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GROWTH RATES AND PREVALENCE OF *PERKINSUS MARINUS* PREVALENCE IN RESTORED OYSTER POPULATIONS IN MARYLAND

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ABSTRACT Since 1995, hatchery-produced juvenile oysters have been planted on numerous natural oyster bars in Maryland in an effort to restore degraded reefs. As part of the monitoring effort, 27 discrete hatchery plantings spanning 10 y of restoration were sampled during late summer and fall 2009. Oyster shell height, dry meat weight, shell weight, and clump height all increased significantly with age. *Perkinsus marinus* infections were low in all sampled populations, but increased with age. These data enable estimates of growth and shell production rates, and highlight the low prevalence of disease in restored Maryland oyster populations. The longevity of these dense patches suggests that local metapopulation restoration may provide substantial ecological services. The trends presented in this study may provide valuable insights for refining management tools, adapting ongoing restoration, and improving population modeling efforts.

KEY WORDS: oyster, restoration, Maryland, *Crassostrea*, *Perkinsus*

INTRODUCTION

For more than 10 y, eastern oyster (*Crassostrea virginica*) hatchery-produced seed (spat-on-shell) has been planted on small sections of degraded natural oyster bars to restore oyster reefs in Maryland's portion of Chesapeake Bay. Data gathered from these discrete plantings are unique in that the sampled populations are of known ages with little to no natural recruitment (Tarnowski 2010). In addition, plantings were located in legally protected sanctuaries and reserves (not open to annual harvest), although, subsequent to sampling, reports of illegal harvesting at many sites were received. The restoration effort presented a unique opportunity to study the size and disease status of individual cohorts of oysters from 2 mo to 9 y of age. The data reported here may be beneficial not only to oyster biologists and restoration and resource managers, but also for use in predictive modeling efforts.

Although the eastern oyster is important both ecologically and economically along the east and Gulf coasts of North America, many aspects of its biology and ecology are still poorly understood. For instance, data concerning the density of *C. virginica* in most parts of Chesapeake Bay are surprisingly absent from the literature. In addition, little is known about geospatial stock–recruitment relationships between parental broodstocks and local spatfall. Furthermore, Maryland and Virginia populations of *C. virginica* suffer from 2 parasitic diseases (*Haplosporidium nelsoni*-MSX and *Perkinsus marinus*-Dermo) that infect oysters most virulently at higher salinities (Ford 1985, Andrews 1996, Burreson & Ragone Calvo 1996). Effects of these diseases on mortality and growth vary substantially through space and time, and have varied in the upper Chesapeake among tributaries (Tarnowski 2010).

Oyster productivity and potential ecological impacts of restored oysters in Chesapeake Bay remain topics of interest for many scientific agencies (Baird & Ulanowicz 1989, Powell 1992, Dekshenieks et al. 2000, Klinck et al. 2001, Cerco & Noel 2007, Cerco & Tillman 2008, Tillman & Cerco 2009, North et al. 2010). However, robust data describing on-bottom growth rates and shell production of *C. virginica* are largely unavailable. Previous restoration studies have relied on growth rate estimates from a number of sources, including floating tray culture and stock assessments (Paynter & DiMichele 1989, Paynter & Burreson 1991, Jordan et al. 2002, Jordan & Coakley 2004). Kraeuter et al. (2007) summarized many published studies regarding oyster growth and noted that studies of oyster growth *in situ* or "on bottom" on natural oyster bars was remarkably lacking in the literature. In addition, recent discussions of shell budgets suggest shell production rates may be limiting in Delaware Bay and Chesapeake Bay (Powell et al. 2006, Mann & Powell 2007, Powell & Klinck 2007). Many of the aforementioned studies depend on an accurate understanding of growth rates and shell budgets in these systems. Presented here are growth rate, disease prevalence, and shell production data from 27 distinct hatchery-produced oyster cohorts planted on 16 oyster bars over a 10-y period of restoration in the upper Chesapeake Bay. These data may facilitate the adaptation of management tools (e.g., aquaculture, managed harvest beds) and modeling efforts, and could improve restoration strategies baywide.

MATERIALS AND METHODS

Juvenile eastern oysters (spat settled onto oyster shell) used to restore oyster reefs were produced at the University of Maryland Center for Environmental Science Horn Point Laboratory oyster hatchery in Cambridge, MD, and planted by the Oyster Recovery Partnership. Planting densities were targeted at 1–2 million/acre although some bars may have received significantly less as a result of variations in production or planting area.

Sixteen oyster reefs of various ages were sampled within sanctuaries or managed reserves in the Maryland portion of Chesapeake Bay (Fig. 1). Managed reserves are defined as areas that are closed to fishing until a specific median size is reached

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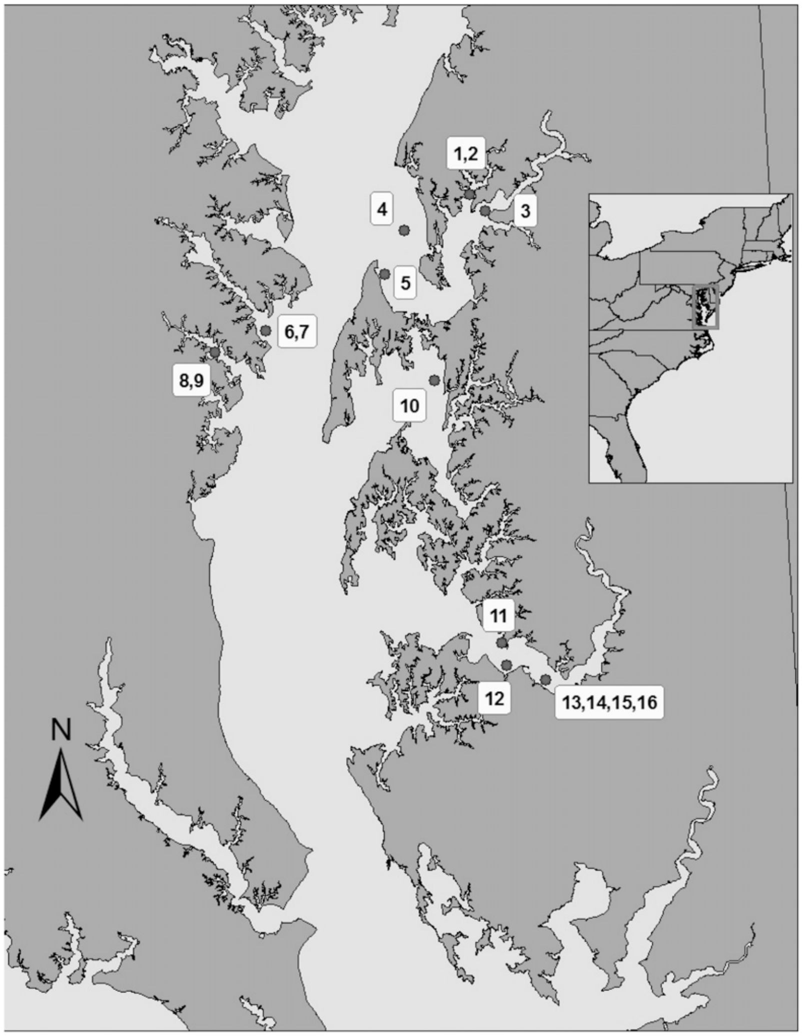

Figure 1. Locations of the oyster bars sampled for this study. 1, Boathouse; 2, Drum Pt.; 3, Spaniard Pt.; 4, Hickory Thicket; 5, Strong Bay; 6, Chinks Pt.; 7, Lake Ogleton; 8, Glebe Bay; 9, Brewers; 10, Mill Hill; 11, Howell Pt.; 12, Green Marsh; 13, Shoal Creek; 14, Bolingbroke Sands; 15, States Bank; and 16, The Black Buoy. Some bars contained multiple, geographically separate plantings, and each planting was treated as a discrete population.

(101 mm). No managed reserves that had been previously opened were sampled. Restoration sites with only 1 planting, or 2 plantings at least 4 y apart, were selected so that distinct cohorts could be identified based on a size frequency analysis. Many reefs had multiple geospatially discrete plantings. From August to October 2009, divers haphazardly collected 50 oysters from each restored reef/planting. If 2 cohorts were expected, 50 oysters of each size class were collected. All oysters collected were the product of restoration plantings of hatchery-produced oysters.

Oysters were returned to the laboratory and stored at 4°C until processed. All live oysters within a sample were enumerated and measured for shell height to the nearest millimeter. All live oysters were shucked, and shell weights were measured to the nearest milligram. Spat (juvenile oysters less than 1 y old) per shell, oysters per clump, and boxes (articulated shells with no oyster tissue) were also tallied. All samples were inspected for the presence of naturally recruited spat.

Oysters processed for dry meat weight (10 per sample) were shucked and the wet tissue was blotted with a paper towel and weighed on a digital scale. The tissue was then placed into a drying oven at 60°C for 72 h and subsequently weighed. Not all samples were processed for dry meat weight.

Sampled oysters were typically found in clumps of 3 or more. Clump height was measured by placing a clump on the laboratory bench and measuring the distance from the laboratory bench surface to the highest shell margin of the clump perpendicular to the laboratory bench. Large clumps in 3-, 4-, and 5-y-old population samples were haphazardly selected to be measured to represent a maximum clump height of those age groups.

Thirty oysters were haphazardly selected from each sample and processed for *P. marinus* diagnosis according to Ray's fluid thioglycollate culture method (Ray 1952, Ray 1966), modified according to Burreson (2009). Small portions of the rectum, gill, and mantle tissue from each oyster were excised and placed in a test tube with 9.5 mL sterile thioglycollate media. Each test tube was inoculated with 0.5 mL of a penicillin/streptomycin mixture and 50 μL of nystatin. After 5–7 days of incubation at 26°C, the tissue samples were removed from the culture media, coated with several drops of Lugol's solution, macerated, and covered with a glass coverslip for inspection under a compound microscope. Enlarged trophozoites were counted for each tissue sample, and infection intensities were assigned based on the number and density of trophozoites visible under 40× magnification. Prevalence was calculated as the percentage of oysters infected, and level of infection intensity was scored (rare, 0.5; very light, 1; light, 1; light to moderate, 3; moderate, 3; moderate to heavy, 5; heavy, 5; very heavy, 5). Weighted prevalence (WP) was calculated as the mean infection intensity score of all the oysters tested.

A total of 27 discrete populations from 16 oyster bars were sampled, 10 of which were reported to have been impacted by illegal harvest. Populations were considered "illegally harvested" by virtue of any one of the following 3 criteria: (1) a Maryland Department of Natural Resources citation or arrest on a specific bar, (2) a report from cooperating watermen, or (3) a eyewitness account from laboratory staff.

Microsoft Excel (2007, Microsoft Corp., Redmond, WA) was used to generate graphs and trend lines in Figures 2–5 and statistical analyses were performed using JMP 5.0.1 (SAS Institute, Inc., Cary, NC).

RESULTS

Live oysters were found at all sites. Divers reported patchy distributions of dense clusters of oysters at many of the sites, and few boxes were found at any of the study sites. Abundance, spatial distribution, and survival were estimated by patent tong surveys and will be reported elsewhere. Samples gathered in this study showed no natural recruits (i.e., oysters smaller than the expected size range for any given planted population).

Sizes at age are presented as shell height and dry meat weight (Table 1). Oyster shell height increased rapidly during the first few years, then more slowly after year 3 (Fig. 2). Oysters planted at 1–2 mm shell height reached a mean shell height of 20.1 ± 6.65 mm (SD) 4–8 wk after planting, and mean shell heights typically reached market size (75 mm) after 2 y. A natural log regression of shell height with age was significant and fit the data well (Ln Regression, $P < 0.0001$, $R^2 = 0.81$, $n = 27$). However, for many older populations where illegal harvesting had been documented (Fig. 2, open points), mean shell height may be underestimated. Thus, a natural log regression of shell height with age was performed for data where no illegal harvesting was documented (years 1–5), which correlated better and may more accurately reflect natural oyster growth rates (Fig. 2 inset, $P < 0.0001$, $R^2 = 0.93$, $n = 17$). Estimated mean shell height at age was higher for these data.

Dry meat weight increased steadily with age (Ln Regression, $P = 0.058$, $R^2 = 0.71$; Fig. 3), such that mean spat dry meat weight was 0.06 ± 0.04 g and increased over time to 2.53 ± 0.64 g at 9 y of age. The low degree of significance observed in the dry meat weight regression was partially a result of a single value more than 3 g for a 4-y-old population at Shoal Creek (Fig. 3). This value was confirmed and was not considered an error, but representative of the high degree of variation in dry meat weight, and indicative of the potential for tissues to grow quickly. A linear regression of the dry meat weight data excluding illegally harvested populations (Fig. 3, inset) was highly significant ($P < 0.0001$, $R^2 = 0.98$).

Disease prevalence was low and WP (the mean infection intensity (see Burreson 2009)) values indicated that expected disease-related mortality should have been low as the low box counts indicated. In populations younger than 6 y of age, *P. marinus* prevalence was less than 40%; however, 7 to 9-y-old populations showed increased prevalence up to 90%. WP was less than 0.8 in oysters up to and including 6 y of age (Fig. 4), whereas 7-y-old oysters had a WP of 1.7 and 9-y-old oysters had a WP of 1.8. Weighted prevalence values above 3 are typically associated with mortality in this region (Tarnowski 2010).

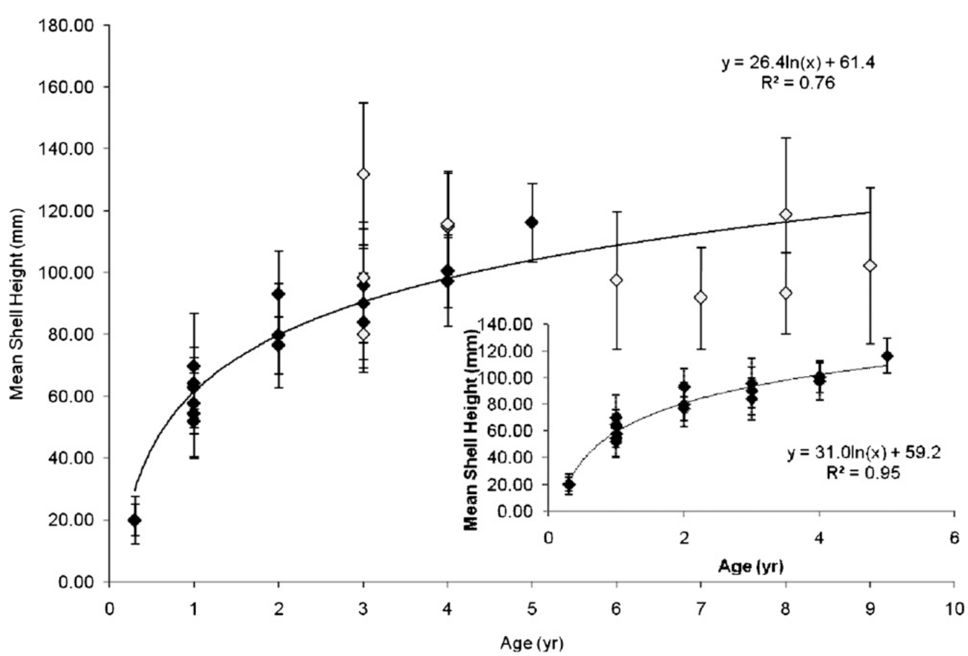

Figure 2. The natural log regression of restored oyster populations sampled in the upper Chesapeake Bay showed that mean shell height increased significantly with age ($P < 0.0001$, $R^2 = 0.7631$). Open points indicate populations impacted by illegal harvest. The natural log regression of populations not impacted by illegal harvesting shows a similar trend, but is an even better fit to the data ($P < 0.0001$, $R^2 = 0.9480$).

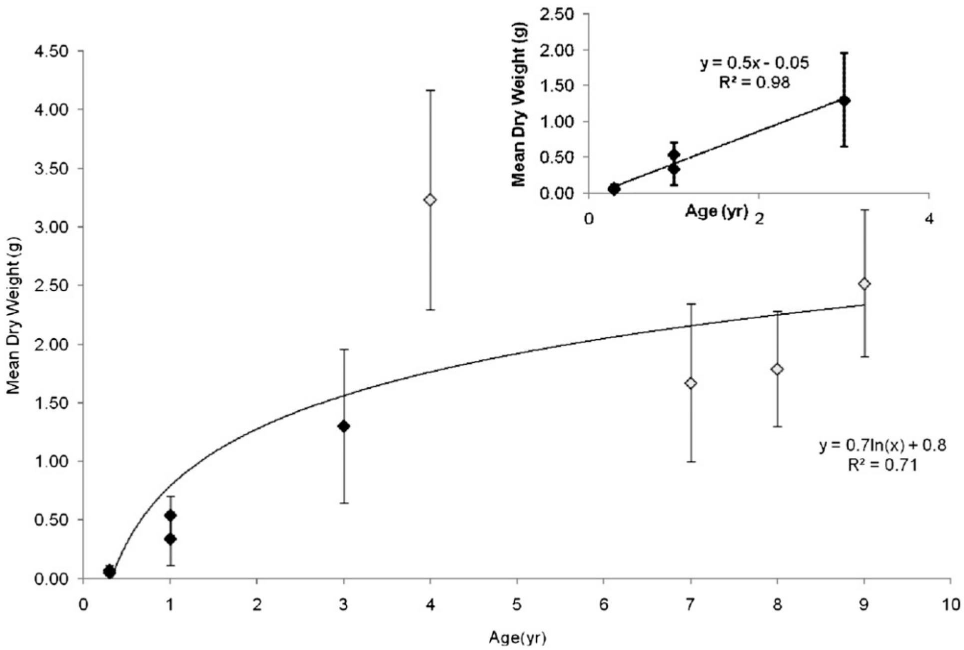

Figure 3. The natural log regression of restored oyster populations sampled in the upper Chesapeake Bay showed that mean dry meat weight increased with age ($P = 0.058$, $R^2 = 0.7057$). Open points indicate populations impacted by illegal harvest. The linear regression of populations not impacted by illegal harvesting shows a significant increase in dry meat weight with age and is an even better fit to the data ($P < 0.0001$, $R^2 = 0.9768$).

Shell weight (Table 1) and clump height increased with age, but showed substantial variability. Shell weight (Fig. 5) significantly increased with age (Ln Regression, $P < 0.0001$, $R^2 = 0.67$). Individual shell weights of more than 200 g were observed in several populations. Shell weight from older populations fell below the regression line, likely a consequence of the aforementioned illegal harvesting. A linear regression of shell weight and age, excluding illegally harvested populations, was significant and showed a tight relationship ($P < 0.0001$, $R^2 = 0.82$). Clump height typically reached 8 cm by 3 y of age, ranging as high as 13 cm in 5-y-old oysters (Fig. 6).

Although mortality was not quantified in this study, box counts served as a crude estimate of oyster death. This is especially true where oysters were collected in clumps, which serve as an informal sampling unit. The observation of few boxes or scars within a clump of 3–10 oysters suggests low mortality and is corroborated by other monitoring data. However, box counts should be regarded as a qualitative estimate of mortality and are likely an underestimate (Mann et al. 2009b). Abundance estimates and long-term mortality will be estimated by patent tongs surveys.

DISCUSSION

Oyster restoration in Maryland has produced several long-lived patchy oyster reefs on previously degraded historical oyster bars. The oysters living on these reefs were planted in areas of relatively low salinity (mean salinities of <12 ppt) with

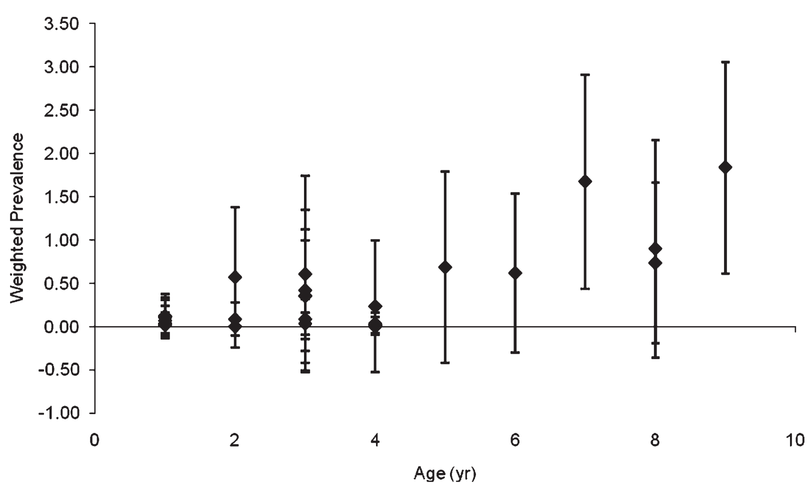

Figure 4. Weighted prevalence of *Perkinsus marinus* infection in sampled oyster populations. Although weighted prevalence increased with age, all sampled populations had weighted prevalence values less than 2.

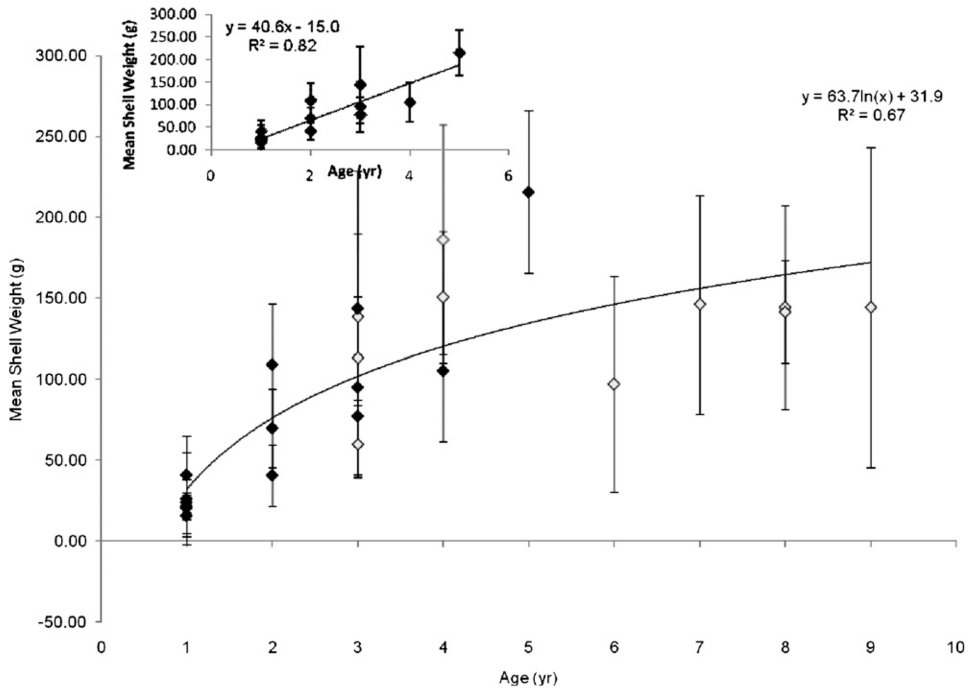

Figure 5. The natural log regression of restored oyster populations sampled in the upper Chesapeake Bay showed that mean shell weight increased with age ($P < 0.0001$, $R^2 = 0.6695$). Open points indicate populations impacted by illegal harvest. The linear regression of populations not impacted by illegal harvesting shows a similar trend, but is an even better fit to the data ($P < 0.0001$, $R^2 = 0.8210$).

the purpose of increasing densities in areas with infrequent natural recruitment. These populations acquired relatively low levels of *P. marinus* infections even after many years, and the patchy reefs created complex benthic structures and have shown remarkable community development (Rodney & Paynter 2006). Although the data sets generated by this ongoing effort may not constitute "successful" restoration per se, they may be valuable in generating measures that could be incorporated into larger assessments and predictive modeling.

Modeling studies for oyster restoration require accurate growth rate and shell budget data (Baird & Ulanowicz 1989, Powell 1992, Dekshenieks et al. 2000, Klinck et al. 2001, Cerco & Noel 2007, Cerco & Tillman 2008, Tillman & Cerco 2009, North et al. 2010). However, growth rate estimates used for management decisions in Maryland have come largely from suboptimal sources such as floating tray culture (Paynter & DiMichele 1989, Paynter & Burreson 1991) and stock assessments (Jordan et al. 2002, Jordan & Coakley 2004). Also, empirical data available in the literature on oyster shell production is rare and based on the contribution of living oysters that contribute their shells to the shell resource when they die. Powell and Mann (Powell et al. 2006, Mann & Powell 2007, Powell & Klinck 2007) argue that shell production rates may be limiting in Delaware Bay and Chesapeake Bay. The results presented here provide empirical data for shell weight with age for oysters up to 9 y old, and provide a statistically robust equation for predicting such production rates in other populations. The trends observed in this study suggest that the growth rate and shell production of oysters in Maryland produce older reefs that provide disproportionately larger ecological services than their younger counterparts (discussed later and see Newell and Langdon (1996)).

Growth Rates

Change in shell height and dry tissue weight with age represent oyster growth rates. The growth curve of shell height with age showed a remarkably good fit even though the data were collected from many different locations, and many populations were impacted by illegal harvesting ($R^2 = 0.7630$). Both curves were highly significant, but note that 4 of the 5 populations older than 6 y fell below the fitted line and were all reported to have been illegally harvested. The growth curve generated for

TABLE 1.

Summary of growth rate and shell budget regressions for all data collected and for populations where no illegal harvesting was documented.

Regression	Data Included	Equation	R^2	P
Shell height (mm)	All	26.4ln(age) + 61.4	0.76	<0.0001
	Without illegally harvested populations	31.0ln(age) + 59.2	0.95	<0.0001
Dry meat weight (g)	All	0.70ln(age) + 0.79	0.71	0.058
	Without illegally harvested populations	0.46(age) – 0.05	0.98	<0.0001
Shell weight (g)	All	63.7ln(age) + 31.9	0.67	<0.0001
	Without illegally harvested populations	40.6(age) – 15.0	0.82	<0.0001

The high R^2 and P values of these regressions indicate their value to estimating oyster growth and shell budgets in Chesapeake Bay.

Figure 6. Typical oyster clump collected from a restored portion of Shoal Creek oyster bar in the Choptank River in Maryland.

the populations without reports of illegal harvesting (Fig. 2, inset) was a better fit ($R^2 = 0.948$). Estimates of growth rates are important for modeling oyster production, and these results will be especially valuable for predicting the growth of oysters in low-salinity waters typical of many Maryland oyster bars. The data show remarkable similarity to those generated by Coakley (2004), who compared fished and nonfished oyster populations, indicating that fishing reduces a population's mean shell height through the preferential harvest of large oysters as the population grows into a harvestable size range. Therefore, the size at age estimates for the oldest ages in this study were likely underestimates. Results presented here are also similar to those of Liddel (2008), who created a unique von Bertalanffy growth equation for oysters in the bay based on different populations, and to the growth estimates created for the demographic model of a recent environmental impact statement on oyster restoration in Chesapeake Bay (Volstad, et al. 2007). Thus, these predictive exercises have been corroborated by the empirical data presented here.

Dry tissue weight (grams dry weight (dw)) are an important reference metric for many biological and ecological parameters. For instance, filtration, clearance, and biodeposition rates in most bivalve studies are reported by grams dw (Newell & Langdon 1996). Dry tissue weight from the sampled populations approached a maximum of 2–3 g after 5 y (Fig. 3), although probably not in a linear fashion as the inset shows. Again, large older oysters may contribute disproportionately to important ecological functions like clearance and denitrification rates (see the later section Ecological Functions; Table 2). Many reports use 1 g dw/oyster as an estimate of adult tissue weight, and therefore may be underestimating mass-based estimates of such traits as fecundity or filtration rate (discussed later).

TABLE 2.

Filtration rates, egg production, and denitrification rates for oysters of various ages.

Age	Weight (g dw)	Filtration (L/h)	Eggs (millions)	Denitrification (g N/y)
Spat	0.06	0.87	0.05	0.14
2 y	0.5	4.09	7.61	0.65
8 y	2.51	13.29	58.3	2.11

Calculations were based on equations for filtration rate, fecundity, and denitrification rates reported by Riisgard (1988), Choi et al. (1993), and Newell et al. (2004), respectively. dw, dry weight.

Perkinsus marinus

Disease has been shown to affect oyster growth and fecundity directly; however, disease prevalence in oyster populations varies temporally with local environmental conditions, especially temperature and salinity (Andrews 1996, Hoffmann et al. 2009). The current conceptual theory of the *P. marinus* life cycle assumes a certain level of subclinical, overwintering infection that is reactivated each year by warming spring temperatures, and accumulates through time (Ragone Calvo & Burreson 1994, Burreson & Ragone Calvo 1996). Because WP values more than 3 are typically associated with mortality in this region (Tarnowski 2010), the *P. marinus* infection levels in these restored populations are generally nonlethal, even though the oysters were up to 9 y old. Similarly, studies using triploid oysters in the Patuxent River reported low levels of *P. marinus* infection both initially and after seasonal intensification (Paynter et al. 2008, Kingsley-Smith et al. 2009). In contrast, oysters deployed experimentally in the Patuxent River by Albright et al. (2007) rapidly contracted lethal levels of *P. marinus* infection at salinities comparable with those observed at all sampling locations. These disparate findings are indicative of the variable nature of *P. marinus* epidemiology and infection rates among tributaries within the Maryland portion of Chesapeake Bay. Restored oyster in the Severn River had lower prevalence and WP values than nearby native oysters, whereas restored oysters in the Chester and Choptank rivers showed disease levels similar to or greater than those in nearby native oysters (Table 3). It is important to note that during periods of oyster growth for the oldest oysters reported here (1999 to 2009), salinities ranged widely at all sites from 1.1–20.2 ppt (W. Romano, NOAA Chesapeake Bay Office, pers. comm.), and included a nearly 4-y drought from 1999 to 2002. The WP values presented in Figure 4, although likely a snapshot of a variable annual trend, characterized the generally low levels of *P. marinus* infection typical of many restored populations found at interim sampling periods. Although boxes are typically thought of as indicators of recent mortality, most of the oysters collected in this study were retrieved as clumps, indicating minimal disturbance since planting (Fig. 5). Thus, we expect many boxes may have been preserved longer than those on annually fished bars, and the lack of mature fouling communities we observed on the inside surfaces of these boxes, such as large barnacles, seemed to bear this out. We would

TABLE 3.

***Perkinsus marinus* prevalence and weighted prevalence (WP) in selected oyster cohorts and nearby wild populations.**

Site	River	Date Planted	Date Sampled	Age	Prevalence	WP	Wild Prevalence*	Wild WP*
Lake Ogleton A	Severn	2008	8/26/09	1	6.67	0.03	73	1.4
Chinks Point	Severn	2008	8/26/09	1	3.33	0.02	73	1.4
Green Marsh	Choptank	2008	8/19/09	1	20.69	0.12	13	0.14
Strong Bay	Chester	2003	10/20/09	6	46.67	0.62	64	1.1
Lake Ogleton B	Severn	2001	8/26/09	8	44.83	0.90	73	1.4
Howell Point	Choptank	2000	8/27/09	9	90.00	1.83	13	0.14

Ages of wild populations were unknown, but the oysters were market size (>76 mm) and thus at least 3 y old.
* Wild data from fall 2009 oyster survey provided by C. Dungan, MD DNR (pers. comm.). Severn data were compared with data from Hackett's Bar, Chester data were compared to Buoy Rock bar and Choptank data compared to Sandy Hill bar.

argue that the absence of significant numbers of boxes in these sanctuaries and within clumps indicates low long-term mortality.

Shell Production

Shell weight (Fig. 5) and clump height (8–13 cm in 3–5 y; Fig. 6) are presented as a contribution to recent analyses of shell budgets in Chesapeake Bay and Delaware Bay (Powell et al. 2006, Mann & Powell 2007, Powell & Klinck 2007, Mann et al. 2009a). These studies postulate that shell production may not keep pace with shell dissolution, burial, and loss. The analyses are based, at least in part, on estimated shell production in portions of Chesapeake Bay or Delaware Bay. The data gathered during this study may be a useful addition to the discussion of shell budgets, especially with regard to the importance of long-lived oysters. Because annual shell addition to the resource is based on oyster mortality, that contribution is limited by the mean size of oysters at the time of their death. In general, the mean shell weight of oysters reported here were much larger than those used by Powell and Klinck (2007) (Fig. 1), although the relationships between shell height and shell weight in both populations were nearly identical. Thus, the older populations of oysters in Maryland may contribute more shell mass to the ecosystem, and therefore may play a relatively larger role in the creation of reefs and maintaining and building reef height despite their low mortality rates. These older communities of oysters are able to survive for a variety of reasons, including the low prevalence of *P. marinus* and the boring sponge *Cliona celata*, which is known to be extremely destructive to oyster shell in higher salinity conditions such as those found in Virginia and Delaware Bay (Pomponi & Meritt 1990).

Shell weight and clump height data from the 16 discrete plantings suggest that shell production on reefs in Maryland would produce significant deposits of calcium carbonate. Individual shell weight increased to 100 g within 3 y (Fig. 5), suggesting that a target density of 100 oysters/m^2 could yield 10 kg/m^2 or, 100,000 kg/ha. Therefore, observed shell production rates, in addition to regular robust recruitment, could substantially augment shell resources on any given reef. Of course, shell contributions by long-lived oysters may be mitigated by lower mortality rates over time, because the models developed in the aforementioned studies require oyster mortality for shell to be contributed to the "shell resource." Also, clump height (Fig. 6) reached 10–12 cm within 4 y, suggesting oyster growth rates might outpace sedimentation rates in many areas. Clump structures remained intact for several years in areas undisturbed by destructive forces, and contribute substantially to reef structure and complexity. Furthermore, increases in shell-based structure and the overall architecture of a reef probably increase faunal abundances (Harding & Mann 2001, Rodney & Paynter 2006).

Ecological Functions

Many ecological contributions of oysters, including water filtration, fecundity, and nutrient removal, have been directly related to dry tissue weight (Riisgard 1988, Cox & Mann 1992, Choi et al. 1993, Newell et al. 2004). Using the data collected in this study, estimates of several ecological contributions of different age oysters can be calculated (Table 2). For instance, Riisgard (1988) postulated that the filtration rate of an oyster was directly related to dry meat weight. Applying those methods to various-age oysters it appears that 8-y-old oysters could filter 15 times more water per hour than a 2-mo-old spat, and 3 times more than a 2-y-old oyster (Table 2). Of course, filtration rates are likely to vary with oyster health and environmental changes (Powell et al. 1992), but the generalization may still be accurate. Similarly, Choi et al. (1993) showed that fecundity in West Bay, TX, oysters was directly related to dry meat weight. Their formula suggests that an 8-y-old oyster could produce about 58 million eggs per year (Table 2), nearly an order of magnitude more than 2-y-old oysters. Finally, data from Newell et al. (2004) show that oysters denitrify about 1.813×10^{-5}g N/L water filtered (Table 2). The data presented in Table 2 suggest that reefs with higher densities of small oysters might match the filtration and denitrification rates of less dense reefs composed primarily of large oysters.

Restoration Challenges and Future Directions

Many studies have shown that restored reefs provide valuable habitat for a wide variety of fauna, and the ecological benefits of oysters in marine protected areas and/or sanctuaries are well documented (Coen & Luckenbach 2000, Harding & Mann 2001, Luckenbach et al. 2005, Rodney & Paynter 2006, Powers et al. 2009). Unfortunately, we know that many, possibly all, of the oyster populations sampled for this study have been impacted by illegal harvest. The effects of illegal harvesting are difficult to quantify, but likely include a reduction in mean oyster size within a population, especially on older reefs, as well as an overall reduction in oyster density. This makes the estimation of natural and disease-related mortality increasingly complex. Illegal oyster harvest is rapidly becoming epidemic in Maryland, with 124 citations issued from July 2008 to February 2010

(Maryland Department of Natural Resources). This activity, paired with low natural recruitment in Maryland, threatens the success of oyster restoration efforts.

A recent report of "unprecedented success" in restoring oysters in the Great Wicomico River was based on a localized natural recruitment event and the survival of a large portion of 1-y-old oysters after shell plantings (Schulte et al. 2009). However, less than 10% of the "restored" population in the Great Wicomico River in Virginia was comprised of oysters older than 2 y (≥70 mm). Given the paucity of large old oysters, that report calls into question the definition of success in oyster restoration. Because oyster survival and recruitment vary with salinity in Chesapeake Bay (high recruitment and low long-term survival in high salinity, low recruitment and high long-term survival in low salinity), a single measure of success may not be appropriate to assess restoration efforts baywide. Mann and Powell (2007) suggest sustainability (e.g., natural recruitment must equal or be greater than annual mortality) should be a requirement of successful oyster restoration. However, they also note that the systemwide goal may be unobtainable, whereas local restoration may prove more profitable for aquaculture and may provide local ecological benefits (Mann & Powell 2007). This may be especially true in Maryland's waters where disease-related mortalities are low (Tarnowski 2010) and patch-specific densities reach more than 200 oysters/m^2. Thus, the longevity of these dense patches suggests that local metapopulation restoration may provide substantial ecological services as one measure of success.

These data lead to several important conclusions. First, oysters planted in the areas studied grew well enough to produce market-size oysters in 2–3 y. These growth rates would likely support a vigorous aquaculture industry. Second, the rates of *P. marinus* infection in the oysters studied were low, suggesting that disease-related mortality would not often threaten an aquaculture industry within the study area. Third, the longevity of oysters in sanctuaries might substantially increase the ecological value of local restoration efforts, at least in terms of habitat creation and enhanced local biogeochemical processes. These results suggest that oyster restoration efforts in Maryland could result in significant success either through oyster production or local reef ecosystem function.

The successes and challenges of oyster restoration in Maryland to date suggest that localized efforts might provide the greatest ecological and economic return. Restoration has historically been spread across the bay in many different areas, diluting the effort in any specific area. The scales at which restoration has been undertaken in Maryland are insignificant compared with the scale of the area across which they have been spread. Thus, any potential ecological signal from the restoration effort has been lost in the noise of environmental variation. However, if the efforts were to be concentrated, the ecological signals might be detected and we might learn how best to restore oysters locally in subestuaries and rivers. Understanding how to maximize the ecosystem benefit of oysters at small scales will give us the knowledge to attempt baywide management and restoration.

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