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Performance of selectively-bred lines of eastern oyster, *Crassostrea virginica*, across eastern US estuaries

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ABSTRACT

Eastern oyster, *Crassostrea virginica*, aquaculture has expanded greatly in recent years, but further growth of the industry is constrained by disease-related losses. Oyster breeding programs supporting the oyster aquaculture industry along the east coast of the US have targeted resistance to three prominent diseases: MSX, Dermo, and ROD, caused by *Haplosporidium nelsoni*, *Perkinsus marinus*, and *Roseovarius crassostreae* respectively. Consequently, selected oyster lines possess some level of resistance and/or tolerance but the extent to which these lines, derived from various programs, perform across diverse growing environments used by industry has not been tested. The performance of six selected eastern oyster lines was evaluated at five sites along the east coast of the US (Maine to Virginia) to 1) identify differences in performance among lines at each site, and 2) identify lines that perform well across all sites. Performance measures included growth, mortality, and yield over a 15-month evaluation period. During unusually high mortality events, subsets of oysters were processed for disease diagnosis. Growth trajectories were similar among lines within a site, but varied significantly across sites (78% of random variance explained). Oysters grown in Rhode Island were largest while oysters grown in Maine were smallest at the end of the study. Mortality varied greatly among lines at each site as well as among sites. Line × site interaction explained 61% of the total random variance in the mortality data. In Maine, extensive mortality was observed early in the year for all lines, coincident with increased ROD prevalence. In New Jersey and Virginia, unusually high mortality was evident in the UMFS, Clinton, and NEH-RI lines during the final months of the experiment when the prevalence of both Dermo and MSX were 100% and <50%, respectively. NEH, DEBY, and hANA lines were less affected, demonstrating that lines selected to perform better in their native site surpassed those selected outside the area. Despite large and significant line × site interaction effects for mortality and yield, NEH, DEBY, and hANA performance was above average across all sites. These findings have important implications for oyster breeding strategies and industry practices.
Statement of relevance: First to evaluate multiple oyster lines across diverse sites.

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1. Introduction

The eastern oyster, *Crassostrea virginica*, has been an ecological, economic, and cultural mainstay of eastern US estuaries for centuries. Overfishing during the 18th and early 19th centuries reduced native populations to a fraction of historic levels, particularly in the Northeast (Kirby, 2004; Beck et al., 2011; Ermgassen et al., 2012). Aquaculture has begun to fill the production void created by the collapsed fishery; however, contemporary issues, such as the quantity and quality of available oyster seed and the introduction and spread of oyster pathogens, continue to constrain the industry's potential (Naylor et al., 2000; Jackson et al., 2001).

Abbreviations: MSX, multinucleated sphere X; ROD, *Roseovarius* Oyster Disease; SSO, seaside organism; CM, cumulative mortality.

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Hatcheries are a critical element of eastern oyster culture. Because natural recruitment in northeastern estuaries can be highly unpredictable and often absent entirely (Thompson et al., 1996; Oviatt, 2004), oyster growers are dependent on hatchery-produced seed to stock their farms. In addition to providing the vast number of seed required to sustain a profitable aquaculture enterprise, hatcheries are in an opportune position to positively impact oyster culture by improving existing oyster germplasm through selective breeding (Allen et al., 1993).

Disease resistance represents a high priority target for selective breeding throughout the Northeast and Mid-Atlantic regions. Since the 1950's, eastern oyster populations have suffered losses from three principal diseases: MSX, Dermo, and *Roseovarius* Oyster Disease (ROD). Exposure of farmed oysters to the causative agents of disease is inconsistent and unpredictable over space and time (Powell et al., 2011). Therefore the use of selective breeding for disease resistance and/or tolerance is necessary to minimize the impact(s) of disease on the culture industry (Dégremont et al., 2015).

MSX, which is caused by the parasite *Haplosporidium nelsoni*, was first detected between 1957 and 1959 as an epizootic resulting in the death of >90% of infected oysters in the lower Delaware Bay (Ford and Haskin, 1982). Although the parasite was initially confined to the Delaware and Chesapeake Bays, it has since invaded estuaries as far north as the Damariscotta River, Maine (Messerman and Bowden, 2012) and as far south as South Carolina (Bobo et al., 1997). For much of the latter half of the 20th century, Dermo disease (caused by the parasite *Perkinsus marinus* and responsible for >50% mortality in affected populations), was primarily a problem in the southeastern US and the Gulf of Mexico; however, by 1992 the disease had spread to nearly every region where eastern oysters are cultured (Ewart and Ford, 1993; Ford and Smolowitz, 2007). The bacterium *Roseovarius crassostreae*, known to cause ROD, has caused annual losses ranging from 40 to 90% in Maine, Massachusetts, and New York since 1988 (Maloy et al., 2007; Barber et al., 1996). The activity of all three diseases is modulated in part by temperature and/or salinity and early management strategies were based on limiting the exposure of juveniles to the disease seasonally (Ford and Tripp, 1996).

By the mid-1960s, it became evident that the progeny of survivors of the initial MSX outbreak were more resistant to the disease than naïve oysters (Ford and Haskin, 1987). This observation led to the inception of the first oyster breeding program in the Northeast targeting disease resistance and within five generations of selection, the negative effects of MSX in Delaware Bay were largely neutralized (Haskin and Ford, 1979; Guo et al., 2008). When Dermo disease expanded into northern waters, it was clear that MSX-resistant oysters were not Dermo resistant (Burreson, 1991). Therefore, selection for Dermo resistance was incorporated into the Haskin Shellfish Research Laboratory (Rutgers University) breeding program in 1992, and the result is the Northeast High survival (NEH) line (Guo et al., 2008). In the late 1990s, a second program, the Aquaculture Genetics and Breeding Technology Center (ABC) at the Virginia Institute of Marine Science, was founded to develop genetically improved (e.g. disease resistant) oyster stocks for industry (Frank-Lawale et al., 2014). Wild Delaware Bay oysters have been selected over multiple generations in the York River, VA, where exposure to both MSX and Dermo is consistent from year to year, to create DEBY, an oyster line with dual resistance (Ragone-Calvo et al., 2003). A third breeding program, initially targeting fast growth in colder waters, was established at the University of Maine in 1986. The founding population for this program was a line developed by Frank M. Flowers Oyster Company and was subsequently selected in Maine. The University of Maine Flowers Select (UMFS) line is derived from the largest 20% of Flowers survivors after 18 months of growth at a location where ROD is enzootic (Davis and Barber, 1999). These and other selected oyster lines are currently used by industry to minimize disease impact.

Performance of selected eastern oyster lines is routinely evaluated at their respective sites of origin to enable continued genetic improvement, but only a handful of studies have examined how well they perform across sites and geographic regions (but see Davis and Barber, 1999; Guo et al., 2003; Rawson and Feindel, 2012; Frank-Lawale et al., 2014). This is an important question for the oyster aquaculture industry in the eastern US because there are few selected lines available and many different growing environments. Eastern oysters thrive in waters ranging from −2° to 36 °C and 5 to 40 ppt. Adult growth is positively correlated with temperature while survival is likely influenced by the effects of temperature and salinity on the distribution of disease-causing organisms (Shumway, 1996).

With the occurrence of oyster culture across varied environmental conditions comes a strong possibility for Genotype × Environment (G × E) interactions. G × E interactions occur when two or more genotypes respond to different environments in different ways (Futuyma, 1998). Predictability of yields across localities can be affected by G × E interactions in agricultural species. Although the presence and magnitude of G × E interactions for specific traits should be considered when developing a breeding strategy, attempts to quantify and characterize them have been modest (Annicchiarico, 2002).

The purpose of this study was to evaluate the performance (mortality, growth, and yield) of six selectively-bred eastern oyster lines from various programs at five grow-out sites ranging from Maine (ME) to Virginia (VA) to 1) identify differences in performance among lines at each site, and 2) identify lines that perform well across all sites. Differences in performance among lines within sites reflect the success of selection and the suitability of specific lines for particular growing environments, while the identification of consistent performers across sites reflects whether breeding programs can be centralized or environment-specific programs are required.

2. Materials and methods

2.1. Oyster lines

Six eastern oyster lines routinely used for aquaculture throughout the Northeast and Mid-Atlantic were chosen for evaluation in this study. The origin, site and extent of selection, and environmental conditions (including potential disease exposure) at selection sites are summarized for each line in Table 1. The UMFS, NEH™ (NEH for simplicity), DEBY, and hANA lines are products of multiple generations of selection for performance, while Clinton and NEH-RI are derived from closed populations of survivors of acute, disease-related mortality events and have not been subject to prolonged, consistent, selection efforts.

2.2. Oyster seed production

All material for this study was spawned during the summer of 2012. The original intention was for all six lines to be spawned at the University of Maine's Darling Marine Center shellfish hatchery; however, spawns for the lines of southern origin (NEH, DEBY, and hANA) were not successful. Subsequently, DEBY and hANA seed were produced at the Aquaculture Genetics and Breeding Technology Center (ABC) at the Virginia Institute of Marine Science, and NEH material was obtained by mass spawning approximately 50 broodstock at Muscongus Bay Aquaculture (Bremen, ME).

UMFS, Clinton, and NEH-RI broodstock were conditioned and spawned as in Rawson and Feindel (2012). In brief, 50 oysters from each line were strip-spawned, eggs fertilized and stocked in 300 l conical tanks. Larvae were reared at 24 °C, ambient salinity (28–30 ppt) and fed a diet of *Isochrysis galbana*, *Pavlova* sp., and *Thalassiosira pseudonana* until set. Post-set oysters were maintained in recirculating upwellers supplied with 24 °C, 28–30 ppt filtered seawater and fed mixed live algae (*Tetraselmis chuii*, *Cheatoceros muelleri*, *Rhodomonas* sp., in addition to those mentioned above) until they reached 2 mm in size.

DEBY and hANA seed were produced according to standard ABC hatchery procedures (Frank-Lawale et al., 2014). One hundred pair