SOURCES OF VARIATION IN HEIGHT TO DRY WEIGHT RATIOS OF THE EASTERN OYSTER *(Crassostrea virginica)*

BY

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ABSTRACT

The Eastern Oyster (*Crassostrea virginica*) has become an increasingly popular species for bioremediation via extractive fisheries in the United States. Shell height has commonly been used to predict soft tissue biomass, which in turn, has been used to predict nutrient removal (mainly nitrogen) from aquatic systems. The reliability of shell height as a predictor of tissue mass, however, has not been established under variable grow-out conditions. Shell height to dry weight relationships of the Eastern Oyster was quantified under similar environmental conditions on the Alabama-Mississippi coast, but different grow-out conditions and oyster ploidy. Dry weight was found to increase more rapidly with shell height for transplanted compared to wild-harvested oysters. Oysters reared in surface cages exhibited more rapid increase in dry weight with shell height compared to oysters reared in mid- or near-sediment waters. In contrast, shell height to dry weight relationships did not differ among types of aquaculture gear used for grow-out. Finally, dry weight increased more rapidly with shell height in triploid versus diploid oysters, despite location in the water column. Significant differences in shell height to dry weight ratios existed in the smallest size class of oysters (< 51 mm) in the extractive method comparison, in all three size classes (25-50 mm, 51-75 mm, ≥ 76 mm) in the depth comparison, and in the largest size class (≥ 76 mm) in the ploidy treatment group. Shell height to dry weight ratios did not vary with age or size class in the gear comparison. Overall, these data highlight that environmental and genetic attributes can alter shell height to dry weight relationships, resulting in site and study-specific allometric variation. Hence, site-specific or study-specific measurements will be essential to accurately apply shell dimensions to predict nutrient removal and associated bioremediation for extractive wild-harvest or aquaculture fisheries.

TABLE OF CONTENTS

INTRODUCTION AND BACKGROUND

The allometric relationship between shell height (the maximum length from hinge to margin) and soft tissue weight has been widely used in bivalve fisheries to convert length measurements to weight equivalents, determine condition, or estimate biomass (Venugopalan & Prajneshu 1997; Park & Oh 2002; El-Sayed et al. 2011; Kellogg et al. 2013*a*). Shell height is particularly favored for this approach because this characteristic is the most common metric used by the U.S. fishing industry to define marketable size for many bivalves (*e.g.*; 76 mm for oysters, *Crassostrea virginica*; Higgins et al. 2011; Carmichael et al. 2012). Shell height is quick and easy to determine, and it avoids the need to sacrifice restored or otherwise marketable bivalve stocks. The abundance of literature suggests that shell height to dry weight relationships for the Eastern oyster tend to be consistent at least within a study (typically reported close to 1-2 g dry weight for a 76 mm oyster; Newell 2004; Higgins et al. 2011). Such empirically established relationships, while largely untested for specific growing conditions, has lead to the assumption that that shell height can be generously applied to predict dry weight without location or study specific measurements.

Recently, allometric relationships have been applied to estimate particle and nitrogen removal by oysters (and other bivalves) to, in turn, predict the potential for bioremediation of anthropogenic nutrient loading (Newell 2004; Harding 2007; Higgins et al. 2011; Carmichael et al. 2012; Kellogg et al. 2013*a*). This approach is possible because filtration rates that affect particle removal and biomass that determines nitrogen assimilation rates are thought to increase predictably as shell height increases (Harding 2007; Higgins et al. 2011). If successful, this approach would be particularly useful to managers, aquaculturists and wild harvesters interested

in application of extractive fisheries as a method for bioremediation around the world (Newell 2004; Higgins et al. 2011; Carmichael et al. 2012; Kellogg et al. 2013*a*).

The Eastern Oyster, *C. virginica*, is a favored species for application of extractive fisheries as a bioremediation method in the U.S. due to its ecological and commercial value and prevalence in coastal waters affected by nutrient loading (Newell 2004; Higgins et al. 2011; Carmichael et al. 2012*a,b;* Kellogg et al. 2013*a*). Ecologically, the Eastern Oyster is important due to its exceptional filtration capabilities, relatively rapid growth, benthic-pelagic coupling services, and the three-dimensional habitat structures formed by their natural aggregations (Gutierrez et al. 2003; Pietros & Rice 2003; Newell et al. 2004; Cerco & Noel 2007; Harding 2007; Kellogg et al. 2013*a*). *C. virginica* has been shown to have a higher capacity for nitrogen removal and associated bioremediation compared to other species due to higher assimilation efficiency and feeding capacity (Newell et al. 2004; Carmichael et al. 2012; Wall et al. 2013). Economically, the National Marine Fisheries Services reports U.S. commercial oyster landings in 2010 amounted to ~ 28 million pounds of meat at a value of ~ $118 million and represented 75% of the national shellfish harvest (Agricultural Marketing Resource Center 2013). This commercial value further increases the attractiveness of growing *C. virginica* for ecosystem services if they can also be harvested and marketed (Newell 2004; Harding 2007; Carmichael et al. 2012).

To successfully use shell height to tissue dry weight relationships for estimating bioremediation or other purposes, the extent to which correlation between these growth metrics is resilient to environmental variation is essential to define. While not specifically tested, there is some evidence relationships between shell height and dry weight vary among age classes (Kraeuter et al. 2007) and locations (Railland & Menesguen 1994; Kraeuter et al. 2007;

Carmichael et al. 2013; Kellogg et al. 2013*a, b*). Dalyrmple (2013) showed potential for decoupling of the height to dry weight relationship in larger sized oysters that lost weight through time (potentially due to senescence or environmental stress). Because soft tissues are readily metabolized, while shell is not, factors that limit feeding and growth could result in loss of soft tissue relative to shell size. Food flux and quality, water depth, and even the type of gear used for aquaculture grow-out are potentially important factors influencing allometric relationships (Newell et al. 2005; Harding 2007; Lord & Whitlach 2012; Mallet et al. 2013; Wall et al. 2013; Walton et al. 2013). Genetic background (ploidy) may also affect allometry. Triploid oysters that are growing in popularity for use in aquaculture due to their relatively rapid growth (Harding 2007; Allen et al. 2012) may have significantly different shell height to dry weight relationships compared to diploid stocks (Harding 2007). This variation highlights potential for inaccuracy of shell dimensions as a predictor of tissue weight, if applied without location or study-specific measurements. Little of this variation, however, has been quantified to understand implications for making generalized estimates of bioremediation capacity and other purposes.

Factors that lead to variation in dry weight at length for bivalves such as oysters should be quantitatively investigated so that predictive models that depend on accurate values for dry weight to define shellfish condition or bioremediation capacity will be accurate. To begin to measure these sources of variation, I compiled and compared published and unpublished datasets on shell height to dry weight relationships for oysters (*C. virginica*) grown in one region under similar environmental conditions (all oysters were grown on the Alabama-Mississippi coast during the same time of year), but varying in grow-out method and ploidy. Specifically, I compared shell height and tissue dry weight between native wild-harvested oysters and native

cage-grown (aquaculture) oysters to determine whether data collected for aquaculture oysters could be applied to wild-harvest to make comprehensive estimates for the extractive oyster fishery. I also compared data for oysters grown at different depths in the water column and using different types of grow-out gear, and between diploid and half-sibling triploid oysters to define variation under different typical aquaculture scenarios. These data will be highly valuable to decision-makers and industry operators concerned with accurately estimating bioremediation potential of extractive shellfishing, including meeting total maximum daily nitrogen load requirements, issuing credits for nitrogen removal, predicting particle removal, and other aspects of bioremediation.

METHODS

Data were compiled from published and unpublished datasets for oysters (*C. virginica*) grown on the Alabama-Mississippi coast during the same time of year (typically May through October). Unpublished datasets were combined with published values to obtain sufficient data for shell height and dry weight comparisons within a single region during the same time period in which environmental conditions were relatively similar. In all cases where unpublished datasets were used, the specific method by which oysters were reared and collected is described in detail within the methods section for each comparison.

Extractive method (aquaculture v. wild-harvest) comparisons

Data pertaining to native wild-harvested and transplanted oysters were obtained from two studies (E. Darrow et al., Dauphin Island Sea Lab, unpublished; W. Walton et al., Auburn University Shellfish Laboratory, unpublished). Native wild oysters were collected by hand in June 2013 from various sites (Bayou Chicot, Bayou Cumbest, Bayou Heron, North Rigolets) in Grand Bay, Mississippi (Darrow et al.) and June 2011 from four restoration sites in Mobile Bay, Portersville Bay, and near Dauphin Island, Alabama (Walton et al. 2013) (Fig. 1). Aquaculture data were used from oysters reared at Bayou Chicot, Bangs Lake, Bayou Cumbest, and Bayou Heron in Grand Bay, Mississippi during June 2012 and May 2013 (hatchery stock was obtained from the Auburn University Shellfish Laboratory on Dauphin Island, Alabama). Aquaculture oysters were grown in 30 cm X 30 cm X 10 cm cages (described in Biancani et al. 2012) at 100 oysters per cage, and suspended 0.25 m – 0.50 m above the sediment.

Depth comparisons

Data for aquaculture oysters grown at different depths in the water column came from E. Darrow et al. (unpublished) and Walton et al. (2013). For these studies similar gear types (modified

plastic-coated wire mesh suitcases) were used at different locations in the water column: 1) floating ~10 cm below the water surface in OysterGro™ 45.7 cm X 88.9 cm X 7.6 cm cages stocked at 150 oysters per bag and 6 bags per cage, 2) suspended mid-water at ~0.5 m above the sediment in 30 cm X 30 cm X 10 cm cages stocked at 100 oysters per cage, and 3) near bottom at 0.25 m above the sediment in 30 cm X 30 cm X 10 cm cages stocked at 100 oysters per cage (Fig. 2). Although the surface cages were larger than mid-water and near sediment cages in overall dimensions, these cages are divided into six sections that are roughly the same size as the individual smaller sized cages. Furthermore, the smaller sized cages were placed in groups of 4, making them similar to the large sized cage in overall footprint in the field. This design is necessary to accommodate conditions at each depth; larger cages are difficult to manipulate on and off bottom and multiple smaller cages are more subject to disturbance at the surface. Hence, this design helped maintain similar physical conditions at each depth. Measured differences in dimension and proximity are not likely to make a significant contribution to differences measured in allometry.

Surface cage data were collected from animals grown May to early September 2011 at Sandy Bay, in Grand Bay, Alabama. Oysters in near sediment cages were grown from June to late September 2011, and oysters in mid-water cages grew from June to early October 2012. Near sediment and mid-water cages were maintained at Bayou Chicot, Bangs Lake, Bayou Cumbest, and Bayou Heron also in Grand Bay, Mississippi.

Gear type comparisons

To test effects of gear type, data were collected from oysters raised in three different forms of floating gear (Walton et al. 2013; Fig. 2). The gear types included OysterGro™ floating cages (Ketcham Supply, 45.7 cm X 88.9 cm X 7.6 cm), adjustable long-line baskets

(BST, Ltd.; triangular with rounded corners; 71.12 cm long X 21.59 cm wide X 20.96 cm high) and floating bags (Chesapeake Bay Oyster Company; 0.91 m X 0.46 m X 10.16 cm high). Oysters were stocked at 66% normal stocking density to avoid overcrowding, which amounted to 150 oysters per bag in OysterGro™ cages and floating bags and 75 oysters per bag for long-line baskets (Walton et al. 2013). OysterGro™ cages and adjustable long-line baskets were given ~24 hours air exposure weekly, and floating bags were flipped on a weekly basis (Walton et al. 2013). All gear types were deployed and maintained in Sandy Bay in Grand Bay, Alabama.

Ploidy comparisons

Ploidy data for *C. virginica* were based on diploid and triploid oysters spawned from common maternal broodstock at the Auburn University Shellfish Laboratory on Dauphin Island, Alabama (Walton et al. 2013). Oysters were deployed at Sandy Bay, Alabama from May 2011 to August or October 2011 at a stocking density of 75 oysters per bag for adjustable long-line baskets and 150 oysters per bag for OysterGro™ cages, floating bags, and LowPro™ bottom cages (Chesapeake Bay Oyster Company, 38.10 cm X 91.44 cm X 121.92 cm; Fig. 2). Bags were stocked with oysters of similar ploidy, with 12 total bags maintained in OysterGro™ and LowPro™ cages (6 of each ploidy) and 6 total bags maintained in the adjustable long-line baskets and floating bags (3 of each ploidy) (Walton et al. 2013).

Measurements

Oyster shell height (longest length from umbo to shell margin) was recorded in millimeters using vernier calipers (to the nearest 0.1 mm). To measure soft tissue dry weight, oysters were shucked and dissected to separate whole tissue from shell and dried at 60° C until constant weight (~ 7 days; Darrow et al.) or at 80° C for 2 days (Walton et al. 2013). Dried

tissue weight was taken to the nearest 0.0001 g, following standard methods (*e.g.*; Harding 2007; Walton et al. 2013).

Statistical analyses

All soft tissue dry weight and shell height measurements were log transformed prior to subsequent statistical comparisons, a method of analysis used by Harding (2007) that allows small differences in the data to be more easily distinguished. All statistical analyses were performed with MiniTab 14 software. In all cases where data from different sources were grouped for comparisons, data were first analyzed via Analysis of Variance (ANOVA) to determine if the data could be combined for subsequent analyses and comparisons. Although shell height to dry weight relationships are fundamentally correlations (shell height does not biologically determine dry weight), we opted to apply regression analyses to our data because this approach is typically used in allometric comparisons to allow one dimension to predict another, and such analyses allow more detailed statistical comparison of co-variance between variables for the purposes of this study. Regression analyses, therefore, were performed on all log transformed shell height and dry weight data to determine the statistical significance of the relationship between these two variables within treatments (*i.e.*; wild-harvested oysters compared to transplanted oysters; surface cages compared to mid-water and near sediment cages; OysterGro^{TM} cages compared to long-line baskets or floating bags; and diploid oysters compared to triploid oysters). Analyses of covariance were performed using a general linear model (GLM) with shell height as a co-variate to identify significant differences between the slopes and/or the y-intercepts between or among treatment groups.

To identify the specific sizes driving observed differences between or among treatments, data were divided into three groups to separate pre-market sizes (typical juveniles, 25-50 mm),

small adults (51-75 mm) and market sized (≥ 76 mm) oysters based on U.S. standards (T. Getchis, East Coast Shellfish Growers Association, 1623 Whitesville Road, Toms River, NJ 08755, USA). These size classes also roughly correlate with major life stages of the Eastern Oyster that could affect growth; oysters experience the most rapid growth and first reach sexual maturity within the 25-50 mm range (sexual maturity is usually reached after 30 mm; Rothschild et al. 1994; Kraeuter et al. 2007), are fully mature but growth slows in the 51-75 mm range, and growth rates further slow and harvest typically occurs at sizes ≥ 76 mm (Kraeuter et al. 2007). Length to dry weight relationships of oysters in each size class with sufficient sample size ($n \geq 10$), were compared between or among treatment groups using Analysis of Variance (ANOVA) with Tukey's Post-Hoc test to identify significant differences. An alpha level of 0.05 was used to define significant differences.

RESULTS

Dry weight to shell height comparisons

Overall, oyster tissue dry weight increased significantly with shell height for all treatments (Fig. 3, Table 1). Tissue dry weight increased more rapidly with shell height in transplanted compared to wild-harvested oysters (test for homogeneity of slopes: $F_{1,1,1} = 30.24$, $P \leq 0.001$; Fig. 3a), and shell height was a better predictor of dry weight for transplanted oysters (Table 1). For shell height and dry weight comparisons among oysters reared at different water depths, tissue dry weight increased most rapidly with shell length for surface cages, followed by near sediment and mid-water depths, respectively (test for homogeneity of slopes: $F_{1,2,2} = 4.76$, $P = 0.02$; Tukey's Post-hoc test $P \leq 0.001$ for all pair-wise comparisons; Fig. 3b). Similarly, shell height was the best predictor of dry weight in cages at the surface compared to mid-water and near bottom treatments (Table 1). In contrast, oysters raised in different gear types at similar depth (floating at the surface) exhibited similar relationships between dry weight and shell height (test for homogeneity of slopes: $F_{1,2,2} = 0.57$, $P = 0.57$; ANCOVA: $F_{1,2,2} = 0.62$, $P = 0.54$; Fig. 3c and Table 2). For ploidy comparisons, tissue dry weight increased more rapidly with shell height in triploid compared to diploid oysters (test for homogeneity of slopes: $F_{1,1,1} = 5.04$, $P = 0.03$; Fig. 3d and Table 1), despite location in the water column (in surface or bottom type cages).

Size class comparisons

To determine the size classes driving differences observed in Fig. 3, mean dry weight to shell height ratios were calculated for different size classes (25-50 mm, 51-75 mm, and ≥ 76 mm) of oysters in the harvest type, depth, and ploidy treatment groups, where significant differences in morphometrics were detected among treatments (Table 2). For wild-harvest

compared to transplant animals, dry weight to length ratios were on average significantly different for the smaller size class (< 51 mm), but not larger sizes (Table 2). For water depth comparisons, significant differences were found at all three size classes (Table 2), and for ploidy comparisons, differences were found at sizes ≥ 51 mm. Sample size was insufficient to allow additional statistical analyses of triploid oysters, oysters maintained at surface depth, and oysters in all three gear types at the 25-50 mm size class or oysters at mid-water depth in the largest ≥ 76 mm size class.

FIGURES AND TABLES

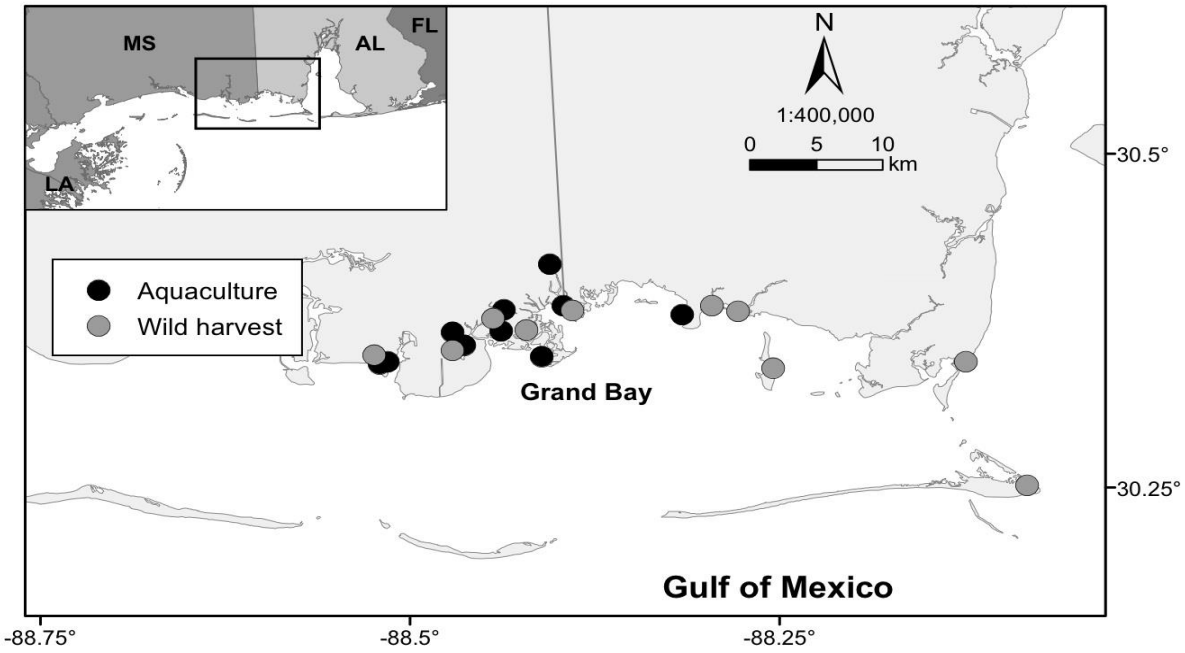

Fig. 1. Locations of wild-harvested and aquaculture-reared oysters in Mississippi Sound on the Mississippi-Alabama coast that were sampled by E. Darrow and W. Walton for this study. Gear, depth, and ploidy samples were collected from aquaculture sites.

Fig. 2. Types of gear in which aquaculture oysters were reared, including A) Surface cages (Oyster Gro™), B) Mid-water cages, C) Near sediment cages, D) Adjustable long-line baskets (BST, Ltd.), and E) Floating bags (Chesapeake Bay Oyster Company).

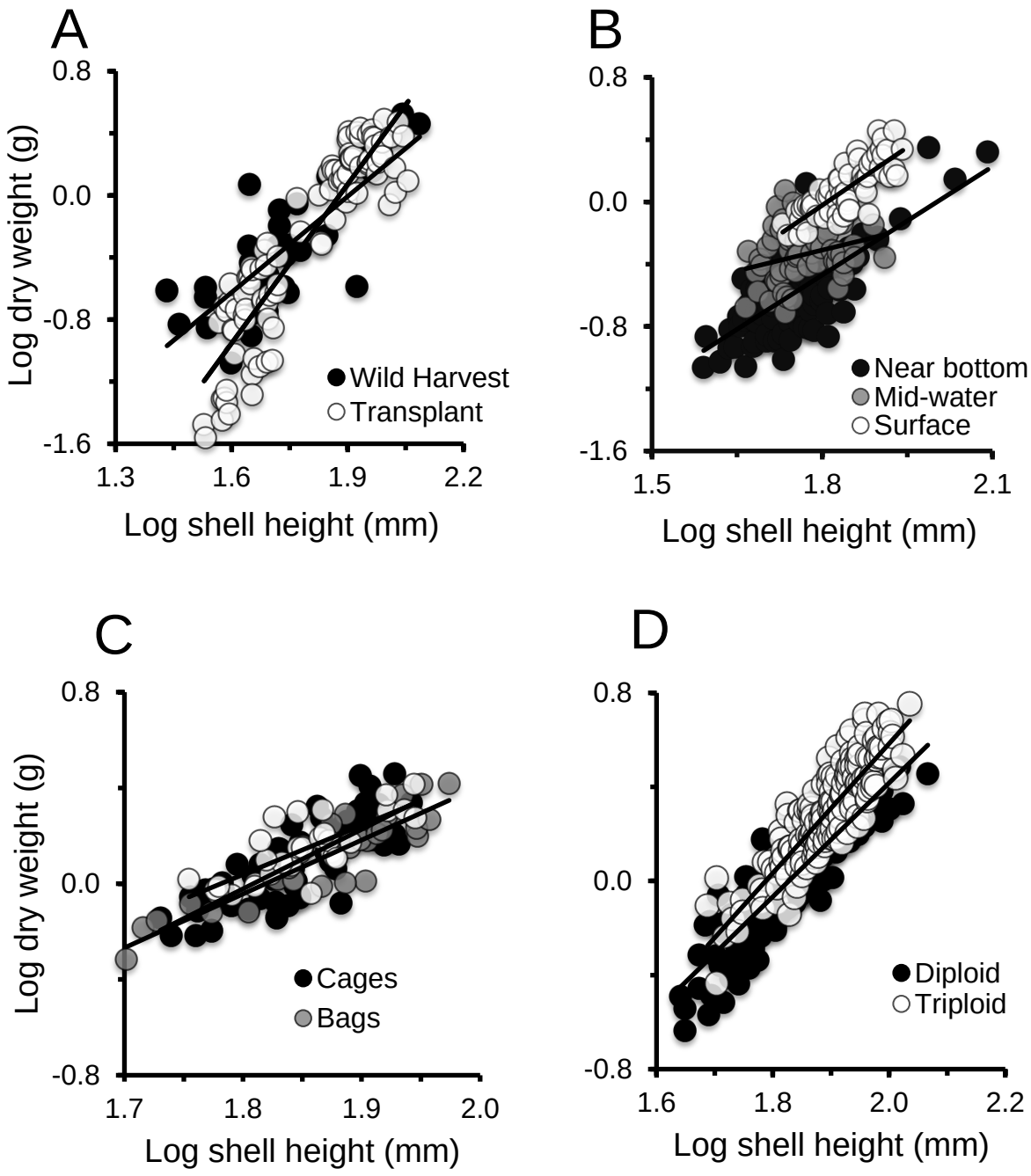

Fig. 3. Relationship between log shell height (mm) and log dry weight (g) for A) wild harvest and transplant oysters, B) oysters reared in cages at different depths in the water column, C) oysters reared in different floating gear types, and D) oysters having different sets of chromosomes.

Table 1. Regression statistics for log transformed shell height (mm) versus dry weight (g) relationships shown in Fig. 3a-d for culture type, transplant location, gear type, and ploidy.

Treatment	Regression Equation	R^2	F_{Reg}	df	P
Harvest type					
Wild harvest	y = -4.00 + 2.10 log (x)	0.66	145.97	1, 75	<0.001
Aquaculture	y = -6.41 + 3.41 log (x)	0.83	472.02	1, 95	<0.001
Depth					
Surface	y = -4.49 + 2.48 log (x)	0.63	102.34	1, 58	<0.001
Mid-water	y = -1.82 + 0.84 log (x)	0.08	4.64	1, 54	0.04
Near bottom	y = -4.65 + 2.32 log (x)	0.51	114.46	1, 110	<0.001
Gear type					
Long-Line baskets	y = -3.65 + 2.05 log (x)	0.60	45.40	1, 28	<0.001
Floating bags	y = -4.18 + 2.30 log (x)	0.79	106.96	1, 28	<0.001
Floating cages	y = -4.49 + 2.48 log (x)	0.63	102.34	1, 58	<0.001
Ploidy					
Diploid	y = -4.42 + 2.42 log (x)	0.79	672.40	1, 178	<0.001
Triploid	y = -4.92 + 2.75 log (x)	0.76	562.32	1, 173	<0.001

Table 2. Mean ± SD dry weight to shell height ratio (DW:SH) of different size classes for each treatment group in which significant differences in shell height and dry weight relationships were found (Fig. 3a, b, c). N/A fields indicate that the sample size was too small (n < 10) for statistical comparison, * indicates significant differences (ANOVA: $P < 0.01$) between mean shell height: dry weight within treatments for each size class.

Treatment	25-50 mm	51-75 mm	≥ 76 mm
Harvest type			
Wild harvest	-0.39 ± 0.17* (n = 31)	-0.12 ± 0.12 (n = 35)	0.06 ± 0.16 (n = 11)
Transplant	-0.53 ± 0.22* (n = 41)	-0.10 ± 0.18 (n = 16)	0.13 ± 0.07 (n = 40)
Depth			
Surface	N/A	0.01 ± 0.07* (n = 44)	0.14 ± 0.07* (n = 16)
Mid-water	-0.26 ± 0.08* (n = 8)	-0.18 ± 0.11* (n = 46)	N/A
Near sediment	-0.44 ± 0.12* (n = 31)	-0.32 ± 0.11* (n = 75)	0.02 ± 0.14* (n =6)
Ploidy			
Triploid	N/A	0.06 ± 0.08* (n = 66)	0.22 ± 0.07* (n = 106)
Diploid	-0.23 ± 0.01 (n = 11)	-0.03 ± 0.09* (n = 122)	0.12 ± 0.06* (n = 48)

DISCUSSION

The findings of this study demonstrate that the predictive relationship between tissue dry weight and shell height in *C. virginica* may vary with factors such as harvest type, depth in the water column, and ploidy. These observations indicate the resulting allometric differences can vary with oyster size or stage of life. Unlike other treatments, similar shell height to dry weight relationships among oysters reared in different gear types was somewhat surprising given that different gear types are known to affect oyster growth rates when shell and dry weight metrics are considered separately (Mallet et al. 2013; Walton et al. 2013). Our results confirm that these differences do not necessarily translate to differences in the relationship between dry weight and shell height. Variation in allometric relationships among the majority of different treatments, however, indicates the potential for error in assuming that shell height (longest length) is equally efficient at predicting soft tissue dry weight under different conditions, even when grown in a single estuary system, during the same general time periods. Hence, while it may be possible to generally use shell height to predict dry weight, with an expected range of predictability from 50-80%; (Table 1), the application of this approach to accurately predict particle or nitrogen removal and capacity for bioremediation will require additional data.

The observation that tissue dry weight increased more rapidly with increased shell height for aquaculture compared to wild-harvested oysters is consistent with previous reports (Paynter & DiMichele 1990; Honkoop & Bayne 2002; Higgins et al. 2011; Lord & Whitlach 2012). Wild oysters growing in natural aggregates are exposed to factors that affect shell and soft tissue growth in different ways compared to caged hatchery-reared oysters, particularly at small sizes. The physical contact insinuated by wild oyster aggregates could reduce individual food intake due to neighbor competition (Frechette & Bourget 1985) or result in changes in shell shape or

structure (Honkoop & Bayne 2002; Marshall & Dunham 2013) that require greater energy allocation to maintain somatic growth. In contrast, cultured oysters are usually stocked at densities to allow for space to grow (as was the case in this study), which reduces density-dependent effects such as crowding and localized competition for food (Frechette & Bourget 1985; Mallet et al. 2013; Marshall & Dunham 2013). It is also likely that native oysters growing directly on the sediment (compared to oysters growing in cages 0.25 m above the sediment) were exposed to higher levels of predation pressure by predators such as the Southern oyster drills (*Thais haemastoma floridana*), which are common in the Gulf of Mexico (Butler 1985). Smaller, thin-shelled oysters have been shown to be especially vulnerable to this species (Butler 1985), and *C. virginica* has been shown to shift from lateral shell growth to shell thickening under such predation pressure (Lord & Whitlach 2012). Size-based predation pressure on young oysters is also consistent with the finding that dry weight to shell length differences was most significant for oysters at smallest size classes (25-50 mm) in this study. Therefore, caged oysters may benefit from lower predation pressure, which allows them to allocate more energy to soft tissue growth rather than shell growth and repair (Paynter & Dimichele 1990; Higgins et al. 2011). This effect may be most detectable in locations where drills and other predators are abundant, such as at the sediment surface (Lord & Whitlach 2012).

Food supply is one of several environmental attributes that varies with depth and may account for allometric differences in oysters reared at different depths. Current speed and organic particulate matter may increase up the water column (Frechette & Bourget 1985; Lenihan 1999), where dry weight to shell height ratios were highest in this study, so that oysters at the surface depth may have access to better food resources compared to those nearer the sediment surface. Frechette and Bourget (1985) showed that mussel (*Mytilus edulis*) tissue mass

increased with increased height above the sediment and that shell growth was unaffected. Although increased food supply near the surface may help explain the highest dry weight to shell height ratios found at the surface depth, one would expect the next highest ratios to exist at the mid-water depth followed by near sediment. This observation, however, was not reflected in the data of this study where ratios were higher for near sediment compared to mid-water depths; thus indicating other factors influencing shell and tissue growth at these locations in the water column. Since mid-water organisms were planted in a different year, interannual variation in other environmental factors may have contributed to lower biomass at the mid-water depth compared to near-sediment. The fact that different gear was used at different depths was unlikely an influential factor since all gear was similar in structure and the depth normalized data obtained from this study showed the insignificance of gear type on shell height to dry weight relationships. Importantly, the differences in dry weight to shell height relationships at all life stages among oysters reared at different depths suggests that the cause of these allometric differences is a consistent effect associated with life in that environment (associated with the physical and chemical environment or food supply) rather than an endogenous or ontogenetic factor, which would be expected to change with life stage.

This study's results are consistent with previously established relationships where dry weight increased more rapidly with shell height in triploid oysters compared to their diploid half-siblings. Other studies have shown more rapid shell (Degremont et al. 2007; Harding 2007; Allen et al. 2012; Dalyrmple 2013; Walton et al. 2013) and soft tissue growth (Degremont et al. 2007; Harding 2007; Dalyrmple 2013; Stone et al. 2013; Walton et al. 2013) in triploid compared to diploid oysters, but these studies have not specifically addressed differences in dry weight to shell height relationships. The fact that the differences in this study were significant

for larger size classes (≥ 51 mm) in which oysters are more likely to be sexually mature, is consistent with the idea that triploid oysters grow rapidly by allocating energy to somatic tissue and shell growth versus gonad development compared to diploid oysters (Allen & Downing 1986; Harding 2007; Allen et al. 2012), resulting in greatest differences among post-reproductive size classes. Although both surface and bottom type cages were used for ploidy comparisons, differences in allometry in this case were dominated by ploidy not cage location. These comparisons confirm that genetic differences and likely other factors that affect endogenous resource allocation have potential to decouple dry weight at length relationships, particularly at certain key life stages, regardless of variation in environmental attributes.

Factors that vary between the hatchery environment and the wild, with water depth, and with genetics can affect growth such that soft tissue mass increases more rapidly than shell length, whether due to a change in shape or resource partitioning. Aquaculture and other activities that will apply allometric measures and derivative growth or biomass estimates, will benefit from studies specifically designed to determine the mechanisms driving the allometric differences. For example, the effects of predators, structure of natural aggregations, food flux and quality, reproductive state or physiological condition, along with presence of other physical or chemical stressors, could be sources of allometric variation that need consideration before applying allometric data within or across different regions to make predictions of biomass based on shell length. To ensure the most accurate and reliable biomass estimates based on allometry will require validation with location and condition-specific measurements.

CONCLUSION

The findings of this study indicate that in addition to environmental factors known to affect oyster growth, there are specific endogenous and exogenous factors that affect the relative relationships between shell height and dry weight, even when major environmental conditions are relatively similar. Hence, while it may be possible to generally use shell height to predict dry weight, with an expected range of predictability from 50-80%, the application of this approach to predict particle or nitrogen removal and bioremediation will require additional data. Our results suggest, at a minimum, data will be needed relative to location (region and depth), season (time of year), age or size class, physiological condition, and genetic stock for the species and grow-out conditions of interest. Factors that lead to variation in dry weight at length for bivalves such as oysters should be quantitatively investigated so that predictive models defining shellfish condition or bioremediation capacity will be accurate.

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