS until achieving approximately 2–6 cm shell height (SH) in size, and tested for ploidy and disease status. Disease-free triploid oysters were shipped to the University of North Carolina-Institute of Marine Sciences (UNC-IMS), where they were held in upwellers prior to initiating field trials. Native oysters were raised at Sloop Point Seafood in raceways until the inception of each experimental trial. Oysters were then cultured in 4.8-mm mesh polyethylene bags that were elevated above the bottom using racks constructed from iron bars and located at approximately 0.1–0.5 m below mean low water (MLW) in research sanctuaries throughout coastal North Carolina.

First Series of Experiments (1999–2000)

Grow-out experiments were performed in 1999 to 2000 to compare growth and survivorship of *C. virginica* versus *C. ariakensis* and *C. virginica* versus *C. gigas* in separate experiments. In December 1999, *C. ariakensis* (mean SH \pm 1 SE = 54.8 \pm 0.9 mm) and *C. virginica* (42.6 \pm 1.0 mm) were placed in 4.8-mm polyethylene (43 \times 48 \times 4 cm) bags on 15 cm-high racks at 1 high-salinity site (>25‰; Chadwick Bay) and 1 site with low (<10‰; Broad Creek) salinity (Fig. 1, Table 1). Abnormal environmental conditions following Hurricane Floyd resulted in extremely low salinity levels at Broad Creek in 2000 (Peterson 2000). Three bags of each species were deployed at each site with 52 oysters per bag. Living oysters were subsequently measured (SH) and counted to assess size and survivorship in March, June, and September/October 2000 at both sites.

C. gigas (31.4 \pm 0.8 mm) and *C. virginica* (29.5 \pm 0.6 mm) were placed in 6 polyethylene bags (50 oysters per bag, 3 bags per species) and deployed in February 2000 on 15 cm-high racks at

each of 2 high-salinity sites in Waters Bay and Chadwick Bay (see Fig. 1). Deployment time for *C. gigas* differed from that of *C. ariakensis* described earlier because of availability of hatchery seed. *C. gigas* was not planted at Broad Creek because its poor performance at low salinities is already well documented (Calvo et al. 1999). Living oysters for the *C. virginica*/*C. gigas* contrast were subsequently measured (SH) and counted in May and August 2000 at both sites. For both the *C. virginica*/*C. ariakensis* and *C. virginica*/*C. gigas* experiments, oyster bags were washed with pressurized water and scrubbed with wire brushes to remove accumulated mud and fouling organisms during each sampling visit.

Second Series of Experiments (2001–2002)

The second series of experiments was initiated in April 2001 and included comparisons of growth, survivorship, *P. marinus* infection and *Polydora* spp. infestation among *C. ariakensis*, *C. gigas*, and *C. virginica*. Three bags of 70 *C. ariakensis* (31.8 \pm 1.0 mm) and 3 bags of 70 *C. virginica* (20.6 \pm 0.3 mm) were placed at each of 4 high-salinity (>25‰; Topsail Sound, Waters Bay, Chadwick Bay and Newport River, see Fig. 1) and 3 intermediate-salinity (15‰ to 25‰; Bay River, Broad Creek and Swan Quarter) sites. In addition, 3 bags of 70 *C. gigas* (18.7 \pm 0.3 mm) were placed at each of the high- and 1 intermediate-salinity (Bay River) sites to determine if slightly reduced salinities negatively impact *C. gigas* growth and survivorship in North Carolina. Bags (4.8-mm mesh, 43 \times 48 \times 4 cm) containing each set of seed oysters were placed on 15 cm-high rebar racks 0.1–0.5 m below MLW. To determine if height above the bottom affects native or non-native oyster growth and survivorship, 3 bags of *C. virginica*, 3 bags of *C. gigas*, and 3 bags of *C. ariakensis* were planted on racks at each of 2 additional heights (on the seabed and 38 cm above the seabed) at 2 sites (Chadwick Bay and Newport River).

Living oysters at high salinities were subsequently measured (SH) and counted in June, October, and November 2001. Living oysters at intermediate salinities were measured (SH) in June and October 2001, and February 2002. Salinity (‰), dissolved oxygen (mg/L), and water temperature (°C) at 0–25 cm beneath the water surface were measured monthly at each site from May to August 2001 during the experiment. Bags were cleaned with pressurized water and brushes monthly during the summer and seasonally during the fall and winter.

At each site, up to 24 oysters (4–8 oysters from each bag per species) were tested in August and October 2001 for prevalence and intensity of the oyster disease *P. marinus* and shell infestation rates by the mud worm *Polydora* spp. When testing for *P. marinus* infections, a 3–5-mm-long section of the rectum was removed from each oyster and analyzed for the presence and intensity of *P. marinus* using Ray's fluid Thioglycollate medium (RTFM) assays (Ray 1952, Ray 1963, Paynter & Burreson 1991). Infection intensity was calculated using the method described by Ray (1954) and Mackin (1962), with infection intensity categorized into the following groups: (0) absent, (1) light, (3) moderate, (5) heavy (Calvo et al. 1999, Lenihan et al. 1999). Average weighted intensity of *P. marinus* then was calculated for each species at each site by multiplying the number of oysters with each infection level by its infection intensity and dividing this sum by the total number of oysters tested. Intensity of *Polydora* spp. shell infestation was rated on a scale of 0 to 4 to describe the approximate percentage of the external oyster shell (right valve only) covered by mud worm tubes ([0] absent, [1] <25%, [2] 25% to 50%, [3] 50% to

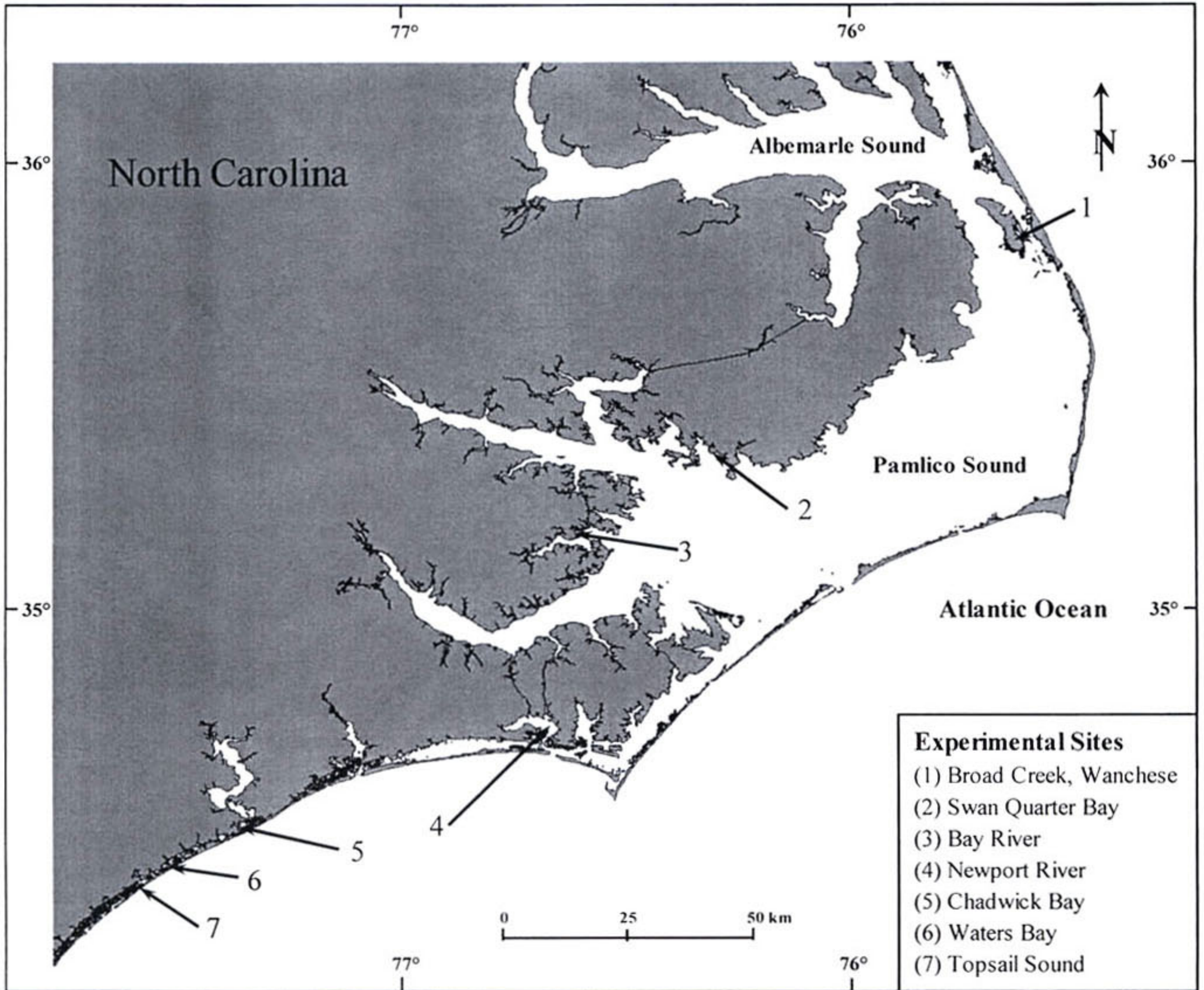


Figure 1. Location of experimental sites where native and non-native oysters were cultivated in 1999 to 2000 and 2001 to 2002 in coastal North Carolina, USA.

75%, and [4] >75% coverage). Weighted intensity was calculated by multiplying the number of oysters with each intensity level by their respective infestation intensity and dividing the sum by the total number of oysters tested.

Statistical Analyses

A series of multifactor ANOVAs was performed to test if growth and survivorship varied between or among oyster species

TABLE 1.

Mean and range of salinity, dissolved oxygen, and temperature from 25 cm below the water surface at field (-0.1-0.5 m below MLW) sites in North Carolina during the second experiment. Each parameter was recorded monthly between May and August of 2001.

Site	County (NC)	Latitude	Longitude	Salinity (‰)		Dissolved Oxygen (mg/L)		Temperature (°C)	
				Mean	Range	Mean	Range	Mean	Range
Broad Creek, Wanchese	Dare	N35°50.530'	W75°37.170'	18	15-22	5.9	4.4-7.6	27.1	21.7-30.1
Swan Quarter Bay	Hyde	N35°23.217'	W76°19.618'	16	15-16	7.2	6.3-8.3	28.6	24.5-30.5
Bay River	Pamlico	N35°11.032'	W76°36.529'	18	16-20	5.5	4.0-7.6	26.7	20.9-29.7
Newport River	Carteret	N34°44.689'	W76°39.679'	34	31-36	5.4	4.0-6.3	25.9	21.0-28.2
Chadwick Bay	Onslow	N34°31.603'	W77°22.574'	38	35-40	5.5	4.3-8.3	25.6	19.5-29.2
Waters Bay	Onslow	N34°26.941'	W77°32.248'	38	35-40	6.6	4.4-9.5	24.0	19.6-27.8
Topsail Sound	Pender	N34°24.417'	W77°35.848'	38	35-40	5.8	3.7-7.7	26.8	19.3-30.8

and whether these patterns were modified by grow-out site. Cochran's test for homogeneity of variances was conducted on all main effects prior to each analysis (Underwood 1981). For datasets that violated this assumption at α of 0.05, fourth-root transformations were performed and transformed data were tested. For experiments conducted in 1999 and 2000, separate 2-way ANOVAs were performed on oyster growth (final SH minus initial SH) and survivorship with site (Chadwick Bay and Broad Creek) and species (*C. ariakensis* and *C. virginica*) as fixed factors. A second set of separate 2-way ANOVAs was performed on oyster growth and survivorship with site (Chadwick Bay and Waters Bay) and species (*C. gigas* and *C. virginica*) as fixed factors. For experiments initiated in 2001, we conducted a series of analyses to compare growth and survivorship of the 3 oyster species within each salinity regimen. At relatively high salinities, we analyzed the effects of site (Chadwick Bay, Newport River, Topsail Sound, and Waters Bay) and species (*C. ariakensis*, *C. gigas*, and *C. virginica*) on growth and survivorship using separate 2-way ANOVAs with fixed factors. The effect of species (*C. ariakensis*, *C. gigas*, and *C. virginica*) on oyster growth and survivorship at Bay River (intermediate salinity) was analyzed using separate 1-way (fixed factor) ANOVAs. For the other 2 intermediate-salinity sites, 2-way ANOVAs were conducted on growth and survivorship with site (Swan Quarter Bay and Broad Creek) and species (*C. ariakensis* and *C. virginica*) as fixed factors. To test the effect of elevating oysters on their growth and survivorship, a 3-way ANOVA was

performed with site (Chadwick Bay and Newport River), species (*C. ariakensis*, *C. gigas*, and *C. virginica*), and elevation (bottom, low, and high) as fixed factors. Student-Newman-Keuls (SNK) *post hoc* tests at α of 0.05 were conducted on all main effects. If an interaction proved significant in 2-way ANOVAs, SNK tests were performed among treatments within each level of a factor. The SNK test was selected because we conducted a balanced experiment with *a priori* predictions and fixed factors (Day & Quinn 1989).

RESULTS

First Series of Experiments

Results of the contrasts between *C. ariakensis* and *C. virginica* varied between the (low-salinity) Broad Creek and (high-salinity) Chadwick's Bay sites. *C. ariakensis* deployed in December grew by September from 55.3 mm SH to 56.9 ± 0.6 mm (mean \pm 1 standard error) at Broad Creek and from 54.3 to 99.3 ± 1.9 mm at Chadwick Bay, while *C. virginica* increased during this period from 42.5 to 51.0 ± 2.2 mm at Broad Creek and from 42.6 to 71.0 ± 0.9 mm at Chadwick Bay. ANOVA revealed a significant effect of the interaction between site and species ($F_{1,8} = 79.1$, $P < 0.0001$; Fig. 2a) on oyster growth (i.e., change in shell height). *C. ariakensis* grew 16.6 mm more than *C. virginica* at the high-salinity Chadwick Bay, but *C. virginica* outgrew *C. ariakensis* by 6.8 mm at the low-salinity Broad Creek (SNK *post hoc* compari-

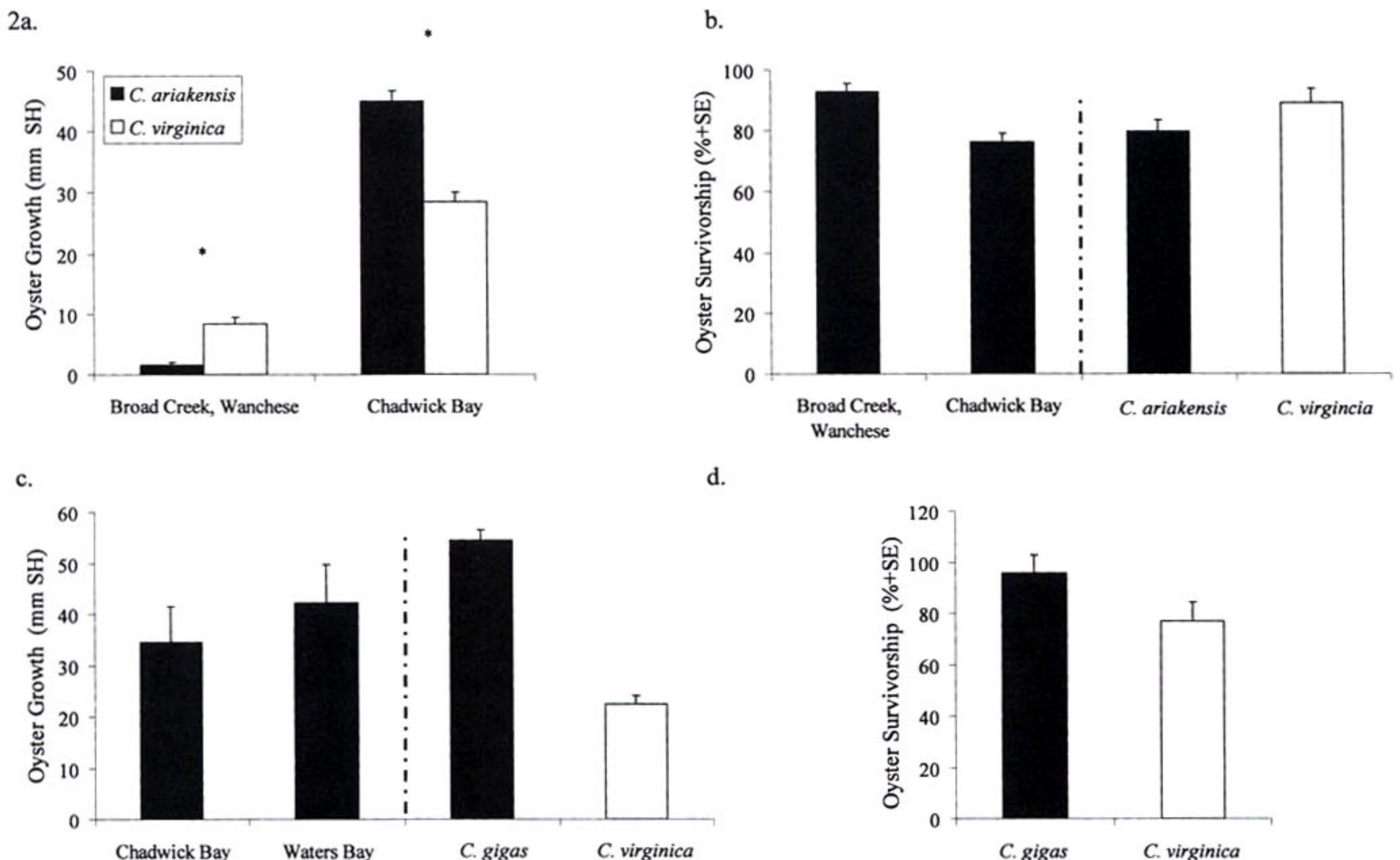


Figure 2. (a) *C. ariakensis* and *C. virginica* growth (final SH to initial SH) from December 1999 to September 2000 at Broad Creek and Chadwick Bay sites (+SE; $n = 3$). Significance levels (* $P < 0.05$; ns $P > 0.05$) presented above bars are from SNK *post hoc* tests conducted to explore the cause of the significant species X site interaction. (b) Oyster (both *C. ariakensis* and *C. virginica*) survivorship at each of the 2 sites and survivorship of *C. ariakensis* versus *C. virginica* after 9 mo of culture (+SE; $n = 6$). (c) Oyster (both *C. gigas* and *C. virginica*) growth at Chadwick Bay versus Waters Bay and *C. gigas* versus *C. virginica* growth from February to August in 2000 (+SE; $n = 6$). (d) *C. gigas* versus *C. virginica* survivorship after 7 mo of oyster culture at Chadwick Bay and Waters Bay (+SE; $n = 6$).

sons; see Fig. 2a). ANOVA revealed that the interaction between site and species did not affect oyster survivorship ($F_{1,8} = 0.3, P = 0.58$). Oyster survivorship at Chadwick Bay was 16.5% higher than at Broad Creek (site effect: $F_{1,8} = 28.4, P = 0.0007$), and survivorship of *C. virginica* was 9.4% higher than that of *C. ariakensis* (species effect: $F_{1,8} = 9.1, P = 0.02$; see Fig. 2b).

Results of the contrasts between *C. gigas* and *C. virginica* did not vary between sites, both of which had similarly high salinities. By the end of August 2000, *C. gigas* deployed in January 2000 grew from 31.3 to 81.3 ± 1.1 mm SH at Chadwick Bay and from 31.5 to 90.2 ± 2.1 mm at Waters Bay, whereas *C. virginica* grew from 29.8 to 48.8 ± 1.7 mm at Chadwick Bay and from 29.1 to 54.8 ± 1.7 mm at Waters Bay. For the contrast between *C. gigas* and *C. virginica*, ANOVA revealed no significant effect of the interaction between site and species on either growth ($F_{1,8} = 0.4, P = 0.56$) or survivorship ($F_{1,8} = 0.4, P = 0.53$). *C. gigas* grew more than *C. virginica* at both sites (species effect: $F_{1,8} = 455.3, P < 0.0001$), and oyster growth was higher at Waters Bay for both species (site effect: $F_{1,8} = 26.6, P = 0.0009$; see Fig. 2c). Survivorship of *C. gigas* was 18.7% higher than that of *C. virginica* across both sites (species effect: $F_{1,8} = 8.8, P = 0.02$; see Fig. 2d). Thus, in these high-salinity sites *C. gigas* grew faster and survived better than the native oyster.

Second Series of Experiments

Salinity, Temperature, and Dissolved Oxygen

Physical parameters were quantified in the summer of 2001 to indicate how variation in these factors might influence patterns of

oyster growth and mortality. Between May and August 2001, mean salinity was 38‰ at Chadwick Bay, Waters Bay, and Topsail Sound and 34‰ at Newport River sites (Table 1). Mean dissolved oxygen ranged from 5.4 to 6.6 mg/L and mean water temperature from 24.0°C to 26.8°C during this period at the high-salinity sites (Table 1). Between May and August 2001, mean salinity was 18‰, dissolved oxygen 5.5 mg/L, and water temperature 26.7°C at Bay River (Table 1). Mean salinity at Swan Quarter Bay (16‰) was slightly lower than at Broad Creek (18‰) between May and August 2001 (Table 1). Mean dissolved oxygen was higher than all other sites at Swan Quarter Bay (7.2 mg/L), and this was the only site for the entire study where relatively low (<4.5 mg/L) dissolved oxygen levels were never recorded (Table 1). Finally, mean water temperature was slightly higher at Swan Quarter Bay (28.6°C) than at Broad Creek (27.1°C; Table 1).

High-salinity Sites

C. ariakensis versus *C. gigas* versus *C. virginica*. Growth and survivorship differed among non-native and native oysters in this set of trials. From April to November 2001, *C. gigas* in high salinity grew from 19.2 to 101.4 ± 2.3 mm SH (means of all 4 sites), *C. ariakensis* from 31.6 to 86.0 ± 2.2 mm, and *C. virginica* from 20.7 to 52.4 ± 1.9 mm. The interaction between site and species did not affect oyster growth ($F_{6,24} = 2.0, P = 0.11$), but each main effect was significant (site: $F_{3,6} = 25.8, P < 0.0001$; species: $F_{2,6} = 346.3, P < 0.0001$). Oyster growth at Waters Bay was greater than all other sites, which did not differ (SNK *post hoc* comparisons; Fig. 3a). *C. gigas* growth was greater

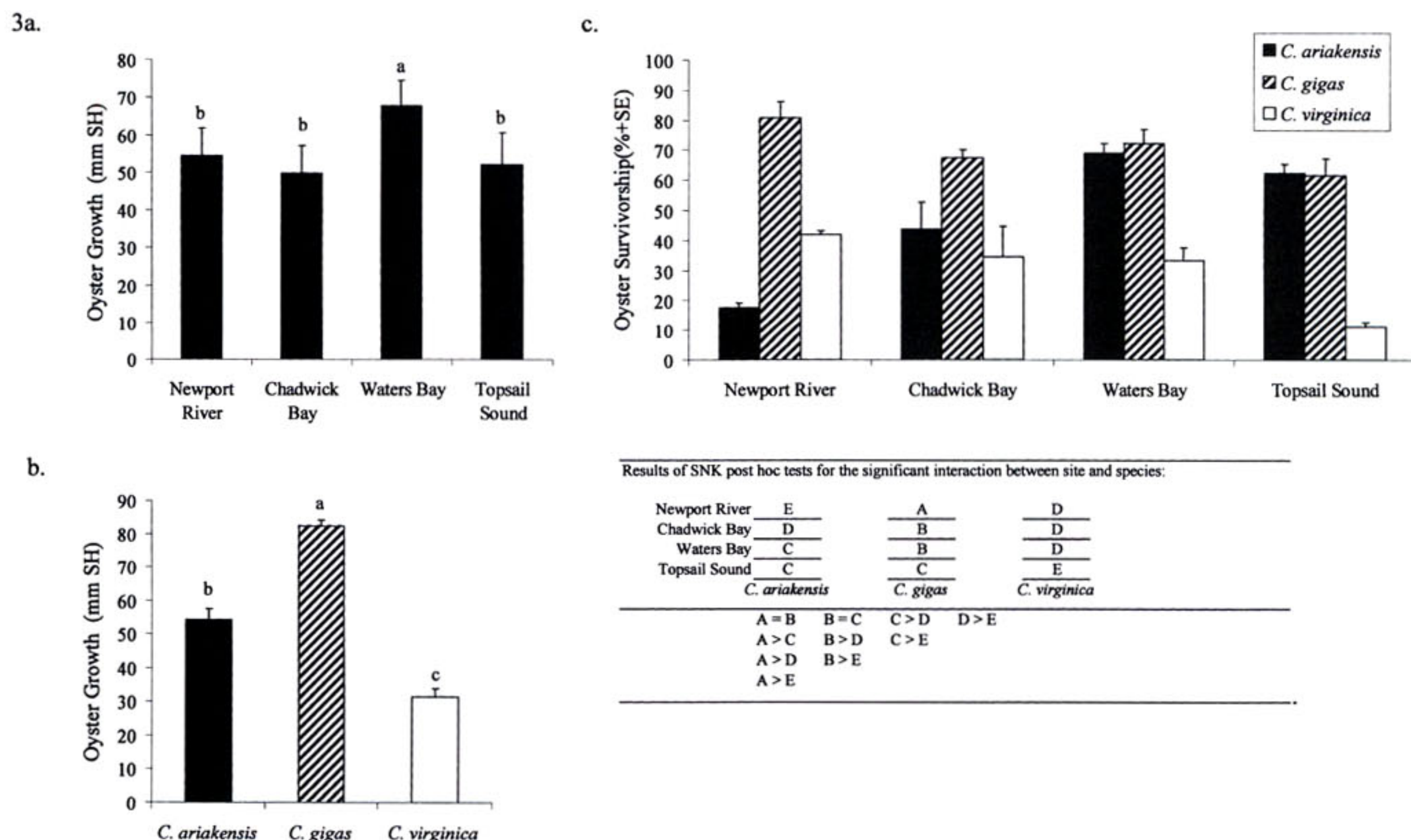


Figure 3. Culture of all 3 species at sites with high salinities from April to November in 2001. (a) The effect of site on oyster growth (final SH to initial SH) of all 3 species combined after 7 mo of culture (+SE; n = 9). Sites with different letters above error bars are significantly different at $P < 0.05$ (SNK *post hoc* tests). (b) The effect of species on growth of each species during oyster culture (+SE; n = 12). (c) The interaction between site and species on oyster survivorship at high salinities (+SE; n = 3).

than that of the other 2 species, and *C. ariakensis* outgrew *C. virginica* (see Fig. 3b). ANOVA revealed a significant interaction of site and species for oyster survivorship ($F_{6,24} = 12.8$, $P < 0.0001$; see Fig. 3c). Survivorship of *C. gigas* exceeded that of *C. ariakensis* at the Chadwick Bay and Newport River sites, and was greater than that of *C. virginica* at all 4 sites (Fig. 3c). Survivorship of *C. ariakensis* exceeded that of *C. virginica* at Topsail Sound and Waters Bay, but was less than that of *C. virginica* at Newport River (Fig. 3c). Finally, survivorship of *C. ariakensis* and *C. virginica* did not differ at Chadwick Bay (Fig. 3c).

Intermediate-salinity Sites

Bay River (*C. ariakensis* versus *C. gigas* versus *C. virginica*). In contrast to the results at the high-salinity sites, both *C. ariakensis* and *C. virginica* exhibited higher growth and survivorship than *C. gigas* at Bay River. From April 2001 to February 2002, *C. ariakensis* had grown from 32.5 to 82.9 ± 1.7 mm SH, *C. virginica* from 20.1 to 56.3 ± 0.02 mm, and *C. gigas* from 16.5 to 43.2 ± 1.1 mm. *C. ariakensis* outgrew both of the other species, and growth of *C. virginica* was greater than that of *C. gigas* (SNK *post hoc*

comparisons; $F_{2,6} = 88.0$, $P < 0.0001$; Fig. 4a). Survivorship did not differ between *C. ariakensis* and *C. virginica*, but survivorship of each was greater than that of *C. gigas* ($F_{2,6} = 52.4$, $P = 0.0002$; see Fig. 4b).

Broad Creek and Swan Quarter Bay (*C. ariakensis* versus *C. virginica*). The pattern exhibited at the other intermediate-salinity site (Bay River) of higher growth of *C. ariakensis* than *C. virginica* but equivalent survivorship was replicated in this set of trials. From April 2001 to February 2002, *C. ariakensis* grew from 31.4 to 62.1 ± 1.0 mm SH at Broad Creek and from 31.1 to 80.7 ± 3.5 mm at Swan Quarter Bay, whereas *C. virginica* increased from 18.8 to 48.8 ± 1.0 at Broad Creek and from 18.9 to 56.5 ± 0.6 mm, respectively, at the 2 sites. ANOVA revealed a significant effect of the interaction between site and species for oyster growth ($F_{1,8} = 7.5$, $P = 0.03$; Fig. 4c). *C. ariakensis* outgrew *C. virginica* at Swan Quarter Bay, but not at Broad Creek (SNK *post hoc* comparisons; Fig. 4c). For both species, growth was greater at Swan Quarter Bay than at Broad Creek (Fig. 4c). ANOVA revealed no significant effect on oyster survivorship of either main effect (site: $F_{1,8} = 0.5$, $P = 0.51$; species: $F_{1,8} = 1.4$, $P = 0.27$) or the interaction between site and species ($F_{1,8} = 2.8$, $P = 0.13$). Mean survivor-

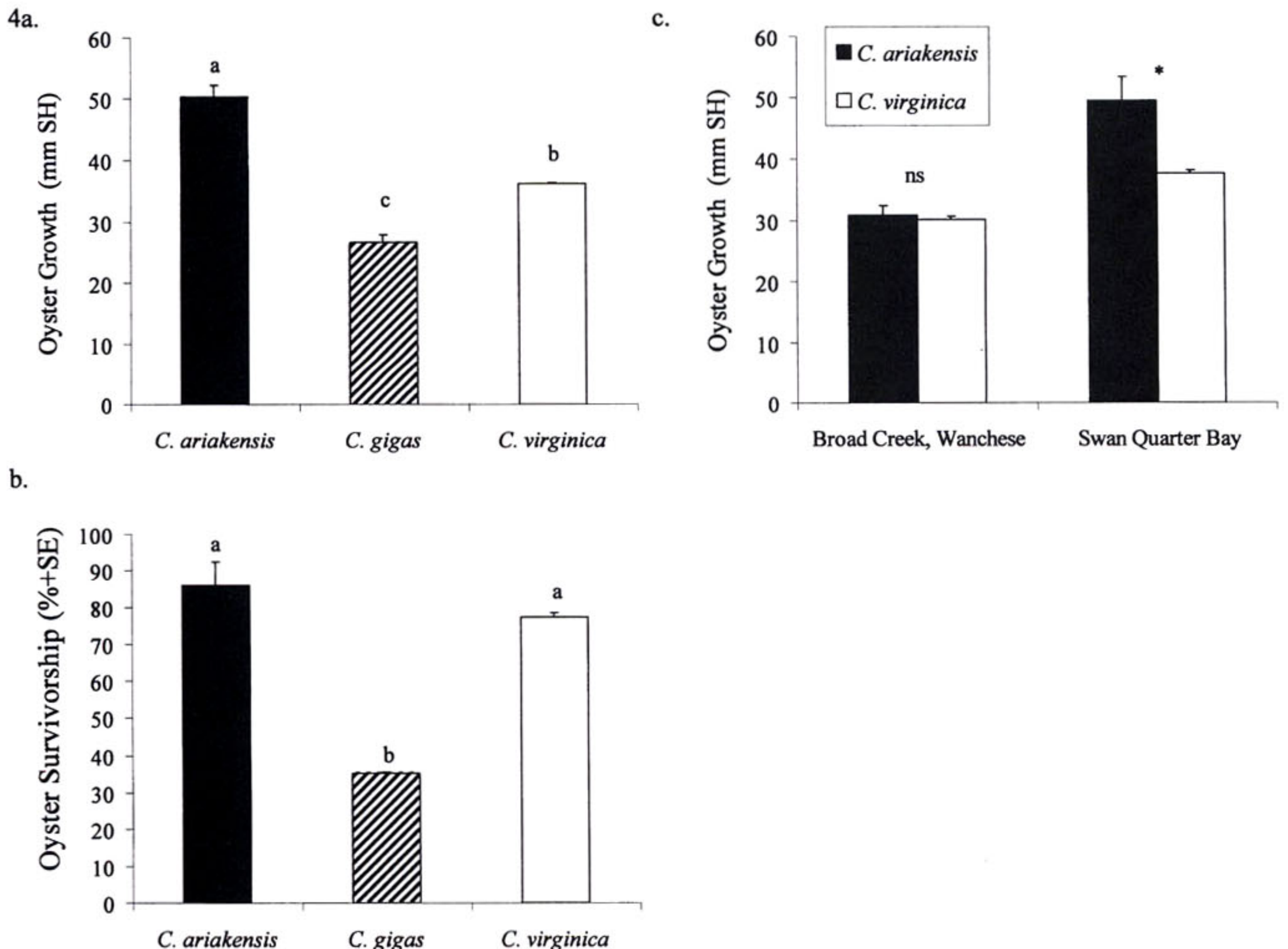


Figure 4. Oyster culture at intermediate-salinity sites from April 2001 to February 2002. (a) Growth and (b) Survivorship of all 3 species at Bay River from April 2001 to February 2002 (+SE; $n = 3$ for both graphs). Species with different letters above error bars are significantly different at $P < 0.05$. (c) *C. ariakensis* and *C. virginica* growth at Broad Creek and Swan Quarter Bay from April 2001 to February 2002 (+SE; $n = 3$). Significance levels (* $P < 0.05$; ns $P > 0.05$) presented above bars are from SNK *post hoc* tests conducted to explore the cause of the significant site X species interaction.

ship at these 2 sites was 74.1 ± 4.2 for *C. ariakensis* and 83.4 ± 7.3 for *C. virginica*.

Oyster Elevation Experiment

C. ariakensis versus *C. gigas* versus *C. virginica*. Elevating oysters enhanced the growth of *C. ariakensis* more than that of the other two oyster species. ANOVA revealed a significant effect of the 3-way interaction among site, species, and elevation for oyster growth (Table 2 and Fig. 5a). Height of oysters did not affect *C. gigas* growth at either site (SNK *post hoc* comparisons; Table 2,

Table 3 and Fig. 5a). *C. ariakensis* growth was greater on high racks than on the bottom at both sites, and was also greater on high-rack racks than on low racks at Chadwick Bay (Table 2, Table 3, and Fig. 5a). *C. virginica* growth was greatest on high racks, intermediate on low racks, and lowest on the bottom at Newport River, but did not differ at Chadwick Bay (Table 2, see Fig. 5a). *C. gigas* growth was greater than that of the other 2 species for all 3 elevations at both sites (Table 2, Table 3, and Fig. 5a). *C. ariakensis* growth was greater than that of *C. virginica* at all 3 elevations at both sites except for the bottom at Chadwick Bay, where the 2 species did not differ (see Table 2 and Fig. 5a).

TABLE 2.

The effect of site (Newport River and Chadwick Bay), species (*C. ariakensis*, *C. gigas*, and *C. virginica*), and elevation (bottom, low rack, and high rack) on oyster growth (change in shell height: SH) and survivorship in 2001 analyzed using separate 3-way ANOVAs.

	Oyster Growth (SH)				Oyster Survivorship			
	df	SS	F	P	df	SS	F	P
Site	1	0.001	3.6	0.06	1	0.079	7.4	0.01
Species	2	0.302	522.4	<.0001	2	1.671	78.2	<.0001
Height	2	0.009	15.9	<.0001	2	0.340	15.9	<.0001
Site × species	2	0.002	3.8	0.03	2	0.333	15.6	<.0001
Site × height	2	0.001	2.0	0.16	2	0.069	3.2	0.05
Species × height	4	0.010	8.5	<.0001	4	0.132	3.1	0.03
Site × species × height	4	0.005	4.6	0.004	4	0.019	0.4	0.78
Residual	36	0.010			36	0.385		

3-way interaction for oyster growth: site × species × height

Species	Newport River			Chadwick Bay		
	Bottom	Low	High	Bottom	Low	High
<i>C. ariakensis</i>	D	C	B	D	D	B
<i>C. gigas</i>	A	A	A	A	A	A
<i>C. virginica</i>	I	H	F	E	G	F

Newport River						Chadwick Bay	
A > B	B = C	C = D	D = E	E = F	F = G	G = H	H > I
A > C	B > D	C = E	D > F	E = G	F > H	G > I	
A > D	B > E	C > F	D > G	E > H	F > I		
A > E	B > F	C > G	D > H	E > I			
A > F	B > G	C > H	D > I				
A > G	B > H	C > I					
A > H	B > I						
A > I							

2-way interaction for oyster survivorship: site × species

Site	<i>C. ariakensis</i>	<i>C. gigas</i>	<i>C. virginica</i>
Newport River	C	A	C
Chadwick Bay	B	A	C

A > B	B = C	
A > C		

2-way interaction for oyster survivorship: species × height

Species	Newport River		Chadwick Bay	
	Bottom	Low	High	High
<i>C. ariakensis</i>	E	E	B	
<i>C. gigas</i>	A	A	A	
<i>C. virginica</i>	E	D	C	

A > B	B > C	C = D	D = E
A > C	B > D	C > E	
A > D	B > E		
A > E			

Notes: Provided also are results of SNK *post hoc* tests (using Bonferroni's adjustment for multiple contrasts to maintain experiment-wise $\alpha = 0.05$) for each significant interaction at $P < 0.05$ for the above analyses.

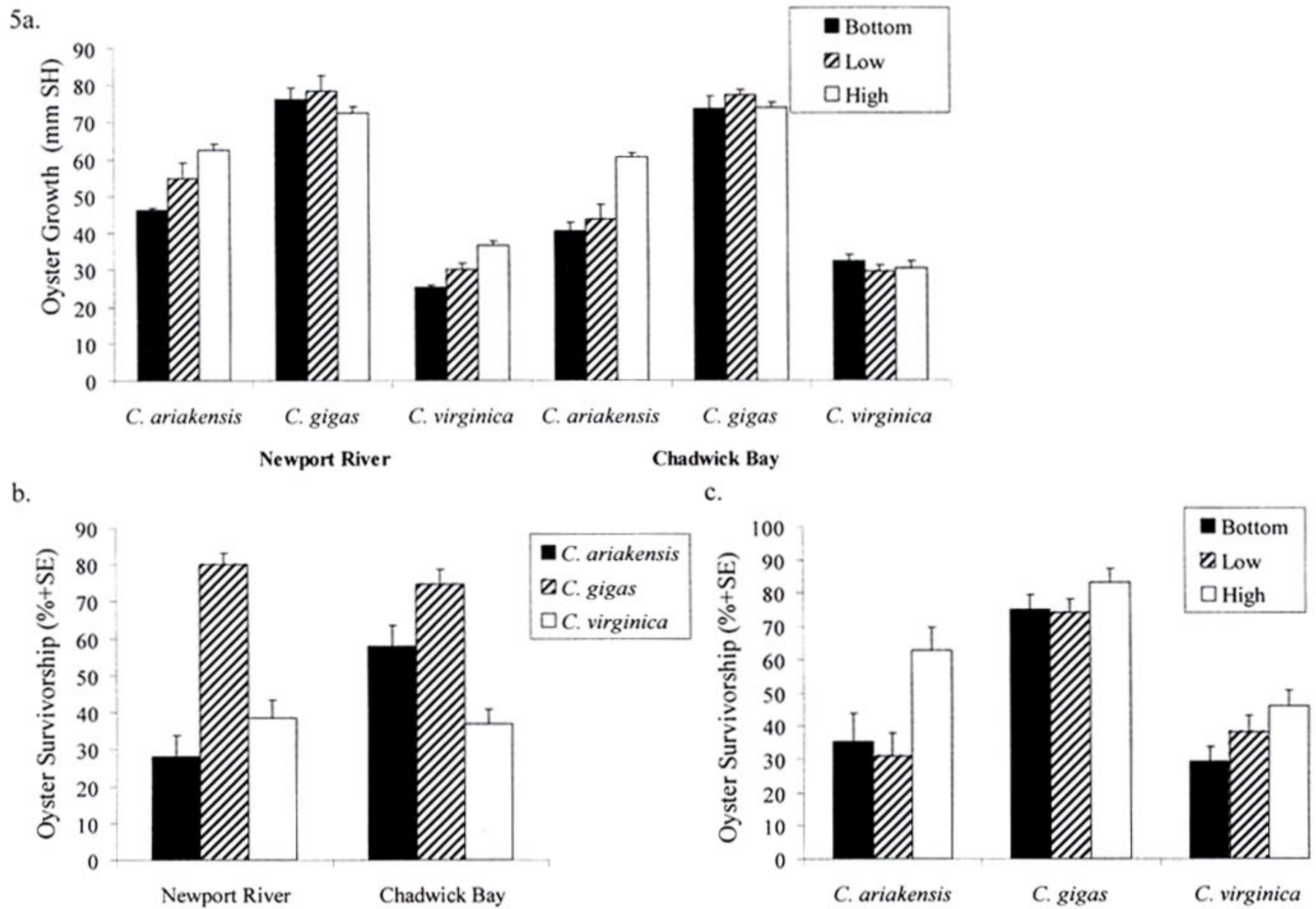


Figure 5. Culture of all 3 species on racks of differing elevations and on the bottom from April to November of 2001 at Newport River and Chadwick Bay. (a) The three-way interaction among site, species and elevation on oyster growth (+SE; $n = 3$). (b) The two-way interaction between site and species on oyster survivorship (+SE; $n = 9$). (c) The two-way interaction between species and elevation on oyster survivorship (+SE; $n = 6$). See Table 2 for results of SNK *post hoc* tests for each of the 3 graphs.

Although ANOVA of oyster survivorship revealed no 3-way interaction among site, species and elevation, all 3 2-way interactions were significant (site X species, species X elevation) or marginally significant (site X elevation; Table 2 and Fig. 5b,c). For the interaction between site and species, *C. gigas* survivorship was significantly higher than that of the other 2 species at both sites (SNK *post hoc* comparisons; Table 2 and Fig. 5b). *C. ariakensis* survivorship was greater than that of *C. virginica* at Chadwick Bay, but survivorship of the 2 species did not differ at Newport

River (Table 2 and Fig. 5b). For the interaction between species and elevation, elevating oysters did not affect survivorship of *C. gigas* (Table 2 and Fig. 5c). In contrast, elevating *C. ariakensis* from the bottom or low racks to high racks increased its survivorship (Table 2 and Fig. 5c). Survivorship of *C. virginica* was greater on high racks than on the bottom, but did not differ from low racks (Table 2 and Fig. 5c). *C. gigas* survivorship was greater than that of the other 2 species at all 3 elevations (Table 2 and Fig. 5c). Survivorship was greater for *C. ariakensis* than for *C. virginica*

TABLE 3.

Initial and final oyster sizes (shell height) of oysters grown at each elevation (bottom, low rack, and high rack) from April to November of 2001 at high-salinity sites (Newport River and Chadwick Bay) in North Carolina.

Site	Elevation	<i>C. ariakensis</i>		<i>C. gigas</i>		<i>C. virginica</i>	
		Initial SH	Final SH	Initial SH	Final SH	Initial SH	Final SH
Newport River	Bottom	30.4	76.8 (0.6)	20.9	97.2 (3.5)	20.4	45.7 (0.5)
	Low	28.9	83.9 (3.8)	19.6	98.0 (4.1)	20.7	50.8 (1.7)
	High	30.4	89.9 (1.1)	20.9	91.7 (1.6)	20.4	57.4 (1.3)
Chadwick Bay	Bottom	30.9	71.5 (1.9)	18.5	91.1 (3.3)	20.1	52.4 (2.0)
	Low	31.0	74.9 (2.8)	19.5	96.7 (1.3)	21.4	51.0 (2.2)
	High	30.9	89.4 (1.1)	18.5	93.4 (1.4)	20.1	50.7 (1.7)

only when oysters were raised on high racks (Table 2 and Fig. 5c). For the marginally significant (Table 2, $P = 0.05$) interaction between site and elevation, elevating oysters affected oyster survivorship only at Newport River, where survivorship of oysters was significantly greater on high racks than on the bottom.

Incidence of Oyster Disease and *Polydora* spp. Infestation

The prevalence (% of oysters infected) and intensity of *P. marinus* infection was extremely low at all sites for oysters tested in both August (1.7% were infected) and October 2001 (3.3% were infected; Table 4). In August, *P. marinus* was detected at only 1 to 2 sites for each of the 3 species, and its average prevalence for any species at any site was never greater than 10.0% (Table 4). In October, *P. marinus* was detected in *C. ariakensis* at 4 of 7 sites, and was most prevalent (16.7%) among *C. ariakensis* on low racks in Newport River and most intense (0.67) among *C. ariakensis* at Topsail Sound (Table 4). Of the 3 species, *P. marinus* was least prevalent and least intense among *C. gigas* and was detected only among *C. gigas* on high racks at Chadwick Bay in October (Table 4). *P. marinus* was detected in *C. virginica* at 4 of 7 sites in October (see Table 4).

In August 2001, the prevalence (% of oysters infected) and intensity of *Polydora* spp. infestation were greatest among *C. ariakensis*, intermediate among *C. gigas*, and almost nonexistent for *C. virginica* (Table 5). Prevalence and intensity of mud worms on *C. ariakensis* shells were very high at Broad Creek and Swan Quarter Bay, intermediate at Chadwick Bay, and very low at the other 4 sites (Table 5). Mud worm tubes were present on over half of *C. gigas* oysters tested at Chadwick Bay, but were present at only 1 of the other 4 sites (6.7% at Waters Bay; see Table 5). Waters Bay was the only site where mud worm tubes were present on *C. virginica* oysters (Table 5). In October 2001, mud worm

prevalence and intensity were greatest among *C. ariakensis* and *C. gigas*, and almost nonexistent among *C. virginica*. Mud worms were present on *C. ariakensis* and *C. gigas* shells at all sites except Waters Bay and Topsail Sound, and were most prevalent and intense at Chadwick Bay (Table 5). For *C. virginica*, mud worms were detected only at Chadwick Bay on high racks. In October, both infestation prevalence and intensity on shells of *C. ariakensis* and *C. gigas* were slightly greater on low racks than on either the bottom or high racks.

DISCUSSION

Critical to any decision on the introduction of non-native species for aquaculture, fisheries, or restoration of ecosystem services once provided by native species is an assessment of the biology of the candidate species in their prospective new environment. The primary motivations for introducing 1 of the 2 non-native oysters to Chesapeake Bay are their presumed resistance to *P. marinus* and *H. nelsoni*, with consequent survival advantages over the native oyster, and their high individual growth rates (National Research Council 2003). Previous studies comparing non-native oysters to *C. virginica* have found that the 2 non-native species tend to grow and survive better than the native oyster (Barber & Mann 1994, Calvo et al. 1999, Calvo et al. 2001), although reducing salinity can decrease or eliminate the growth and survivorship advantages of *C. gigas*. Barber and Mann (1994) demonstrated that growth and survivorship of *C. gigas* grown in the Chesapeake Bay were negatively impacted by salinities below 20‰. Similarly, Calvo et al. (1999) found that growth and survivorship of *C. gigas* in Chesapeake Bay were reduced at an intermediate salinity range of 15‰ to 25‰ in contrast to sites with salinities consistently above 25‰. They also noted that the individual growth rate of *C. gigas* was no longer greater than that of *C. virginica* at this intermediate-salinity

TABLE 4.

Prevalence and intensity of the oyster disease *Perkinsus marinus* among native and non-native oysters grown at 7 field sites in North Carolina. *P. marinus* prevalence and intensity were examined in August and October of 2001.

Experimental Height	Broad Creek Low	Swan Quarter Bay Low	Bay River Low	Newport River			Chadwick Bay			Waters Bay Low	Topsail Sound Low
				Bottom	Low	High	Bottom	Low	High		
August 2001											
<i>C. ariakensis</i>											
% infected	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	6.7%	0.0%	6.7%	0.0%
Weighted intensity ^a	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.07	0.00
<i>C. gigas</i>											
% infected			5.6%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
Weighted intensity			0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>C. virginica</i>											
% infected	0.0%	0.0%	0.0%	0.0%	10.0%	0.0%	0.0%	0.0%	0.0%	7.1%	0.0%
Weighted intensity	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.07	0.00
October 2001											
<i>C. ariakensis</i>											
% infected	7.1%	0.0%	0.0%	0.0%	16.7%	0.0%	0.0%	0.0%	14.3%	0.0%	13.3%
Weighted intensity	0.07	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.29	0.00	0.67
<i>C. gigas</i>											
% infected			0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	7.7%	0.0%	0.0%
Weighted intensity			0.00	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.00
<i>C. virginica</i>											
% infected	13.3%	0.0%	6.7%	0.0%	0.0%	0.0%	14.3%	0.0%	0.0%	7.7%	0.0%
Weighted intensity	0.13	0.00	0.07	0.00	0.00	0.00	0.14	0.00	0.00	0.38	0.00

^a Infection intensity was calculated using the method described by Ray (1954) and Mackin (1962), with infection intensity categorized into the following groups: (0) absent, (1) light, (3) moderate, (5) heavy (Calvo et al. 1999, Lenihan et al. 1999). Average weighted intensity of dermo then was calculated for each species at each site by multiplying the number of oysters with each infection level by its infection intensity and dividing this sum by the total number of oysters tested.

TABLE 5.

Prevalence and intensity of mud worm *Polydora* spp. infestation among native and non-native oysters grown at 7 field sites in North Carolina. Mud worm infestation levels were quantified in August and October of 2001.

Experimental Height	Broad Creek Low	Swan Quarter Bay Low	Bay River Low	Newport River			Chadwick Bay			Waters Bay Low	Topsail Sound Low
				Bottom	Low	High	Bottom	Low	High		
August 2001											
<i>C. ariakensis</i>											
% w/ <i>Polydora</i>	100.0%	86.7%	0.0%	0.0%	0.0%	0.0%	33.3%	26.7%	23.8%	0.0%	0.0%
Weighted intensity	3.00	1.40	0.00	0.00	0.00	0.00	0.89	0.33	0.48	0.00	0.00
<i>C. gigas</i>											
% w/ <i>Polydora</i>			0.0%	0.0%	0.0%	0.0%	66.7%	40.0%	66.7%	6.7%	0.0%
Weighted intensity ^a			0.00	0.00	0.00	0.00	1.27	0.80	1.27	0.07	0.00
<i>C. virginica</i>											
% w/ <i>Polydora</i>	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	7.1%	0.0%
Weighted intensity	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00
October 2001											
<i>C. ariakensis</i>											
% w/ <i>Polydora</i>	28.6%	46.2%	60.0%	0.0%	16.7%	28.6%	92.3%	100.0%	64.3%	0.0%	0.0%
Weighted intensity	0.93	0.92	1.53	0.00	0.17	0.29	1.31	3.00	1.79	0.00	0.00
<i>C. gigas</i>											
% w/ <i>Polydora</i>			50.0%	13.3%	53.8%	0.0%	66.7%	100.0%	69.2%	0.0%	0.0%
Weighted intensity			1.60	0.13	0.77	0.00	1.67	2.00	1.54	0.00	0.00
<i>C. virginica</i>											
% w/ <i>Polydora</i>	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	9.1%	0.0%	0.0%
Weighted intensity	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00	0.00

Intensity of *Polydora* spp. shell infestation was rated on a scale of 0 to 4 to approximate the percentage of the oyster shell covered by mud worm tubes ([0] absent, [1] <25%, [2] 25–50%, [3] 50–75%, and [4] >75% coverage; Calvo et al. 1999). Weighted intensity was calculated by multiplying the number of oysters with each intensity level by their respective infestation intensity and dividing the sum by the total number of oysters tested.

level. Calvo et al. (2001) found low mortality rates for *C. ariakensis* over a wide spectrum of salinities (<15‰, 15‰ to 25‰, >25‰), suggesting that the physiology of *C. ariakensis* is influenced less by salinity than that of *C. gigas*. High *C. virginica* mortality rates in 2 of these studies (Barber & Mann 1994, Calvo et al. 2001) were primarily caused by the parasitic protozoan *P. marinus*, which is one of the largest impediments to native oyster aquaculture and recovery of native oyster fisheries in the estuaries of Maryland and Virginia. Prior to our study, growth and survivorship of the two non-native species had yet to be compared along the Atlantic coast of the United States, though Robinson and Langdon (1993) found that *C. gigas* growth was greater than that of *C. ariakensis* at sites on the West coast.

Results of our study provide clear evidence that the 2 non-native oysters, *C. gigas* and *C. ariakensis*, differ dramatically from one another and from the native eastern oyster, *C. virginica* in critical biologic rates (Table 6). As anticipated from previous studies done in the Chesapeake Bay (Barber & Mann 1994, Calvo et al. 1999), we found that *C. gigas* grows faster and survives at higher rates in high-salinity waters (25‰ to 36‰) than in 15‰ to 25‰ salinities. At the high-salinity sites, *C. gigas* exhibited consistent and substantial growth and survival advantages over the other 2 species (i.e., 162.4% higher growth than *C. virginica* and 54.1% higher than *C. ariakensis* and 33.1% higher survivorship than *C. virginica* and 22.3% higher than *C. ariakensis*). Thus, at high salinity, performance of the non-native *C. gigas* greatly exceeds that of the native eastern oyster in both biologic traits critical to production, namely growth and survivorship. From previous research (Barber & Mann 1994) and our own more limited data, the survivorship advantage of *C. gigas* could be related to greater resistance to *P. marinus* infection. At the 1 site of intermediate salinity (15‰ to 25‰) where we deployed *C. gigas*, it was sig-

nificantly outperformed in both growth and survival by the native eastern oyster, *C. virginica*. Therefore, any enthusiasm for introduction of *C. gigas* to Chesapeake Bay or the Pamlico Sound must be tempered by the realization that in the vast majority of the waters of these estuaries salinities favor the native eastern oyster.

Our results from deploying *C. ariakensis* in the small-scale grow-out trials confirm some previous conclusions from analogous research in Chesapeake Bay (Calvo et al. 2001) while providing new insights as well from direct contrasts with *C. gigas* and from our tests of elevation impacts. We first demonstrated in cold-season trials that salinity levels below 10‰ virtually inhibited all net growth and caused high mortality of *C. ariakensis*, thereby serving to help define one environmental and thus geographic limit to its successful culture. A site with salinity consistently below 10‰ proved unsuitable to achieve net growth in winter and simultaneously induced high mortality. The native eastern oyster actually significantly outperformed *C. ariakensis* at this low-salinity site in both growth and survival. However, the native oyster would have required an additional 3 to 4 y to achieve market size based on observed growth rates of *C. virginica* from this site, rendering such environments poor candidates for its culture also.

At sites of intermediate salinity (15‰ to 25‰), *C. ariakensis* significantly outgrew *C. gigas* by 35.9% and *C. virginica* by 24.5%. At intermediate salinity, *C. ariakensis* survivorship was 42.1% higher than that of *C. gigas*, but it did not differ significantly from *C. virginica*. However, the absence of a survival advantage of *C. ariakensis* over *C. virginica* in our study is misleading. By the time our trials were terminated, *C. ariakensis* had already reached a legally harvestable size (76.2 mm SH in North Carolina), whereas the more slowly growing native oyster had not. Using observed growth rates of *C. virginica* in our study, approximately 2–10 additional months of culture would have been re-

TABLE 6.

Summary of results from experimental culture of native (*C. virginica*) versus non-native (*C. ariakensis* and *C. gigas*) during 1999–2000 and 2001–2002 in North Carolina.

	Year	Site	Species Compared	Elevation	Results	
					Individual Growth	Survivorship
1. High-salinity (>25‰) sites						
	1999–2000	Chadwick Bay	<i>C. ariakensis</i> versus <i>C. virginica</i>	Low elevation	aria > virg	virg > aria ^a
	1999–2000	Chadwick Bay	<i>C. gigas</i> versus <i>C. virginica</i>	Low elevation	gigas > virg	giga > virg
	1999–2000	Waters Bay	<i>C. gigas</i> versus <i>C. virginica</i>	Low elevation	gigas > virg	gigas > virg
	2001–2002	Waters Bay	All 3 species	Low elevation	gigas > aria > virg	aria = gigas > virg
	2001–2002	Topsail Sound	All 3 species	Low elevation	gigas > aria > virg	aria = gigas > virg
Elevation experiment						
	2001–2002	Newport River	All 3 species	Bottom	gigas > aria > virg	gigas > aria = virg
	2001–2002	Newport River	All 3 species	Low elevation	gigas > aria > virg	gigas > virg > aria
	2001–2002	Newport River	All 3 species	High elevation	gigas > aria > virg	gigas > aria > virg
	2001–2002	Chadwick Bay	All 3 species	Bottom	gigas > aria = virg	gigas > aria = virg
	2001–2002	Chadwick Bay	All 3 species	Low elevation	gigas > aria > virg	gigas > aria = virg
	2001–2002	Chadwick Bay	All 3 species	High elevation	gigas > aria > virg	gigas > aria > virg
	2001–2002	Newport River	<i>C. ariakensis</i>	All 3 elevations	high = low > bottom	high > low = bottom
	2001–2002	Newport River	<i>C. gigas</i>	All 3 elevations	bottom = low = high	bottom = low = high
	2001–2002	Newport River	<i>C. virginica</i>	All 3 elevations	high > low > bottom	high > bottom
	2001–2002	Chadwick Bay	<i>C. ariakensis</i>	All 3 elevations	high > low = bottom	high > low = bottom
	2001–2002	Chadwick Bay	<i>C. gigas</i>	All 3 elevations	bottom = low = high	bottom = low = high
	2001–2002	Chadwick Bay	<i>C. virginica</i>	All 3 elevations	bottom = low = high	high > bottom
2. Intermediate-salinity (15–25‰) sites						
	2001–2002	Broad Creek, Wanchese	<i>C. ariakensis</i> versus <i>C. virginica</i>	Low elevation	aria = virg	aria = virg
	2001–2002	Swan Quarter Bay	<i>C. ariakensis</i> versus <i>C. virginica</i>	Low elevation	aria > virg	aria = virg
	2001–2002	Bay River	All 3 species	Low elevation	aria > virg > gigas	aria = virg > gigas
3. Low-salinity (<10‰) site ^b						
	1999–2000	Broad Creek, Wanchese	<i>C. ariakensis</i> versus <i>C. virginica</i>	Low elevation	virg > aria	virg > aria

^a *C. virginica* had not reached marketable size by the end of the experiment. Therefore, the 2–9 months of additional estimated grow-out would be expected to lead to much more mortality from dermo and other sources.

^b Abnormal environmental conditions following Hurricane Floyd resulted in extremely low salinity levels at Broad Creek in 2000 (Peterson 2000).

quired to achieve market size. The several additional months of warm water exposure required to complete grow-out of *C. virginica* would almost certainly have elevated its mortality, perhaps even dramatically if *P. marinus* infection had increased as expected (Lenihan et al. 1999).

At sites of high salinity, growth of *C. ariakensis* consistently and significantly exceeded that of the native *C. virginica* in all 5 trials where this contrast was set up. However, *C. ariakensis* survivorship was highly variable and unpredictable even using the environmental information on actual salinity, temperature, and DO variation that we collected. Over the 5 trials comparing *C. ariakensis* to *C. virginica* at high salinity, *C. virginica* survived at a significantly higher rate in 2 cases, *C. ariakensis* survived better in 2 cases, and no significant difference was detected in the remaining contrast. The high variability in the survivorship results for these 2 species at high salinity differs from the consistent advantage of *C. ariakensis* previously demonstrated in the Chesapeake Bay study of Calvo et al. (2001).

Comparison of triploid non-native oysters with diploid *C. virginica* could partly explain why non-native oysters outgrew *C. virginica* because reduced gamete production in triploids generally results in enhanced somatic growth (Barber & Mann 1994). Allen and Downing (1986) and Davis (1989) documented that triploid *C.*

gigas outgrow diploid *C. gigas*, particularly during the reproductive season. However, in a previous study with triploid *C. gigas* and *C. virginica*, *C. gigas* growth was nearly double that of triploid native oysters at high salinities (Calvo et al. 1999), suggesting that growth results in our study are only slightly confounded by differences in ploidy status among species.

A second potential limitation of this study was that the size and condition of oysters differed among species at the beginning of each experiment. In particular, *C. ariakensis* were approximately 10 mm (SH) larger than either of the other two species at the beginning of the experiment. *C. ariakensis* were raised at VIMS until they were large enough to be tested for ploidy status prior to use in this study. Because the proportional growth in oyster biomass increases with each incremental gain in shell height, an incremental gain in shell height for a larger oyster represents greater growth in biomass than the amount of biomass growth from a similar gain in shell height of a smaller oyster. Therefore, in this study growth rates of *C. ariakensis* are likely underestimated relative to the other two species. In particular, differences in growth rates between *C. gigas* and *C. ariakensis* were likely overestimated at high salinity sites, and *C. ariakensis* growth advantages over *C. virginica* and *C. gigas* (at low salinities) were probably underestimated. Another important consideration is that these oyster spe-

cies differ in morphology, so that an incremental change in SH for each species does not necessarily represent a uniform change in oyster biomass. Comparison of oysters tissue weights of larger (80–110 mm SH) oysters that did not differ in SH determined that *C. ariakensis* tissue weight was approximately twice that of *C. virginica* and one-third greater than *C. gigas* tissue weight (Grabowski et al. 2003). Thus, comparing growth rates by quantifying changes in shell height also underestimated *C. ariakensis* growth relative to the other two species.

Our experiment that varied the elevation of oysters from culture on the bottom to racks of 2 different heights, 15 cm and 38 cm, provides some insight into why the relative advantage of *C. ariakensis* may change among sites even with salinity held constantly high. Varying elevation off the bottom had no detectable impact on growth of *C. gigas* and did not change the survivorship advantage that *C. gigas* held over both other oysters. However, culturing *C. ariakensis* on the bottom consistently reduced its growth rate. Growth of *C. virginica* also exhibited lower growth in bottom culture at 1 of the 2 sites, but the native oyster was sufficiently less sensitive to the bottom environment such that the statistically significant growth advantage held by *C. ariakensis* over *C. virginica* at both rack elevations disappeared on the bottom at one site. Similarly, *C. ariakensis* held a detectable survivorship advantage over *C. virginica* only on high racks. Because the concentration of suspended sediments decreases dramatically with elevation in the water column in estuaries and suspended sediments can interfere with suspension feeding (Rhoads & Young 1970), our results from the manipulation of elevation of culture imply that *C. ariakensis* is more sensitive to elevated turbidity than the other two oysters. Consequently, variation in suspended sediment load may help explain the high variation in *C. ariakensis* survivorship among high-salinity sites. Such sensitivity to bottom culture implies that *C. ariakensis* may experience difficulty in becoming established in more turbid regions of estuaries.

Although results of our manipulation of culture elevation imply greater sensitivity of *C. ariakensis* to turbidity, it is doubtful that this explanation accounts for all the variation in its survivorship among high-salinity sites. Other factors varied among sites, such as extensive shell fouling by barnacles and tunicates at Newport River and Chadwick Bay, which may have contributed to mortality. Higher mortality rates could also be a consequence of the parasite *Bonamia* sp., which has caused extensive mortality among juvenile oysters in laboratory and field trials conducted at UNC-IMS (Bishop et al. unpublished data). Rearing organisms in hatcheries often results in extreme genetic bottlenecks (Gaffney et al. 1996, Launey & Hedgecock 2001), which could increase cultured species' susceptibility to parasites and diseases. In the absence of the ability to predict mortality from known independent environmental variables that could be measured *a priori* at any prospective aquaculture site, the possibility of high mortality renders culture of *C. ariakensis* in high salinity a very risky proposition.

Creating any structures rising more than 15 cm off the bottom in North Carolina waters requires growers to obtain a water column lease in addition to the standard bottom lease. Because water column leases historically have been very difficult to obtain in North Carolina and cost an additional \$100 per acre, advantages of using high racks must outweigh the added expense. Elevating oyster racks from 15 to 38 cm increased oyster growth and survivorship of *C. ariakensis* at both sites, growth of *C. virginica* at Newport River, and survivorship of *C. virginica* at both sites. The magnitude of the effects of increasing rack height from on the

bottom and at 15 cm to 38 cm was greatest for *C. ariakensis*, whereas elevating oysters to 38 cm did not affect growth or survivorship of *C. gigas* at either site. Elevating oysters from the bottom to 15 cm generally did not affect growth or survivorship for any of the 3 species. Our results suggest that oyster growers culturing *C. virginica* or especially *C. ariakensis*, but not *C. gigas*, might consider obtaining a water column lease, though a complete bioeconomic evaluation of whether increased growth and survivorship outweigh the additional costs should be considered first.

Our results from trial culture comparing the performance of 2 non-native oysters to the native eastern oyster provide reasonably clear conclusions. *C. gigas* consistently outperforms both other oysters in growth and survivorship in high-salinity waters, but does less well than the other 2 oysters in intermediate salinity. At high salinity, *C. ariakensis* can suffer extremely high mortality, perhaps in part from exposure to high turbidity or the parasite *Bonamia* sp., but the environmental determinants are not well enough known to predict where survival will be good or bad. Consequently, on the basis of unpredictable and occasionally massive mortality, culturing *C. ariakensis* at sites of high salinity is risky. On the other hand, *C. ariakensis* has a substantial growth advantage over both of the other 2 oysters at intermediate salinity and likely also has a survivorship advantage. The range of viable salinities for successful culture of *C. ariakensis* does not extend below approximately 10‰; however, in the range of 15‰ to 25‰, this oyster grows faster and suffers less from the oyster diseases that plague *C. virginica*. Elevation of *C. ariakensis* during culture should be a viable strategy to increase survivorship and growth, but the cost-benefit ratio of obtaining water column leases should be examined further in North Carolina. Incorporation of all these results into a bioeconomic model is now necessary to quantify and compare the additional value that could be generated from higher growth and/or survivorship rates of non-native species relative to the risks associated with introducing a non-native species.

Because oyster consumers in eastern North Carolina prefer *C. virginica* over either non-native species when consumed raw and *C. gigas* when eaten cooked (Grabowski et al. 2003), differences (if any) in the price of each species for both raw and steamer markets must be incorporated into economic evaluation of the profitability of culturing non-native oysters. Given that the added cost of producing triploid oysters to avoid wild introduction is high and non-native oysters may be somewhat less palatable, culture of triploid non-native oysters may prove economically non-viable. Making non-native oysters available for aquaculture may, however, lower the probability of unsanctioned and uncontrolled introduction of reproductively capable non-native oysters into the environment (National Research Council 2003), thereby reducing the risk of potentially dire ecologic impacts of introducing a non-native species (i.e., competition with native species, unintentional introduction of additional predators and/or diseases, etc.). Finally, potential ecosystem benefits (i.e., water filtration, habitat provision) of promoting bivalve aquaculture should also be considered in deciding about permits for culturing non-native oysters. The question of whether to attempt to establish breeding, self-replicating populations of a non-native oyster entails consideration of many more issues, but requires more biologic information on potential risks versus economic and ecosystem benefits.

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