CULTURE OF SINGLE EASTERN OYSTERS, *Crassostrea virginica* (GMELIN, 1791), IN THE INTERTIDAL ZONE OF A TIDAL CREEK IN COASTAL GEORGIA, USA

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Abstract

The productive subtropical waters of the southeastern United States support rapid growth rates for commercial bivalve species. In this region, the Eastern oyster *Crassastrea virginica*, suffers low intensities of disease, and natural spatfall is abundant. Unique challenges associated with an intertidal distribution and heavy fouling and sedimentation rates, however, have thus far precluded the development of oyster aquaculture operations in Georgia. As consumer demand for seafood rises, there is mounting pressure and tremendous potential to diversify successful clam farms through the development of unique grow-out techniques for oysters. Growth, survival, and spat fouling for the species were documented in mesh bags that were placed 1 m off the bottom at five different intertidal heights ranging from -0.5 m to 1.5 m from mean low water. The present findings indicate that oysters should not be cultured in the particular intertidal zone in which they naturally occur in Georgia, but instead can be grown to market size (76 mm) in approximately one year and kept as single oysters by placing near the spring low water mark in an off bottom cage. These findings will significantly contribute to future endeavors to establish an environmentally-friendly and sustainable oyster aquaculture industry in Georgia.

Introduction

Globally, 97% of oysters consumed are farmed and comprise a \$3.1 billion industry; however, the United States only comprises about 2% of this production (FAO Fishery Statistics 2008). The Eastern oyster, *Crassostrea virginica* (Gmelin 1791) is the commercial oyster species of importance on the East and Gulf coasts of the United States (Bahr and Lanier 1981; Carriker and Gaffney 1996). Aquaculture techniques vary geographically, representing regional differences in oyster biology and ecology and social, economic and environmental variables throughout this range (Galtsoff 1964; Bahr and Lanier 1981; Carriker and Gaffney 1996; White and Wilson 1996; MacKenzie, 1996; Kennedy et al. 1996; Kennedy and Sanford 1999). Each region has its own particular set of production limitations; the Chesapeake Bay industry has been significantly impacted by disease and spat availability, whereas the Gulf of Mexico was crippled by hurricane Katrina in 2005 and the British Petroleum oil spill in 2010.

In Georgia, oyster aquaculture has been limited to directly planting cultch materials in the mid intertidal zone where the species predominantly occurs. Food limitations set a maximum intertidal height of approximately 1.5 m above mean low water, and sediment encroachment and heavy fouling limit the lower intertidal zone (Bahr 1974; Bahr and Lanier 1981; Adams et al. 1994; Moroney and Walker 1999). Oyster spawning is protracted (April through October) with peak settlement rates generally ranging between 70 - 300 oysters/0.01 m² but sometimes reaching above 2,000 oysters/0.01 m² (Heffernan et al. 1989; O'Beirn et al. 1994, 1995, 1996a, b; Thoreson et al. 2005). This prolific reproductive capability and the limited habitat niche produces crowded reefs comprised of long irregular shaped oysters with a high shell ratio to meat. These "coon" oysters are not deemed suitable in appearance for the lucrative half-shell trade but were once a desirable shucked resource for canneries (Oemler 1894; Burrell 1997, 2003; Kirby 2004). Today's markets are limited and most oysters are consumed at local "roasts" where the clusters are steamed over a fire and then hand shucked at communal outdoor dining tables. In 2009, 8,626 kg of oysters worth \$81,265 were commercially harvested (Commercial Data Landings Georgia Department of Natural Resources). The fishery is regulated through a 76 mm legal size and by restricting harvesting to handpicking during daylight hours in the fall, winter, and early spring months.

The Georgia clam aquaculture industry currently ranks third in value after the blue crab and shrimp fishery. As traditional fisheries continue to collapse, new shellfish harvesting areas are being classified to meet an increasing interest from displaced fishermen to enter clam aquaculture. Demonstration of successful culture techniques for single oysters for the half shell trade could be the stimulus for the diversification and enhancement of shellfish farming. The challenges are not restricted to an overcatch of spat. Other problems include heavy fouling by sea squirts and sponge borers (e.g. *Cliona* sp.) and intense sedimentation rates that can suffocate shellfish beds and make maintenance and harvesting operations labor intensive. On the other hand, the pathogen Perkinsus marinus which plagues more northern populations does not present as significant a threat (Reece et al. 2001; Power et al. 2006; Manley et al. 2009b). The productive, subtropical waters support high growth rates often reducing the grow-out of commercial species by more than half that required in more northern waters (Heffernan and Walker 1988). A recent oyster restoration research project using commercial spat sticks indicated potential to recruit and grow oysters to a marketable size prior to the succeeding spawning season (Manley 2007). The state of Georgia also has ample marketing potential for home-grown oysters. The 28-county area of metropolitan Atlanta has a population of more than 4.7 million. Clearly, research into different cultivation techniques is warranted, the benefits of which could extend into South Carolina and northeastern Florida which share the same physical, chemical and biological parameters that control the oyster species' intertidal distribution.

Materials and Methods

The project site selected was a stretch of intertidal bank devoid of oyster reef, near the Ridge River mouth, a tidal creek near Creighton Island in McIntosh County, Georgia (Figure 1). Naturally occurring oyster beds nearby were identified and the range between the highest and lowest intertidal heights for the beds vertical distribution was transferred and marked at the study site using PVC poles. The upper and lower limits of this natural distribution were labeled levels four and two, respectively. The mid point of the vertical distance between these levels was called level three. The vertical distance from three to the upper and lower limit was then added to these levels to result in levels five and one, marked above and below the natural range, respectively. Fifteen replicate schedule 40 PVC frames (50.8 mm external diameter) measuring 1 m square in length and width and 1.5 m in height were constructed. A cross piece was provided on the top to support a $1m^2$ mesh bag. Each vertical leg was 1.5 m long and two opposite sides were connected with crosspieces 0.5 m from the bottom to allow the frames to sink and anchor themselves into the mud, but also to maintain the bags 1 m above the substrate. Three frames were arranged with their tops in line with each of the five intertidal levels and spaced at least 1 m apart from each other both horizontally and vertically. Mesh bags measuring 1 m² were prepared using 15.87 mm stretch sized heavy duty high density polyethylene diagonal netting. The bag seams were sewn using 4.76 mm diameter polypropylene rope. The approximate location of the mesh bags in relation to mean low water was determined on a calm weather day with a zero meter low tidal height by measuring the vertical distances in meters from the water line at dead low to the top of each PVC frame at each respective level. The height at level two approximated mean low water, and there was approximately 0.5 m between each successive level.

Oyster seed was purchased from a South Carolina hatchery in January 2009. One hundred individual oysters from this hatchery shipment were randomly selected and measured for length, width, and height with Vernier calipers (to nearest 0.1 mm) and weight on an electronic balance (to nearest 0.1 g). The initial mean sizes of oysters purchased from the hatchery were as follows: shell length (mm) 19.43 ± 0.30 ; width (mm) 16.49 ± 0.64 ; height (mm) 5.88 ± 0.15 ; and weight (g) 1.00 ± 0.04 . Each intertidal height treatment mesh bag received 1,750 seeds. Every two weeks the frames and bags were inspected at low tide to remove fouling organisms and check for damage and predators. Every two months each bag was opened and 35 oysters were randomly selected. Their lengths were determined and the number of living versus dead noted to provide a measure of mortality rates. The living oysters were placed back into the bags. At the termination of the experiment, each replicate was retrieved and the lengths, widths and weights of 100 randomly selected oysters per bag were obtained as well as a count of living and dead oysters and the number of of oysters that remained single versus those that had spat attached. ANOVAs were used to determine differences in growth (length, width, height, and weight), mortality, and percent single across intertidal height treatments.



Figure 1. The project study site on the Ridge River Mouth near the Sapelo River, McIntosh County, Georgia.

Results

The intertidal treatments spanned a vertical intertidal elevation of approximately 2 m. The lowest level was situated approximately 0.5 m below mean low water and was exposed only on the lowest spring tides, and level 5 was located in the zone occupied by Spartina alterniflora (Loisel). A biweekly cleaning schedule was sufficient to maintain the cages free from fouling organisms and simply involved brushing the cages with a stiff brush. Figure two presents the bimonthly mean shell lengths using all replicates for each intertidal level from January 2009 through February 2010. Only two intertidal levels produced oysters with a mean shell length greater than market size (76 mm), the mid and lowest levels, three (76.73 \pm 1.05 mm) and one (78.62 \pm 0.61 mm), respectively. For the other treatments the growth rate was inversely proportional to the intertidal height, with level five generating the lowest sizes (37.24 \pm 0.50 mm). The lowest level, one, also displayed a linear constant growth curve, with oysters adding approximately 5 mm of length per month, and described by the equation: length = 4.61(# months) + 21.06, $R^2 = 0.99$. Most other treatments had an exponential growth phase during the summer which tapered off into the fall and winter months. Single factor ANOVA tests detected significant differences (p < 0.001) between the mean scores for shell length (F = 379.66), width (F = 387.59), height (F = 181.98) and total wet weight (F = 294.51) for the three replicates combined for each intertidal level. Tukey's HSD confirmed significant differences at p < 0.01 for all level mean combinations, but did not detect a significant difference between lengths for levels one and three nor for heights between two and three. At the termination of the experiment in February 2010, each size parameter was consistently smaller as the intertidal height increased with the one exception of shell length which was significantly greater in level three than in level two (Figures 3, 5).

Mortality percentages were square root transformed and then analyzed with ANOVAs. When all replicates for each intertidal treatment and each sampling period were combined, the only significant difference detected was between the lowest level one, and the highest level five (F = 3.68, p < 0.05). Generally the lower level had the least mortality rate and the highest intertidal level had the greatest mortality (Figures 4, 5). When each sampling period was treated independently, there were no significant (p < 0.05) differences in mortality rates between treatments for April (F = 3.03, p = 0.07), June (F = 2.11 p = 0.15), August (F = 0.71, p = 0.60) or November 2009 (F = 3.45, p = 0.05). In February 2010, however, there were significant intertidal differences (p < 0.001) in mortality (F = 14.06, p = 0.0004). Tukey's HSD test revealed significant differences at p < 0.05 between levels two and three, and four and five and at p < 0.01 between levels one and two, one and five, and three and five. Throughout the study the highest mortality percentages were found in each intertidal level in November 2009, with a replicate in level two peaking at 33.65 %. At the termination of the experiment, the mean mortality rates ranged from 4.03 % at level one to 19.67 % at level five. The rates at the other levels in decreasing order were 18.33 % at 2, 9.30 % at four and 6.33 % at level three.

The percentage of oysters remaining single after the growing period was also square root transformed and revealed significant differences using an ANOVA test (F = 9.13, p < 0.01). Oysters from the lower level one and the upper level five were the only ones in which all oysters remained single (Figure 5). Between 34 and 82 % of the oysters grown between levels two and four, the natural oyster distribution range attracted spat and became dense clusters. It should be noted that 76 to 83% of clustered oysters were successfully broken up to provide an oyster suitable for the roast market. The mid intertidal level, three, had the least amount of single oysters with values for replicates ranging from 26 to 31%. Tukeys's HSD revealed significant differences at p < 0.05 between levels one and two, and between levels two and five. Greater significance (p < 0.01) was described between levels one and three, and five and three.



Figure 2. Bimonthly mean shell lengths (mm) for oysters from three combined replicates at five different intertidal levels (1 = -0.5 m < MLW, 5 = 1.5 m > MLW) grown in the Ridge River, McIntosh County Georgia between January 2009 and February 2010.



Figure 3. The final mean (\pm standard error) total wet weight (g), shell width (mm) and shell height (mm) for oysters in each replicate that were grown at five different intertidal levels (1 = 0.5 m below MLW, 5 = 1.5 m above MLW) in the Ridge River, McIntosh County Georgia between January 2009 and February 2010.



Figure 4. Bimonthly mean mortality rates (%) for oysters from three combined replicates at five different intertidal levels (1 = 0.5 m below MLW, 5 = 1.5 m above MLW) grown in the Ridge River, McIntosh County Georgia between January 2009 and February 2010.



Figure 5. The final mean shell length (mm \pm standard error), the percentage of oysters remaining as singles, and the mortality rates (%) for oysters in each replicate that were grown at five different intertidal levels (1 = 0.5 m below MLW, 5 = 1.5 m above MLW) in the Ridge River, McIntosh County Georgia between January 2009 and February 2010.

Discussion

To date, Georgia's commercial oyster aquaculture has been limited to placing cultch shell directly onto the substrate or breaking up naturally occurring reefs to take advantage of wild sets. In order to alleviate the challenges imposed by heavy sedimentation and predation rates, and to maximize growth rates, future oyster aquaculture efforts will need to move away from bottom culture towards growing seed in off-bottom systems. In order to produce single restaurant quality oysters, these off-bottom techniques will need to consider vertical zonation patterns associated with intertidal fouling rates, and the timing and size of seed deployment. The limited availability of hatchery produced seed should not negatively impact the development of aquaculture efforts. Many of the top oyster producing nations successfully collects natural spatfall using varied cultch materials (Matthiessen 2001). Treatments using PVC sticks coated in cement slurry have already proven particularly effective at cheaply recruiting high densities of spat and facilitating the easy removal of intact seed in Georgia's waters (Manley et al. 2009a).

Off bottom growout systems have been previously investigated in coastal Georgia's waters, however none achieved the success observed with the current trials at the lowest intertidal level. Heffernan and Walker (1988) produced market sized oysters in 18 months in suspended pearl nets but suffered intense fouling and high mortality rates. Treatments were only 15 cm off the bottom substrate though which may have provided insufficient clearance from the sediment water interface. Manley et al. (2009b) documented good growth and survival in subtidal pearl nets but determined that fouling would be preventative for commercialization. Adams et al. (1994) and Moroney and Walker (1999) investigated on and off-bottom techniques and determined that off-bottom culture resulted in the greatest growth and survival rates, but unfortunately also the greatest spat fouling rates. Adams et al. (1994) determined higher densities could have an effect on reducing the fouling rates and Moroney and Walker (1998) and Manley et al. (2009c) both documented lower spat recruitment rates in more sheltered environments further up tidal creeks. Manley (2007) produced legal sized oysters in less than one year by allowing recruited oysters to growout on French Spat collectors. This was a significant result as it meant ovsters could reach market size prior to the commencement of the second spawning season and therefore remain single. Commercial problems with this technique, however, were the high costs of the sticks and the high percentages of oysters and sticks destroyed while attempting to remove and separate them into singles (Manley et al. 2009b). Therefore, the recommendations to date were to grow oysters off the bottom when possible but to transfer to the bottom, stock in high density, or transplant far up tidal creeks during the spawning season.

The current research indicates that a trade off between survival and growth to minimize spat fouling may not be necessary. Oysters at the three middle levels which represent the natural intertidal distribution for oysters in Georgia had good growth, but became so heavily fouled with oyster spat that by the end of the experiment, it was almost impossible to tell the original oyster from the clusters formed by newly recruited spat. However, moving beyond the natural distribution range, a zone approximately 0.5 m below mean low water has proved to be optimal, producing unfouled single market sized oysters with the largest widths, heights, lengths and weights. Growing rates were consistent throughout the year (~ 5 mm per month) and oysters grown here had the lowest mortality rates. Fouling of the mesh bags was also adequately maintained with a biweekly cleaning schedule. Wild oyster seed collected during the spawning season can be grown to an approximate 20 mm size in 2- 3 months on sticks (Manley 2007). This seed could then be grown to market size in approximately one year using the system described by the current research. The production of a market size single oyster in such a time period is significantly faster than occurring anywhere on the eastern seaboard and presents enormous aquaculture potential.

As the traditional commercial fisheries in Georgia continue to decline, aquaculture is seen as a method to enhance the economic viability of many small rural coastal Georgia communities. With the expansion of clam aquaculture in Georgia, shellfish growers wish to diversify into other possible opportunities in aquaculture. This research presents opportunity but also identifies further needs starting with the reproduction of these trials at another location to determine if the results were site or year specific. Additional trials should determine if the cages perform as well when placed less than 1 m off the substrate where they would provide less of an impediment to navigation and present less potential user conflicts. Commercial off-bottom aquaculture operations may also prove objectionable from an aesthetic point of view, but public outreach could be effective at alleviating some of these concerns.

The quality and appearance of the single oysters produced should be assessed for the halfshell trade. Marketing efforts should also evaluate demand for a smaller sized "boutique" oyster. The 76 mm legal size of Georgia's oysters is not biologically warranted. Legal sizes are most frequently established to ensure resource sustainability by allowing individuals to attain the size and age at first maturity to allow them to spawn and contribute to commercial stocks before being harvested. In Georgia, oysters sexually mature and spawn in their first year (O'Beirn et al. 1996b). A smaller size limit would reduce the growing time even more and would also reduce the amount of culled oysters wasted when clumps are broken up for the roast markets. Aquaculture trials may also be warranted in the subtidal zone. It is not known why oysters do not naturally occur as subtidal reefs in Georgia, but it has been theorized that post settlement process affect the survival rates of spat in this environment (Kenny et al. 1990; O'Beirn et al. 1996a). Finally, adequate permitting policies need to be established to facilitate the commercial application of new off-bottom techniques. The growth and expansion of the industry will also require permitting amendments to assess and authorize mechanized systems on shellfish leases.

Literature Cited

- Adams M.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.
- Bahr, L.M., Jr. 1974. Aspects of the structure and function of the intertidal oyster ref community in Georgia. Dissertation, University of Georgia, Athens, 149 pp.
- Bahr, L.N. and W.P. Lanier. 1981. The ecology of intertidal oyster reefs of the south Atlantic Coast:A community profile. U.S. Fish and Wildlife Service, Office of Biological Services, WashingtonD.C. FWS/OBS-81/15. 105 pp.
- Burrell, V.G. 1997. Molluscan shellfisheries of the South Atlantic region of the United States. In: Mackenzie, C.L., V.G. Burrell, A. Rosenfield, and W.C. Hobart, (eds.). 1997. The history, present condition and future of the molluscan fisheries of North and Central America and Europe, Volume 1, Atlantic and Gulf Coasts. U.S. Department of Commerce, NOAA Tech. Rep. 127, 234pp.
- Burrell, V.G., Jr. 2003. South Carolina Oyster Industry: A history. V.G. Burrell, Publ., 1 Gadsden Way, Charleston, SC
- Carriker, M. R. and P. M. Gaffney. 1996. A catalogue of selected species of living oysters (*Ostreacea*) of the world. In: V. S. Kennedy, R. I. E. Newell, A. F. Eble, Eds., The Eastern Oyster *Crassostrea virginica*. Maryland Sea Grant College, College Park, pp. 1-18.

FAO Fisheries and Aquaculture Information and Statistics Service. FAO yearbook. Fishery and Aquaculture Statistics. 2006. Rome, FAO. 2008. 57p.

Galstoff, P.S. 1964. The American Oyster. Fisheries Bulletin 64: 1-480.

- 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). Journal of Shellfish Research 8: 61-70.
- Heffernan P. B. and R.L. Walker. 1988. Preliminary observations on oyster pearl net cultivation in coastal Georgia. Northeast Gulf Science 10: 33-43.
- Kennedy, V. S. and L. P. Sanford. 1999. Characteristics of relatively unexploited beds of the eastern oyster, *Crassostrea virginica*, and early restoration programs. In: M. W. Luckenbach, R. Mann and J. A. Wesson, editors. Oyster reef habitat restoration: a synopsis and synthesis of approaches. Gloucester Point, VA: Virginia Institute of Marine Science Press. pp. 25-46.
- Kennedy, V.S., R.I.E. Newell and A.F. Eble. 1996. The Eastern Oyster *Crassostrea virginica*. College Park, Maryland, USA, Maryland Sea Grant College Publication UM-SG-TS-96-01.
- Kenny, P.D, W.K Michener and D.M. Allen. 1990. Spatial and temporal patterns of oyster settlement in a high salinity estuary. Journal of Shellfish Research 9: 329-339.
- Kirby, M.X. 2004. Fishing down the coast: historical expansion and collapse of oyster fisheries along continental margins. Proceedings of the National Academy of Sciences of the United States of America, 101: 13096-13099.
- MacKenzie, C.L., Jr. 1996. History of oystering in the United States and Canada, featuring the eight greatest oyster estuaries. Marine Fisheries Review 58: 1-87.
- Manley, J. 2007. Oyster reef restoration for developing essential fish habitat in coastal Georgia. Master Thesis, Department of Marine Biology, Savannah State University

- Manley, J., A. Power and R.L. Walker. 2009a. Comparison of techniques for off-bottom culture of the eastern oyster, *Crassostrea virginica* (Gmelin, 1791), in Georgia. Occasional Papers of the University of Georgia Marine Extension Service, Vol. 6, 16 pp.
- Manley, J., A. Power and R.L. Walker. 2009b. Effect of submergence depth on the eastern oyster, *Crassostrea virginica* (Gmelin, 1791), growth, shell morphology, shell characteristics, *Perkinsus marinus* infection, and mortality in oysters cultured intertidally off-bottom in Georgia. Occasional Papers of the University of Georgia Marine Extension Service, Vol. 5, 21 pp.
- Manley, J., A. Power and R.L. Walker. 2009c. 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, Athens, Vol. 3, 15 pp.
- Matthiessen, G.C. 2001. Oyster Culture: Fishing News Books Series. 176pp. Wiley-Blackwell Science Ltd.
- Moroney, D.A. 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.
- Moroney, D. and R.L. Walker. 1999. The effects of tidal and bottom placement on the growth, survival and fouling of the eastern oyster *Crassostrea virginica*. Journal of the World Aquaculture Society. 30: 433-442.
- O'Beirn, F.X., P.B. Heffernan and R.L. Walker. 1994. Recruitment of *Crassostrea virginica*: A tool for monitoring the aquatic health of the Sapelo Island National Estuarine Research Reserve. University of Georgia, School of Marine Programs, Marine Technical Report No. 94-2, 42 pp.

- O'Beirn, F.X., P.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.
- 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.X., 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.
- Oemler, A. 1894. The past, present, and future of the oyster industry of Georgia. Bull. U.S. Fish. Comm. 13: 263-272.
- Power A., B. McCrickard, M. Mitchell, E. Covington, M. Sweeney-Reeves, K. Payne and R. Walker. 2006. *Perkinsus marinus* in coastal Georgia, USA, following a prolonged drought. Diseases of Aquatic Organisms 73: 151–158.
- Reece, K.S., D. Bushek, K.L. Hudson and J.E. Graves. 2001. Geographic distribution of *Perkinsus marinus* genetic strains along the Atlantic and Gulf coasts of the USA. Marine Biology 139: 1047-105.
- Thoresen, M., M. Alber and R.L. Walker. 2005. Trends in recruitment and *Perkinsus marinus* parasitism in the eastern oyster, *Crassostrea virginia*, within the Sapelo Island National Estuarine Research Reserve (SINERR). University of Georgia, School of Marine Programs, Marine Technical Report No. 05-1, 33 pp.
- White M. E. and E. A. Wilson. 1996. Predators, pests, and competitors. In V. S. Kennedy, R. I. E. Newell, and A. F. Eble (Editors), The Eastern oyster, *Crassostrea virginica*, p. 559-579. Md. Sea Grant Program, Coll. Park.