

**EFFECT OF SUBMERGENCE DEPTH ON EASTERN OYSTER,
Crassostrea virginica (GMELIN, 1791), GROWTH, SHELL
MORPHOLOGY, SHELL CHARACTERISTICS, *Perkinsus marinus*
INFECTION, AND MORTALITY IN OYSTERS CULTURED
INTERTIDALLY OFF-BOTTOM IN GEORGIA**

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Abstract

Clam farmers in Georgia would like to diversify into culturing oysters, *Crassostrea virginica* (Gmelin, 1791), but no technique currently exists for producing a quality single oyster for the lucrative raw and cocktail markets. This study evaluated the growth, shell morphology and characteristics, *Perkinsus marinus* (Levine, 1978) infection rates, and mortality of single oysters cultured in pearl nets. Oysters were grown in a non-stationary setting at a consistent and variable water depth at the Marine Extension Service dock in the Skidaway River from October 2005 to April 2006. Three replicate 9-mm mesh pearl nets each stocked with 200 oysters gathered from spat collectors were suspended in a non-stationary manner at the two-hours above- mean-low water mark to experience submergence at variable depths over a full tidal range in treatment one. Treatment two was attached to a float system that allowed three replicate 9-mm mesh pearl nets to rise and fall with the tide while keeping oysters ~0.5-meter below the surface when the tide was two-hours above-mean-low water mark or higher. Oysters in both treatments grew from a mean shell height of 17 mm to 38.4 ± 1.43 (S.E.) mm in floating pearl nets and to 38.0 ± 1.27 mm in hanging pearl nets which were not significantly ($P=0.7432$) different. Oyster growth rates were correlated with seasonal water temperatures. There were no significant differences in shell height to shell length ratio ($P=0.6472$), condition index ($P=0.3662$), percentage of chalky deposits ($P=0.4227$), or percent shell pigmentation ($P=0.7800$) during April 2007. No oyster mortality, *Perkinsus marinus* infection, or mud blisters occurred throughout the study. Oysters did not reach the legal-market size of 76 mm during the course of this research, but potential for the development of single oysters of 50-mm size for the cocktail trade was determined.

Introduction

Oyster farming has been very successful in many parts of the United States, as well as, worldwide (Castagna *et al.* 1996). In Georgia, oysters *Crassostrea virginica* (Gmelin, 1791) are marketed primarily for the fall/winter sack trade and are used in local oyster roasts. Oyster reefs are destroyed by oyster fishers who break up the clusters of oysters in hopes of obtaining singles. Due to an increasing global demand for and the value of raw single oysters intended for the halfshell trade, clam farmers in Georgia would like to diversify into culturing single oysters.

Presently, wild harvest of oysters is a small business in Georgia mostly for the sack trade with landings of only 7,247 kg of meat valued at \$65,250 in 2007. Although Georgia has abundant natural oyster stocks, quality single oysters are rare. Oysters exhibit a high reproductive capacity resulting in a high rate of larval oyster recruitment. Mature oysters start spawning in April/May (Heffernan *et al.* 1989, O’Beirn *et al.* 1996a, 1997) with early spring recruits growing rapidly, sexually maturing within two months (O’Beirn *et al.* 1996b) and spawning in summer/fall. Spawning and recruitment continue into October (O’Beirn *et al.* 1995, 1996a,c, 1998, Manley 2007, Manley *et al.* 2009). With monthly recruitment as high as 204,700 spat per square meter per month (Thoresen *et al.* 2005), overcrowding on natural oyster reefs results in oysters exhibiting shells that are long, thin and narrow. Likewise, oysters from overcrowded beds in Georgia and South Carolina tend to have narrow and thin shells (Carriker, 1996). Oysters that are elongated and do not have a cupped appearance are generally not preferred in the lucrative raw oyster bar market. Consumer demand for high-grade single oysters, current oyster prices, and an abundance of natural oyster spat suggest that Georgia can develop an oyster aquaculture industry if single oysters can be produced. If the shellfish industry in Georgia is going to compete with oyster industries from other states and countries, it must meet the consumer demand for an aesthetically pleasing single oyster of “raw bar quality” (i.e., suitable for sale in oyster bars).

This study evaluates growth rate, shell morphology and characteristics, *Perkinsus marinus* infection rates, and mortality of wild oyster spat grown in a non-stationary setting at consistent and variable water depths for the purpose of developing a market-grade oyster for the halfshell industry.

Materials and Methods

Oyster spat were collected using 2.0-cm diameter PVC sticks coated in a cement slurry mixture composed of 1/3 portland, 1/3 sand, and 1/3 garden lime (Manley *et al.* 2008). Spat collectors were deployed at Tybee Cut, a small tidal creek between Cabbage and Wilmington Islands in Wassaw Sound, Georgia during mid August 2006 (Figure 1). One-hundred individual collectors were placed in close proximity to each other along the creek bank adjacent to a live natural oyster reef at approximately two-hour above-mean-low water. Spat collectors were gathered in September 2006, and oysters were detached from the collectors and separated into single oysters.

Six 9-mm-mesh pearl nets were stocked with 200 oysters at a mean size of 17.07 ± 0.38 (S.E.) mm in shell height (hinge to lip) during October 2006. Three pearl nets were suspended from the Marine Extension Service dock on the Skidaway River, Skidaway Island, Georgia (Figure 1). Nets were suspended at a height approximately two-hours-above the mean-low-water mark, similar to that of the adjacent natural oyster reefs. Individual nets were weighted with a brick attached underneath to hold them in place during the tidal cycle.

Three additional 9-mm mesh pearl nets were deployed in a similar manner at the same site, except they were attached to a crab-trap float that held them suspended ~0.50-meter below the surface of the water. Thus, the nets rise in the water column with the incoming tide, but are left suspended in the intertidal zone along with the hanging nets at low tide. At low tide both treatments were aligned parallel to each other and received equal air exposure and submergence time. Pearl nets were deployed on 26 October 2006, and the study was terminated on 17 April 2007.

Each month (November 2006 to April 2007), 32 randomly selected oysters per replicate were measured for oyster height (from hinge to lip), length (across the abductor muscle), and width (across two valves) to the nearest 0.1 mm with Vernier calipers. Fifty oysters per replicate were evaluated each month to determine the mortality rate. On 17 April 2007, 32 oysters per treatment type were randomly selected from combined replicates and were evaluated for oyster index condition, presence of the oyster pathogen, *Perkinsus marinus*, percent shell pigment, percent chalky

deposits in shells, and number of mud blisters caused by the polychaete, *Polydora websteri* Hardman, 1943, on the interior of the shell.

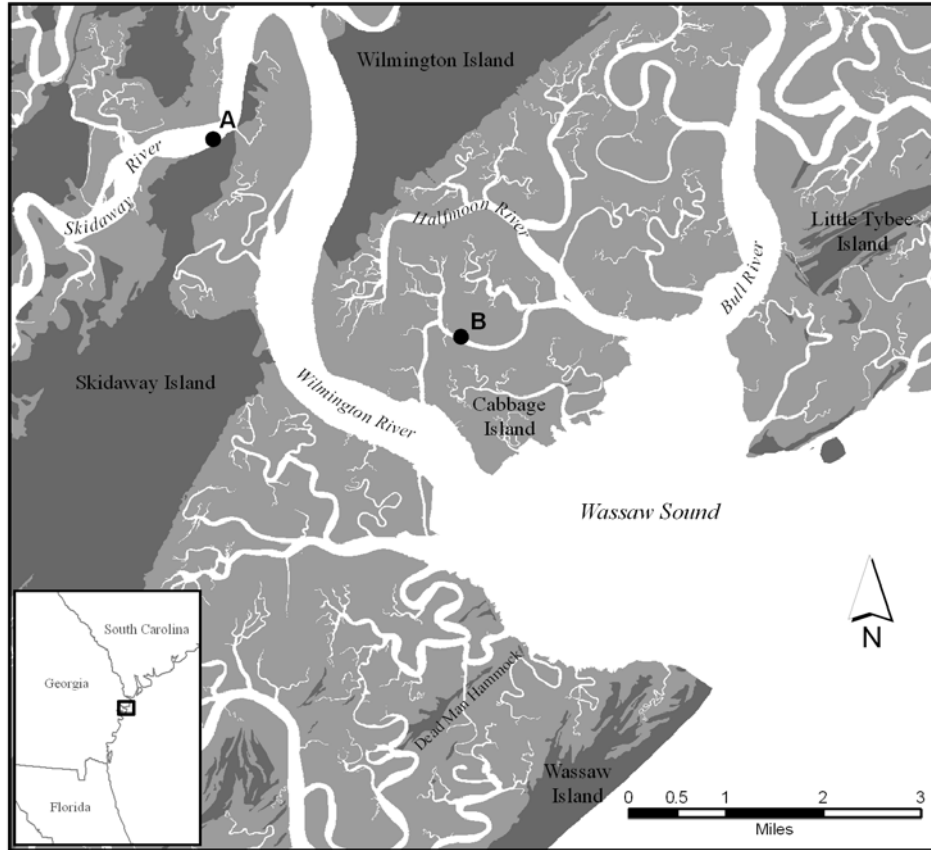


Figure 1: Location of spat collection in Tybee Cut (B) and oyster grow out at the Marine Extension Service dock on the Skidaway River (A), Skidaway Island, Georgia

Shell area covered by purple pigment and chalky deposits was determined by measuring the shell area covered by these artifacts and dividing them by the total area of the shell X 100.

Condition index was determined based on the methods of Lawrence and Scott (1982). Each oyster was measured for shell length and weighed (total weight, *g*). Subsequently the shell was opened, and the meat was placed on an aluminum foil dish and then dried in an oven at 67°C for forty-eight hours to obtain a dry weight. Empty oyster shells were also dried at room temperature

for twenty-four hours and subsequently re-weighed. The internal cavity volume was determined by subtracting the shell weight (g) from the total weight (meat and shell). The condition index was calculated by the following formula: (dry meat weight in grams) (100) / (internal cavity volume in centimeters cubed).

Ray's fluid thioglycollate medium assay (Ray 1952) was used to assay rectal tissue from oysters according to procedures outlined by Powell & Ellis (1998). Each sample was examined microscopically with a dissecting scope and an intensity index of *Perkinsus marinus* infection assigned according to Craig *et al.*'s (1989) semi-quantitative scale. Mean infection intensity indices were calculated for each treatment by averaging the intensity index score of each oyster including uninfected individuals (score = 0) at each site. Values range from a low of 0 to a high intensity level of 5.

Water temperature and salinity data were collected from the Skidaway River off the Marine Extension Service dock at 0800 hr each work day by using a hand-held thermometer and a refractometer.

One-way Analysis of Variance (ANOVA) and Tukey's Studentized Range Test ($\alpha = 0.05$) using SAS for PC (SAS Institute Inc., 1989) were carried out. All proportional data were arcsine transformed prior to statistical analysis (Sokal and Rohlf 1981).

Results

While oysters were suspended from the Marine Extension Services dock in the Skidaway River, the mean water temperature changed from 27.2°C in September 2006 to 12.2°C in February 2007 and rose to 23.9°C in May 2007. Salinity increased from 26.6 PSU in September to 30.6 PSU in November 2006 and decreased to 25.4 PSU in March 2007 before rising to 28.6 PSU in May 2007 (Figure 2).

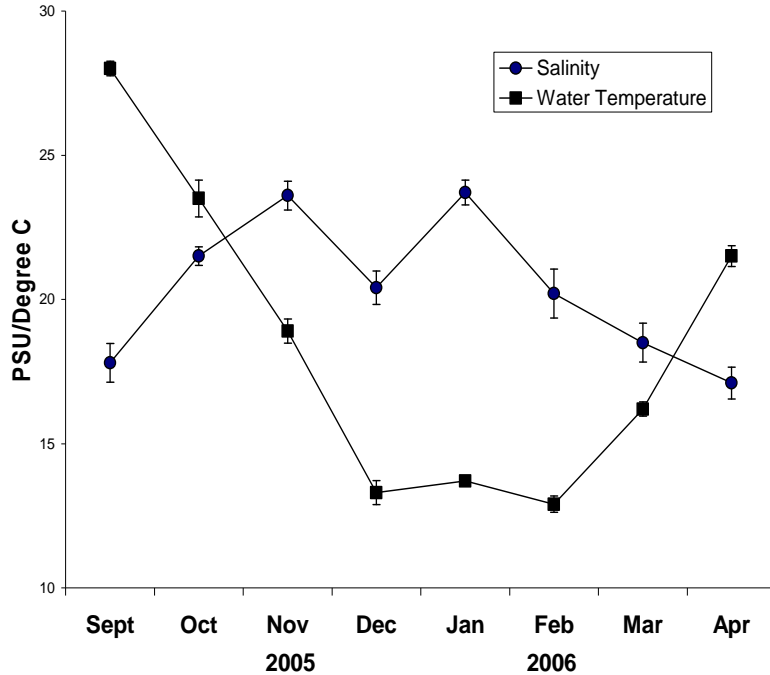


Figure 2: Water temperature ($^{\circ}\text{C} \pm \text{S.E.}$) and salinity ($\text{PSU} \pm \text{S.E.}$) taken from the Marine Extension Service dock on the Skidaway River, Skidaway Island, Georgia

Oysters in both treatments grew from a mean shell height of 17 mm to 38.4 ± 1.43 (S.E.) mm in floating pearl nets and to 38.0 ± 1.27 mm in hanging pearl nets (Figure 3). The size of oysters in floating and hanging nets were not significantly ($P=0.7432$) different. No significant difference in shell height occurred on any of the sampling dates from October 2006 to April 2007. Growth rates (Figure 4 and 5) reflected seasonal patterns. The lowest growth rate values occurred between January and February (0.0038 mm/day and 0.02 mm/day, respectively). No significant differences in shell height to shell width ratios (Figure 6) or shell height to shell length ratios (Figure 7) occurred in any sample period with the exception of the shell height to shell length ratio found in January 2007 ($P=0.0022$). The condition index of oysters in April was not significantly different ($P=0.3662$), nor was the percentage of chalky deposits ($P=0.4227$) nor the percentage of shell pigmentation ($P=0.7800$) in oysters (Table 1). No oyster mortality, *Perkinsus marinus* infection or mud blisters occurred in any oysters.

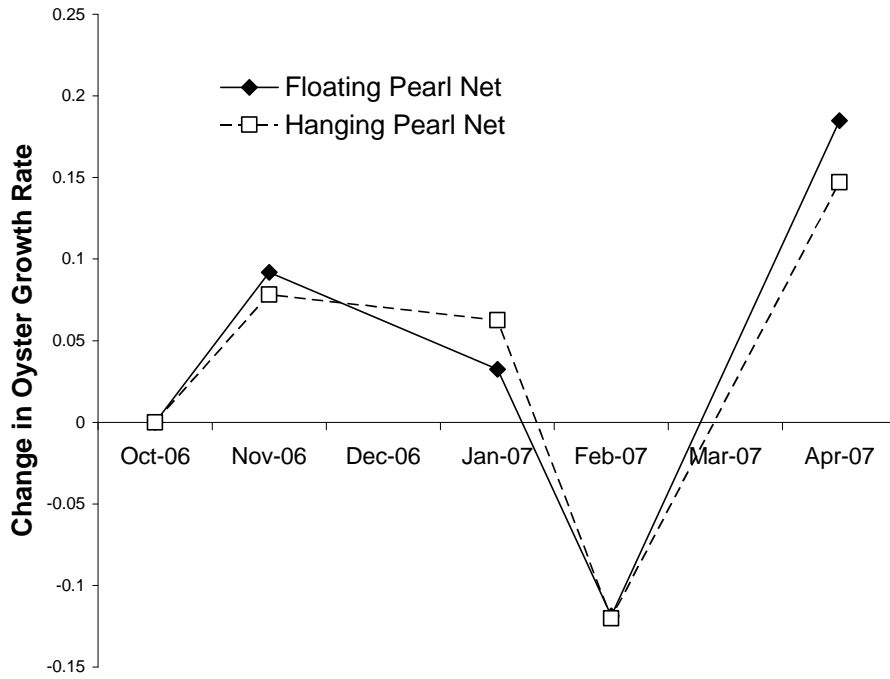


Figure 3: Growth of oysters placed in 9-mm mesh pearl nets floating or suspended in the Skidaway River, Georgia.

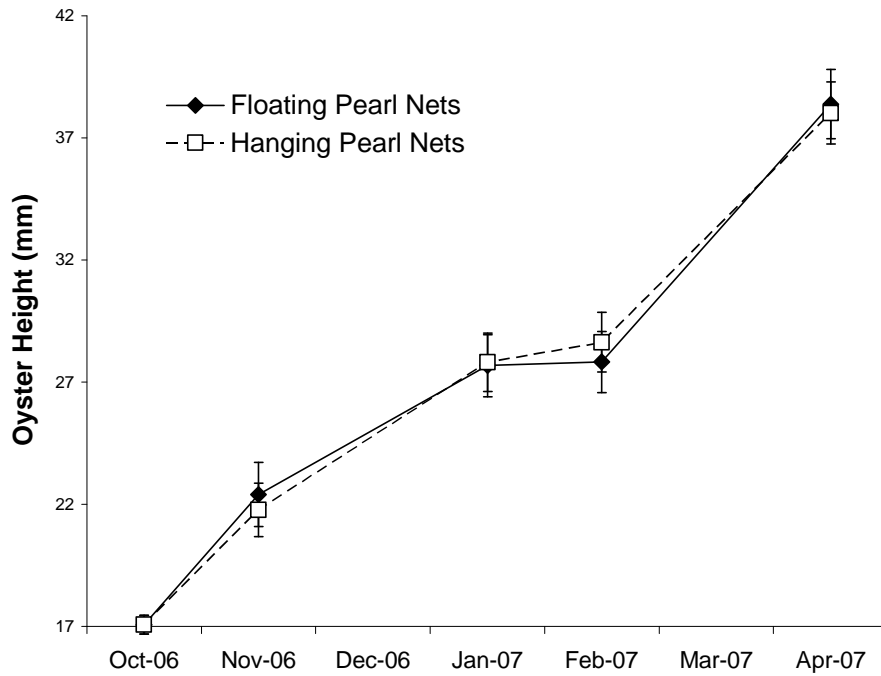


Figure 4: The rate of growth of oysters placed in hanging or floating 9-mm mesh pearl nets suspended in the Skidaway River, Georgia.

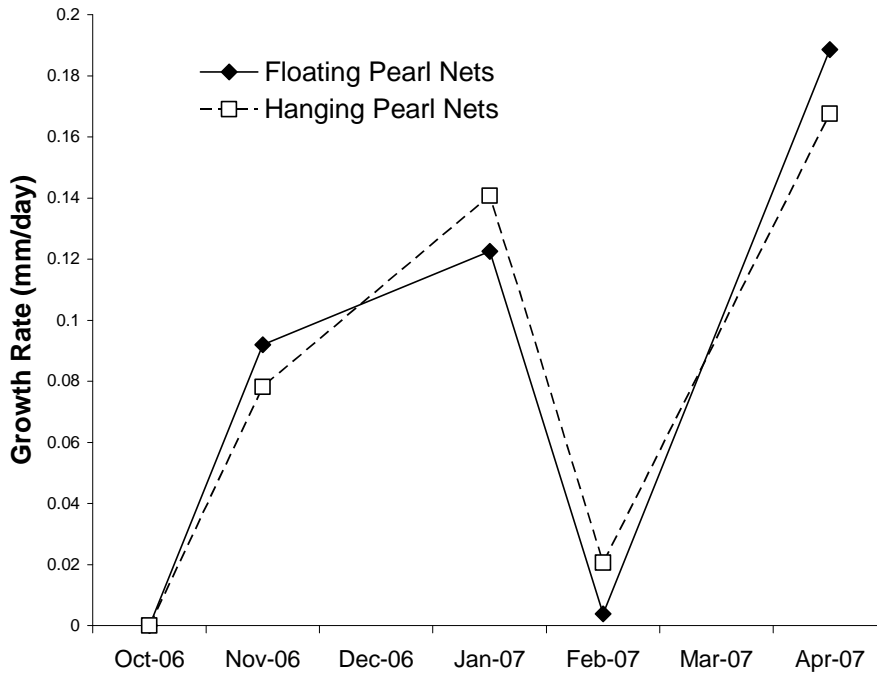


Figure 5: The rate of growth of oysters placed in hanging or floating 9-mm mesh pearl nets in the Skidaway River, Georgia.

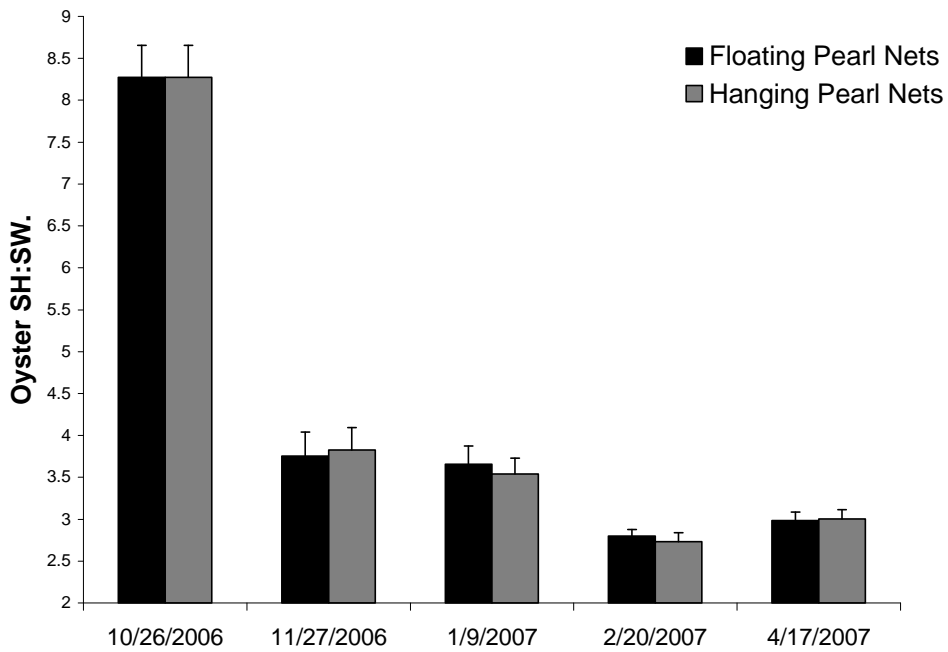


Figure 6: Comparison of oyster shell height to shell width ratio for oysters cultured in hanging or floating 9-mm mesh pearl nets in the Skidaway River, Georgia.

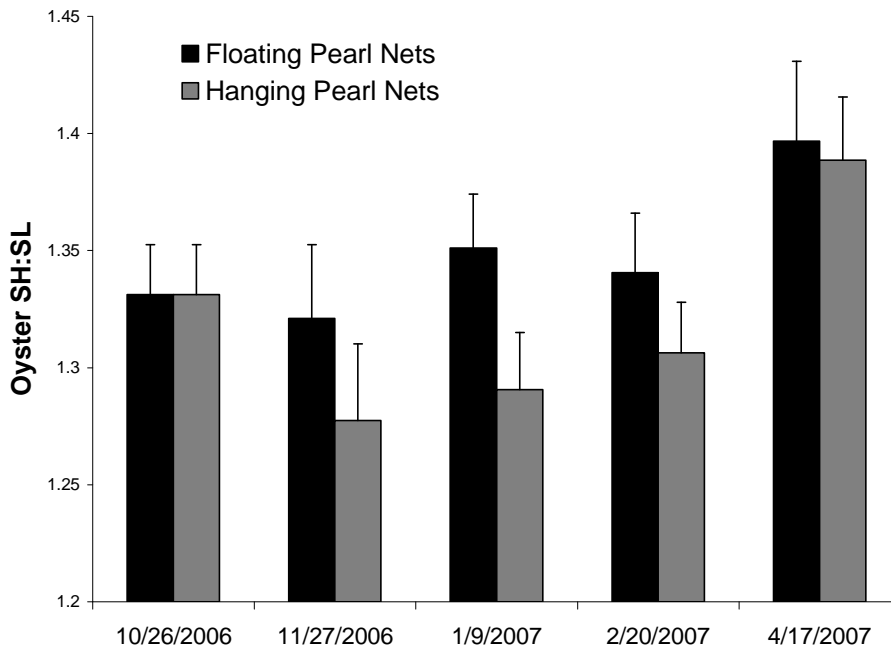


Figure 7: Comparison of oyster shell height to shell length ratio for oysters cultured in hanging or floating 9-mm mesh pearl nets in the Skidaway River, Georgia.

Table 1. Analysis of Variance results for condition index, percent chalky shell and percent pigmentation of shell between oysters grown in hanging and floating bags. Data are means \pm standard errors. Different letters indicate if significant differences in means occur.

	Condition Index (P=0.3662)	% Chalky (P=0.4227)	% Pigmentation (P=0.7800)
Hanging	16.0 \pm 0.34 a	5.2 \pm 0.92 a	15.3 \pm 2.60 a
Floating	16.4 \pm 0.26 a	4.4 \pm 0.86 a	16.7 \pm 2.80 a

Discussion

This study documents that once the tide floods there are no real differences between growing oysters in pearl nets suspended off-bottom, near the bottom or nets floating just below the surface. In both treatments, oysters were suspended in the intertidal zone for the same length of time. The only difference was that those suspended 0.5-m below the surface were compared to others that were suspended approximately 0.6-m above the bottom. The negligible difference in growth rates is probably due to the fact that Georgia estuarine waters are well-mixed and vertically homogeneous (Pritchard 1967, 1971), so that food is evenly distributed throughout the water column. Oysters are effective filter feeders. While heavy silt loads are known to hinder oyster growth (Loosanoff 1948, Loosanoff and Tommers 1948), oysters in this study were located well above the point where sediments might interfere with growth.

Oyster spat separated into singles (mean = 17 mm in shell height) and placed into pearl nets in October grew to a mean height of 38 mm by the following April. The legal size for harvesting oysters in Georgia is 76 mm (3 inches). Thus, oysters had not approached marketable size by spring prior to the start of the spawning season in May. Heavy oyster spat recruitment occurs from May through October (O'Beirn *et al.* 1995, 1996a, c, Thoresen *et al.* 2005, Manley *et al.* 2009). This prolonged recruitment event would foul the single oysters over spring, summer and early fall and turns them into clusters. This results in an inferior product when the oysters are ultimately harvested for the fall/winter sack trade market. The culture method did produce single oysters over fall and winter which could be used in the lucrative raw or cocktail markets if they had grown larger than 50 mm. Both treatments produced highly attractive oysters with a distinctly more ovate appearance (personal observation by senior author) as was reflected in the shell height to width and shell height to length ratios (Figure 6 and 7).

The live oyster cocktail market will purchase a 50-mm size oyster (Jacobsen, 2007). In this study only 9.4% and 11.5% of the oysters from the hanging and floating pearl nets, respectively, were greater than 50-mm in size. Thus, there is potential for using pearl nets to culture single oysters if growth rates can be increased or the season extended, and a cocktail oyster market is developed

for Georgia. It is also important to note that oyster spat used in this research were collected at the end of September. The collectors were only deployed late in August. Thus, the oysters were not able to utilize the full potential of the spring/summer growth season. If spat were instead collected in May from sticks deployed in April as opposed to August, the oysters used in this research may have had sufficient time to achieve 50-mm size in time for the winter market. Manley (2007) showed that oysters which recruited to sticks deployed in April in the intertidal zone of Stacy Creek, Duplin River, Sapelo Island were able to grow to a marketable size (76 mm) within 9-10 months. These oysters, which recruited in April, reached a mean size of 50 mm by November. It is feasible that spat collected in April/May and placed into growing areas with low-to-no natural oyster recruitment could grow to a 50-mm size in time for the fall/winter oyster markets in Georgia. O'Beirn *et al.* (1996c), Moroney and Walker (1998), and Manley *et al.* (2009) observed lower spat recruitment rates in the upper reaches of coastal creeks and rivers than in areas near the mouth or in the sound. In an ongoing seven-year oyster spat monitoring study in the Duplin River, Sapelo Island, little-to-no oyster settlement occurs at the headwater (Lumber Dock) site, while heavy spat fall occurs in the middle river (Jack Hammock) and near the mouth (Marsh Landing) (Walker unpublished data).

Oyster growth was appreciable in all months except February (Figure 5). The growth rate dropped to almost zero in February but increased again by March. This can be explained by two factors. First, water temperatures were at their lowest in February; shellfish growth decreases at lower water temperatures. Secondly, in Georgia January marks the start of gametogenesis (Heffernan *et al.* 1989, O'Beirn *et al.* 1996b). Consequently, for the next two-to-three months much of the oysters' energy is devoted to sexual maturation process at the expense of its growth rate.

Stocking density plays a major role in determining growth rate. In general, the higher the stocking density of oysters, the slower the mean growth. Oysters of 15-mm shell height were stocked at densities of 50, 100, and 200 oysters per 6-mm mesh pearl nets and suspended from rafts in either a sheltered creek or in the open sound in an earlier study in Georgia (Heffernan and Walker 1988). Oysters suspended from a raft in the sound in October grew to a mean size of 47.2 mm at 100 oysters per net to 42.8 mm in nets stocked at 300 by March 31. Oysters suspended from a raft in a sheltered creek ranged in size from 34.3 mm at the stocking density of 50 to 32.3

mm at 200 by the end of March. Oysters grown at 50 and 100 stocking densities were significantly larger than those in the higher stocking densities. An optimum stocking density of 100 oysters per net (equals 1,077 oysters m⁻²) was determined. Oysters in the open sound grew to a mean of 55.2 mm at a density of 50 and to 52.1 mm at 300 by June. Oysters from the sheltered creek grew to mean size of 50.3 mm at a stocking density of 50 to 45.6 mm at 200 oysters per net. The majority of the oysters from the raft in the sound and those at the stocking density of 50 in the creek would be marketable for the cocktail trade by the end of May. Adams *et al.* (1994) found no significant differences in oyster size when grown in mesh bags at densities of 200, 500 and 1,000 m⁻² in Georgia. It is possible that oysters grown in the present study could have achieved a greater size if grown at a lower density of 100 oysters per net.

Intertidal exposure time can also affect oyster growth. Greater exposure reduces the available feeding time for filter feeders. Nets were positioned so that they were equal to where naturally occurring oysters inhabit the intertidal zone (i.e., at approximately two-hours above-mean-low water mark). Thus, they are out of the water for three-to-four hours per low tide. Thus, six-to-eight hours of feeding time is lost per day. For *Mercenaria mercenaria* (Linné, 1758) and *Spisula solidissima* (Dillwyn, 1817) clams cultured at various intertidal heights in Georgia, growth was significantly reduced with aerial exposure times (Walker and Heffernan 1990). Oysters from the earlier study in Georgia (Heffernan and Walker 1988) were suspended below the surface from a floating raft and thus were able to feed for longer periods of time than oysters in this study. This could account for their greater size. Oysters should be suspended lower in the intertidal zone to increase growth; however, they should not be suspended in the subtidal zone. Some intertidal exposure time is necessary to control fouling organisms (hydroids, bryozoans, sea squirts, sponges, etc.) and reduce cleaning costs of nets and possibly reduce oyster mortality rates.

Placing bags subtidally or suspending them from rafts so that they are constantly in water increases growth only if the nets are kept clean. Walker (1998) found that pearl nets containing blood arks, *Anadara ovalis* (Bruguère, 1789), suspended from the dock at the same site of this study had to be cleaned of sea squirts, *Molgula manhattensis* (DeKay, 1843), biweekly especially during the summer. Labor costs involved in constantly cleaning the oysters and pearl nets prevent this subtidal

culture from being profitable. Shellfish and their containers need to have some tidal exposure each day in order to control the massive fouling of nets by marine organisms. Thus, a farmer needs to sacrifice some growth to eliminate the labor costs of constantly cleaning the pearl nets. Pearl nets could be placed lower in the intertidal zone to decrease exposure time and thus increase feeding opportunity.

The prevalence of the oyster parasite, *Perkinsus marinus*, in Georgia oysters occasionally leads to epizootic events (Lewis *et al.* 1992). *P. marinus* generally infects the oyster in the first year of life, but mortalities due to the disease occur after the second summer (Andrews 1988). Oysters in this study were not infected with *P. marinus*, which is surprising since the disease is highly prevalent both where the seed were collected and where they were cultured in pearl nets (Power *et al.* 2006). A prolonged drought in Georgia ended in spring 2005, and river salinity conditions were normal during 2006. It is possible that the disease was less prevalent in this study because river salinity levels were lower than normal. Low salinity conditions are known to decrease the prevalence and intensity of *P. marinus* in oysters (Andrews 1988).

Potential exists for developing an oyster aquaculture industry in Georgia. The best method involves gathering oyster spat from natural sets and separating them into singles. Single oysters can be placed into pearl nets or mesh bags and grown to a 50-mm size for sale in the raw cocktail market. Oyster shell shape and appearance are becoming more important factors than oyster size. There is a rapidly growing market for smaller sized ovate and deeply cupped oysters [e.g., the Kumamoto oyster *Crassostrea sikamea* (Amemiya 1928) is commonly sold at 38 mm to 50 mm (1.5-2 inches) in shell height (Brake *et al.* 2003; Jacobsen 2007) on the west coast of the U.S.]. Small-sized gemlike oysters are usually preferred by first-time oyster eaters and are increasingly common in raw oyster bars (Jacobsen 2007). This shift towards smaller oysters is very beneficial for Georgia's oyster industry, since a nicely shaped smaller oyster can be grown here in less than a year. Less than 5.2% of oysters grown in this study had chalky shells and less than 16.7% had the purple shell pigmentation which reduces their marketability. Oysters from the pearl nets had a high condition index in April, which is indicative of excellent oyster meat quality. The high condition index is related to the reproductive stage of oysters in Georgia as they are fully ripe at this time prior to the

initiation of spawning in late April to early May. After the release of gametes during spawning, the condition index of oysters rapidly declines. With the tremendous productivity of its estuaries, Georgia has the potential to dominate the oyster industry as it once did in the early 1900's (Harris 1980). To accomplish this, we must change the legal-minimal harvest size of oysters. Lowering the minimal legal size to at least 50.8 mm (2 inches) would help the industry.

Minimal-legal-size limits are imposed to protect the resource by allowing individuals in the population to reproduce at least once prior to harvest. A legal size of 76 mm (3 inches) is currently in effect in Georgia. Oysters in Georgia, however, do not need protection since vast areas of oyster reefs are closed to commercial fishing, and there is an overabundance of oyster spat in Georgia's waters (O'Beirn *et al.* 1995, 1996a,c, 1998, Thoresen *et al.* 2005, Manley 2007, Manley *et al.* 2008, 2009), oyster spawn from April/May until October (Heffernan *et al.* 1989). Oysters spawned in April/May become sexually mature within two-to-three months at a size of approximately 40 mm and contribute to fall recruitment (O'Beirn *et al.* 1996). A 76-mm legal size for the commercial harvesting of oysters in Georgia makes little sense.

Literature Cited

- Adams, P., R.L. Walker, and P.B. Heffernan. 1994. The effects of stocking density, bag mesh size, and bottom sediment on the growth and survival of the eastern oyster, *Crassostrea virginica*, with emphasis on controlling oyster spat fouling. *Journal of Applied Aquaculture* 4:25-44.
- Andrews, J.D. 1988. Epizootiology of the disease caused by the oyster pathogen *Perkinsus marinus* and its effects on the oyster industry. *American Fisheries Society Special Publication* 18:47-63.
- Brake, J., F. Evans, and C Langdon. 2003. Is beauty in the eye of the beholder? Development of a simple method to describe desirable shell shape for the pacific oyster industry. *Journal of Shellfish Research* 22(3): 767-771.
- Castagna, M. M.C. Gibbons and K. Kurkowski. 1996. Culture Application. In: Kennedy, V., R.I.E. Newell and A.F. Eble (eds). *The Eastern Oyster Crassostrea virginica*. A Maryland Sea Grant Book, College Park, MD pp. 675-690.

- Carriker, M.R. 1996. The Shell and Ligament. In: Kennedy, V., R.I.E. Newell and A.F. Eble (eds).
The Eastern Oyster *Crassostrea virginica*. A Maryland Sea Grant Book, College Park, MD pp.
75-168.
- Craig, M.A., E.N. Powell, R.R. Fay, and J.M. Brooks. 1989. Distribution of *Perkinsus marinus* in Gulf
coast oyster populations. *Estuaries* 12:82-91.
- Harris, D.C. 1980. Survey of the intertidal and subtidal oyster resources. Georgia Department of
Natural Resources, Coastal Resources Division, Brunswick. 44 pp.
- Heffernan, P.B. and R.L. Walker. 1988. Preliminary observations on oyster pearl net cultivation in
coastal Georgia. *Northeast Gulf Science* 10:33-43.
- Heffernan, P.B., R.L. Walker and J.L. Carr. 1989. Gametogenic cycles of three marine bivalves in
Wassaw Sound, Georgia II *Crassostrea virginica* (Gmelin 1791). *Journal of Shellfish Research*
8:61-70.
- Jacobsen, R. 2007. A geography of oysters: the connoisseur's guide to oyster eating in North
America. Bloomsbury, USA, 304 pp.
- Lawrence, D.R. and G.I. Scott. 1982. The determination and use of condition index of oysters.
Estuaries 5:23-27
- Lewis, E.J., F.G. Kern, A. Rosenfield, S.A. Stevens, R.L. Walker, and P.B. Heffernan. 1992. Lethal
parasites in oysters from coastal Georgia, with discussion of disease and management
implications. *Marine Fisheries Review* 54:1-6.
- Loosanoff, V.L. 1948. Effects of turbidity on feeding of oysters. *Proc. Natl. Shellfisheries Assoc.*
1947:40-44.
- Loosanoff, V.L. and F.D. Tommers. 1948. Effects of suspended silt and other substrates on rate of
feeding of oysters. *Science* 107:69-70.
- Manley, J. 2007. Oyster reef restoration for developing essential fish habitat in coastal Georgia.
Savannah State University, Masters Thesis
- Manley, J., A. Power and R.L. Walker. 2008. Wild eastern oyster *Crassostrea virginica* spat collection
for grow-out in Georgia. *Occasional Papers of the University of Georgia Marine Extension
Service*, Vol. 2, 16 pp.

- Manley, J. A. Power and R.L. Walker. 2009. Patterns of eastern oyster, *Crassostrea virginica* (Gmelin, 1791), recruitment in Sapelo Sound, Georgia: Implications for commercial oyster culture. Occasional Papers of the University of Georgia Marine Extension Service, Vol. 3, 14 pp.
- Moroney, D. and R.L. Walker. 1998. Recruitment patterns of the eastern oyster, *Crassostrea virginica*, along a creek gradient in House Creek, Little Tybee Island, Georgia. *Journal of Shellfish Research* 17:1085-1091.
- O'Beirn, F.X., R.L. Walker, M.L. Jansen and P.B. Heffernan. 1998. Microgeographic variation of gametogenesis and sex ratios in *Crassostrea virginica*. *Transactions of the American Fisheries Society* 127: 298-308.
- O'Beirn, F.X., R.L. Walker and M.L. Jansen. 1997. Reproductive biology and parasite (*Perkinsus marinus*) prevalence in the eastern oyster, *Crassostrea virginica* within a Georgia tidal river. *Journal of Elisha Mitchell Scientific Society* 113: 22-36.
- O'Beirn, F.X., P.B. Heffernan and R.L. Walker. 1996a. Recruitment of the eastern oysters, *Crassostrea virginica*, in coastal Georgia: Patterns and recommendations. *North American Journal of Fisheries Management* 16: 413-426.
- O'Beirn, F., P.B. Heffernan, R.L. Walker and M.L. Jansen. 1996b. Young-of-the-year oyster, *Crassostrea virginica*, reproduction in coastal Georgia. *Estuaries* 19:651-658.
- O'Beirn, F.X. R.L. Walker, M.L. Jansen and C.R. Spruck. 1996c. Recruitment, gametogenesis and parasite (*Perkinsus marinus*) prevalence in the eastern oyster, *Crassostrea virginica*, within Sapelo Island National Estuarine Research Reserve. University of Georgia, School of Marine Programs, Marine Technical Report 96-1, Athens
- O'Beirn, F., R.B. Heffernan and R.L. Walker. 1995. Preliminary recruitment studies of the eastern oyster, *Crassostrea virginica*, and their potential applications, in coastal Georgia. *Aquaculture* 136:231-242.
- Powell, E.N. and M.S. Ellis. 1998. "*Perkinsus marinus* assay." In: Sampling and Analytical methods of the National Status and Trends Program Mussel Watch Project: 1993-1996 Update. NOAA Technical Memorandum NOS ORCA 130. G.G. Lauenstein and A.Y. Canstilla (eds). Pp 228-233.

- Power, A., B. McCrickard, M. Mitchell, E. Covington, M. Sweeney-Reeves, K. Payne and R.L. Walker. 2006. *Perkinsus marinus* in coastal Georgia, USA, following a prolonged drought. *Diseases of Aquatic Organisms* 73:151-158.
- Prichard, D.W. 1967. Observations of circulation patterns in coastal plain estuaries. In: G.H Lauff (ed.), *Estuaries*. Am. Assoc. Adv. Sci. Publ. 83.
- Pritchard, D.W. 1971. Estuarine hydrography. In: J.R. Schubel (ed.), *The Estuarine Environment, Estuaries, and Estuarine Sedimentation*. Am. Geol. Inst. Short course lecture notes, Washington D.C.
- Ray, S.M. 1952. A culture technique for the diagnosis of infections with *Dermocystidium marinum*, Mackin Owen and Collier, in oysters. *Science* 166:360-361
- SAS Institute Inc. 1989. *SAS User's Guide: Statistics, version 6*. Cary, North Carolina: SAS Institute
- Sokal, R.R. and F.J. Rohlf. 1981. *Biometry*, second edition. W.H. Freeman and Company, New York
- Thoresen, M., M. Alber and R.L. Walker. 2005. Trends in recruitment and *Perkinsus marinus* parasitism in the eastern oyster, *Crassostrea virginica*, within Sapelo Island National Estuarine Research Reserve (SINERR). University of Georgia, School of Marine Programs, Marine Technical Report 05-1, Athens
- Walker, R.L. 1998. Growth and survival of the blood ark, *Anadara ovalis* (Bruguère, 1789), in coastal Georgia. *Georgia Journal of Science* 56:192-205.
- Walker, R.L. and P.B. Heffernan. 1990. Intertidal growth and survival of northern quahogs, *Mercenaria mercenaria* (Linnaeus, 1758), and Atlantic surf clams, *Spisula solidissima* (Dillwyn, 1817), in Georgia. *Journal of the World Aquaculture Society* 21:307-313.