Oyster Discourses

A Collection of Discussions
from the
Maryland Fall Oyster Survey Reports
2000 -Present

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Cover Photo: M. Tarnowski and Jodi D. Baxter discussing oyster findings during the Fall Survey. (Photo: Robert Bussell)

Introduction

These Discussions follow the trajectory of Maryland's oyster population over the last quarter of a century. During the 1990s the population was buffeted by disease outbreaks, culminating in the devasting four-year millennial epizootics, which by 2002 had claimed almost 60% of the oysters. As a result, harvests collapsed to their lowest point in 150 years. The situation appeared so bleak that serious consideration was given to introducing a non-native species as a replacement for the native *Crassostrea virginica* (ACOE 2008).

It is remarkable to witness the extent that the population has rebounded from this dark period. Certainly, there have been setbacks along the way, but the overall trajectory has been upward. Although the epizootics ended after 2002, in reality this rebound took place over a relatively short time span, beginning with the strong recruitment event in 2010. The Biomass Index, a measure of the number and size of oysters, has increased five-fold in recent years from its nadir in 2001. Landings reached their highest level in 35 years during 2022-23 season, only to be surpassed the following season. Recruitment has been above the 40-year median over the last five years, including a widespread, once-in-a-generation spatset in the Potomac River and other normally low-recruitment areas. And there is evidence that some populations may be developing disease resistance or tolerance. Granted, there is a distance yet to go for a full recovery (however that is defined), but the resiliency demonstrated by this species is truly impressive.

The Discussions herein are arranged chronologically. They review the salient findings of each year, delving in depth on a topic to provide background information to better understand the nuances of the data and expressing issues of concern or attainment. Several gaps exist in the annual order when Discussions were not included in those Fall Survey reports.

The reader will recognize several recurring topics through the years; these can be considered variations on a theme. Central to these Discussions, these topics revolve around primary population metrics (recruitment, disease, mortality, biomass), habitat considerations (shell cultch), and environmental drivers (freshwater discharge). Unavoidably, the interannual variability in streamflow and its profound influence on Maryland's oyster population and this small suite of metrics results in this repetition of topics, though with details specific to a particular year – every year brings a different story.

By consolidating these Discussions into one document, the hope is that it will give a historical perspective on this dynamic period for Maryland's oysters, provide a scientific background for the observations from the Fall Survey, and compile a literature review of value to individuals working with Chesapeake oysters.

1996-2000 Fall Surveys

Maryland Department of Natural Resources
M. Homer and R. Scott
February, 2001

It is clear that oyster mortality since the late 1980s has been strongly influenced by levels of freshwater discharge into the Chesapeake Bay. During this period, the temporal pattern of *P. marinus* infection changed from acute (epizootic) to chronic on the majority of oyster bars in Maryland (Table 7). This profoundly changed the nature of *P. marinus'* impact on oyster populations. Before chronic conditions occurred, *P. marinus* infections would build up over a one to three year period. After an intense outbreak, the protozoan would then become undetectable in all but a few of the regional oyster populations. Once chronic infections became established in oyster populations, however, intense outbreaks became more frequent and their periodicity largely controlled by freshwater discharge into the Bay (Ford and Tripp 1996). Since oysters situated in the lower salinity zones have been relatively safe from parasite-induced mortality, these areas have become increasingly important to the commercial fishery. However, these lower salinity populations have received little or no recruitment since 1991 and are at risk from high freshwater discharges as evidenced from the 1993, 1994, 1996, and 1998 freshets (Table 1). Given the chronic nature of *P. marinus* infections, low and even average freshwater discharges into the Chesapeake Bay tend to exacerbate oyster infection levels. In addition, low flow conditions have generally resulted in *H. nelsoni* epizootics. This parasite can cause more rapid mortality in oysters than does *P. marinus* , kills a wider range of oyster year classes than does *P. marinus*, and typically produces a severe spike in mortality (Smith and Jordan 1992).

During the 1996-2000 period, *P. marinus* disease pressure steadily increased, similar to the pattern observed between 1991-1993. What differs between the two periods, however, is that the later period exhibited increases in both the overall level of parasite intensity (Figure 7) and the frequency of sample mean intensity levels of 3.0 or greater (Figure 11). While about 40 to 50% of the Chesapeake Bay oyster bars (as represented by the Disease Bar set) from 1991-1993 had *P. marinus* population infection levels of 3.0 or greater, over 67% of oyster bars had infection levels of 3.0 or greater in 1999 and 2000.

A severe *H. nelsoni* epizootic occurred in 1999, the second such since 1990. Unlike the 1992 outbreak, however, the 1999 epizootic persisted through 2000. The brevity of the 1992 infection was clearly associated with the 1993 freshet. Since the mid-1980s, both the geographic range of *H. nelsoni* epizootics and associated mortalities have substantively increased in Maryland (MDNR 1988; Krantz 1990).

Compared to the 1985-2000 mean observed total mortality, the 1996-2000 mortality levels were not unusually high. However, the Baywide mean mortality (less fishing mortality) average from 1985-2000 was substantially greater than those that may be found in records from previous periods (MDNR 1975-1984).

Although records of oyster mortality prior to 1975 are spotty and occasionally anecdotal, it appears that before the introduction of *H. nelsoni* and impacts from *P. marinus* outbreaks, mass natural mortality of oysters in Maryland's Chesapeake Bay was generally associated with freshets and occurred in the lower salinity areas. Since the onset of parasitic infections, mass mortalities have become more common and severe and increasingly widespread. This trend is clearly reflected in the historical records of the Annual Fall Dredge Survey and the commercial harvest yields. The period from 1996 through 2000 indicated no change in this pattern.

The 1996-2000 period included three of the lowest spatfall intensity indices on record and the second highest since 1939, the year to which this index was back-calculated (Krantz, 1996). Such volatility in spatfall intensity has been, at least from 1939, a signature of larval settlement in Maryland waters. Since the mid-1980s, however, high spatfall intensity years have generally been followed by periods of high *P. marinus* infection pressure and *H. nelsoni* epizootics, resulting in substantial year class losses. This pattern has been reflected in declining commercial fishery yields during this period, and in substantial changes and shifts in regional production.

2003-04 Fall Surveys

M. Tarnowski
MDNR Publ. No. 17-1072005-62
December 2005

Influence of Freshwater Discharge

It is clear that oyster mortality since the late 1980s has been strongly influenced by the volume of freshwater discharge into the Chesapeake Bay, with freshets directly killing oysters and drought resulting in higher disease levels. Since oysters inhabiting the lower salinity zones have been relatively safe from parasite-induced mortality, these areas have become increasingly important to the commercial fishery. However, these lower salinity populations receive only sporadic recruitment on the order of once per decade, increasing the fishery's reliance on the State Repletion Program. Furthermore, they are at risk from high freshwater discharges as evidenced by mortalities attributed to the 1993, 1994, 1996, and 1998 freshets (MDNR 2001).

Despite the large volumes of freshwater input during 2003 and 2004, no significant oyster mortalities were observed as a consequence. Potentially adverse impacts due to the exceptionally high flows of 2003 were likely buffered by the elevated salinities of the preceding year.

While freshets may be short-term catastrophic events, the establishment of salinity-regulated oyster parasites in Chesapeake Bay has had severe long-term consequences on the oyster populations. Salinity is one of the principal environmental factors controlling oyster diseases. *Perkinsus marinus* mean prevalence and infection intensity and *H. nelsoni* percent frequency of occurrence are inversely related to freshwater inflow. Given the osmotically tolerant character of enzootic *P. marinus* (Dungan and Hamilton 1995), reduced freshwater discharges result in increasing infection prevalences, infection intensities, and mortalities. Even average discharges do not appear to ameliorate the distribution and effects of *P. marinus* infections. *Haplosporidium nelsoni* is even more strongly controlled by freshwater influences than *P. marinus*. Accordingly, low flow conditions have generally resulted in *H. nelsoni* epizootics. This parasite can cause rapid mortality in oysters, kills a wider range of oyster year-classes than does *P. marinus*, and typically contributes to a severe spike in mortality during drought conditions (Smith and Jordan 1993).

The Entrenchment of Dermo Disease

Since the mid-1980's, the pattern of *P. marinus* infection changed from acute (epizootic) to chronic (enzootic) on the majority of oyster bars in Maryland (Table 7). This profoundly changed the nature of the impact of *P. marinus* on oyster populations. Before chronic conditions occurred, *P. marinus* infections would build up over a one to three year period. After an intense outbreak, the parasite would then become undetectable in all but a few of the regional oyster populations. Once chronic infections became established in oyster populations, however, intense outbreaks became more frequent, with their periodicity largely controlled by freshwater discharge into the bay (Ford and Tripp 1996). This shift in infection pattern is reflected in a dramatic change in oyster mortalities. Prior to the widespread establishment of *P. marinus* in the mid-1980's, annual mortality averages ranged between 5% and 10%. Since then, bay-wide annual mortalities have averaged about 30%, with many areas suffering over 50% and some even 80% total observed mortality during high-salinity periods.

The establishment of enzootic conditions for dermo disease is evidenced by increased prevalences over a wide geographic extent for a sustained time period. Each year since 1990, *P. marinus* has been detected on at least 95% of all Disease Bars sampled. However, there were refuges where prevalences were lower than average. From 1990 to 1998, low prevalences typically occurred in samples from low-salinity bars in the upper Chesapeake Bay and the low-salinity reaches of the tributaries, where freshets could exert some controlling influence on the parasite. During the 1999-2002 drought this pattern broke down, with Disease Bars in low-salinity areas exhibiting dermo disease prevalences of 90% or more. After two years of above average freshwater flows, the sustained widespread distribution of *P. marinus,* even though at low to moderate infection intensities, indicates that dermo disease is still enzootic throughout most of the tidal waters of the state as of November 2004.

As an extreme example of disease taking hold in a normally low-salinity population, the occurrence of *P. marinus* on Beacon Bar in the Potomac River in 2002 has profound implications for management and research. It demonstrates that remote oyster bars in low-salinity areas can be infected by dermo disease despite the miles-wide absence of repletion activity that may transplant potentially infected seed oysters. That is, even oysters on far upstream bars can be infected through natural processes during high-salinity periods. It also suggests there is no consistent refuge from dermo disease for oysters in most Maryland waters. With the establishment of dermo disease in upstream areas previously thought to be safe from infection, these oyster populations are now subject to three problems: the potential for dermo disease-related mortality, the "cure" for parasite infection (freshets) that can be more devastating than the disease, and a low frequency and rate of recruitment. The resulting limitations on management will certainly confound efforts to enhance oyster populations in these areas.

The Advance and Retreat of MSX Disease

Since the mid-1980s, both the geographic range of *H. nelsoni* epizootics and associated mortalities have substantively increased in Maryland (MDNR 1988; Krantz 1990). The last *H. nelsoni* epizootic, the most severe on record, was associated with a four-year period of drought and low freshwater inflows to Chesapeake Bay (Figure 2). Similarly, the 1987, 1991-92, and 1995 epizootics were associated with below-average freshwater discharges. On the other hand, no MSX disease epizootic occurred in 1997 despite low annual average freshwater inflow. Due to the relatively high flows that occurred during the spring period, drought conditions did not prevail until mid-summer. Both the 1991-1992 and the 1995 epizootics were followed by unusually high freshwater inputs into the Chesapeake Bay during 1993-94 and 1996. These freshets were largely responsible for subsequent dramatic contractions in the distribution of *H. nelsoni*. Similarly, by Fall 2004 MSX disease had been purged from much of Maryland by two years of consistently high freshwater flows.

Spatfall

The poor spatfall indices in 2003 and 2004 were not surprising, given the high freshwater flows during those years. Because of the proximity of the two primary sources of freshwater input for the bay, the Susquehanna and Potomac Rivers, and the large distance to the Atlantic Ocean with its high-salinity waters, spatfall in Maryland is extremely sensitive to river flows.

Although oyster reproduction and settlement have minimum salinity requirements, elevated salinities do not necessarily guarantee a good spat set. As the 2002 data demonstrate, only a few areas experienced a noteworthy spat set, while other formerly productive areas received little if any. On a speculative note, while a stock-recruitment relationship has yet to be demonstrated for oysters, it might be that in 2002 some areas were so devastated by disease mortalities that broodstock densities fell below a minimum threshold required for successful reproduction.

Extreme variability in spatfall intensity is a historic characteristic of larval settlement in Maryland waters. The 1991-2002 period included four of the lowest annual spatfall intensity indices on record as well as the second and third highest since 1939, the year to which this index was back-calculated (Krantz 1996). However, Friedman's Two-Way Rank Sum Test produced what appears to be an anomaly, with the extremely strong index year of 1997 (second-highest on record) grouped only in the middle tier of yearly spatfall rankings. This index was exceptionally high because of the influence of a few bars with high spat counts. In contrast, the 1991 spatfall (third-highest on record) was far more widespread. Since the spatfall intensity index is calculated as an arithmetic mean, a few Key Bar sites with unusually high spatfall intensities can unduly influence the index. In contrast, Friedman's Test incorporates a geographic component by ranking the yearly spatfall intensities of each Key Bar. Rankings eliminate the problem of bias to the index resulting from unusually high spat counts on a small number of bars. The data from 1991 and 1997 clearly indicate the utility of a statistically-based ranking index, such as Friedman's Test, that more accurately defines spatfall intensity on a bay-wide basis.

Mortality

Observed mortalities in 2003 may have been overestimated due to the persistence of boxes greater than a year old. Despite the fact that prevalences and intensities of *P. marinus* infections were both statistically ranked in the lowest level tiers, the average observed mortality for 2003 fell to the middle group. In fact, the 2003 mortality estimate was higher than the 20-year average. This suggests there was a residual from the large death assemblage of 2002 that remained as boxes through the 2003 survey, well beyond the assumed shell-articulation span of one year.

Areas in the bay that received notable spatfalls in 2001 and 2002, such as the Point Lookout Oyster Sanctuary, have benefited from good survivorship during the subsequent two years and now have flourishing oyster populations. In contrast, since the mid-1980's high spatfall intensity years in elevated salinity areas have generally been followed by periods of high *P. marinus* infection pressure and *H. nelsoni* epizootics, resulting in substantial year class losses.

Prior to the introduction of *H. nelsoni* and impacts from *P. marinus* outbreaks, mass natural mortality of oysters in Maryland's Chesapeake Bay was generally associated with freshets and occurred in lower-salinity areas. Since the wholesale onset of parasitic infections, mass mortalities have become more common, severe, and increasingly widespread. Both the geographic ranges of *H. nelsoni* epizootics and their associated mortalities have substantially increased in Maryland waters (MDNR 1988; Krantz 1990). Increasing frequency of *P. marinus* lethal sample infection prevalences is also associated with widespread mortalities. This trend is clearly reflected in both the historical records of the Annual Fall Survey and the commercial harvest yields. The period from 1999 through 2002 indicated a strengthening of this pattern. Similarly, as infection levels of both parasites dropped in 2003 and 2004, so too did mortalities.

The Eastern oyster in the Maryland Chesapeake Bay has demonstrated modest and variable levels of recruitment in comparison to other regions along the East Coast of the United States. Historically, this sporadic recruitment had been compensated for by the high degree of survivorship in the Maryland population relative to other regions. With bay-wide annual total observed mortalities averaging over 30% since 1990, the resilience of the population has been severely compromised.

2006 Fall Survey

Mitchell Tarnowski
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August 2007

Failure of Disease to Intensify

In June, 2006 Virginia Sea Grant released an advisory bulletin warning oyster growers of anticipated high dermo disease levels. Virginia Institute of Marine Sciences scientists based this projection on the mild temperatures of the previous winter and the drought gripping the Chesapeake region that spring, conditions that are conducive to an epizootic outbreak of dermo disease. Biologists in Maryland had similar expectations for dermo disease in their portion of the bay. Compounding the impending problem was that streamflows had returned to normal in 2005 after two wetter than average years, allowing salinities to rise. Consequently, dermo disease levels in the southern Maryland portion of the bay were also anticipated to have increased to the point where large-scale disease-related oyster mortalities could be expected. The stage was set for an oyster disaster. It didn't happen.

As the VSG advisory was being prepared and released, the drought had broken and the Chesapeake watershed was buffeted by rains. Freshwater input to the Bay jumped from a sluggish 44,000 cfs in May to a brisk 91,000 cfs in June. Above average streamflows persisted for much of the remainder of the year. The timing of this freshwater inundation, just as increasing water temperatures were approaching the point where *P. marinus* begins proliferating in earnest, likely spared the oyster populations in the southern part of Maryland from much higher disease-related mortalities.

As a consequence of the early summer freshwater surge, observed mortalities in 2006 were the lowest since 1989. However, there were disturbing mortality trends, particularly in the southern portion of Maryland. Observed mortalities in Tangier Sound, which had been the premier oyster producing region in the state, were well above the state-wide average. Also, oysters at the Pt. Lookout power-dredge sanctuary, which has a thriving population based largely on the 2001 year class, were heavily infected by *P. marinus.* This sanctuary, which already suffers from an above-average observed mortality of 28%, has been on the verge of even higher die-offs for the past two years. The well-timed decrease in salinity during 2006 was just sufficient to stave off a catastrophe. Nevertheless, the stage is set yet again for heavy mortalities if summer salinities and water temperatures become favorable for *P. marinus*.

Factors Influencing Natural Mortality

Non-fishing mortality in oysters may be attributed to any of a suite of causes, including, but not limited to, predation, starvation, smothering by sediment, low dissolved oxygen, and freshets. However, the overwhelming factor in natural mortalities of oysters over the past 20 years has been disease. Prior to the introduction of *H. nelsoni* and impacts from *P. marinus* outbreaks, sporadic mass natural mortality of oysters in Maryland's Chesapeake Bay was generally associated with freshets and occurred in the lower salinity areas. Outside of these infrequent events, however, annual mortality averages ranged between 5% and 10%. Since the onset of parasitic infections, mass mortalities have become more common, severe, and increasingly widespread. Following the widespread establishment of *P. marinus* in the mid-1980's, bay-wide

annual mortalities have averaged about 30%, with some areas suffering over 80% total observed mortality.
Higher salinities favor both MSX and dermo disease, while lower salinities purge MSX disease from Maryland waters and may reduce, but not entirely eliminate, the prevalence and/or intensity of dermo disease.

The highest total observed mortalities during the past two decades are associated with elevated frequencies of MSX disease associated with higher than average salinities. An increasing trend in observed mortality and MSX disease frequency occurred during the drought years of 1999-2002. Beginning in 2003, the continued decline in observed mortalities can be correlated with a reduction in the geographic range and depression of MSX disease prevalence and intensity over the past four years, resulting from unfavorable salinity regimes.

In the absence of MSX disease, and under current conditions of average to below average salinity, the activity of dermo disease becomes the dominant measurable influence on observed mortality. Even though the annual mean prevalence has decreased from record highs during 1999-2002, this disease still affects approximately 60% of the oyster population, and is present throughout the range of oyster habitat in Maryland. However, infection intensities have dropped to below lethal levels over a wide geographic range, and observed mortalities have continued a 4-year decline. The exception where mortalities, primarily of market oysters, have not declined to as great an extent is in the higher salinity waters of the Tangier Sound region.

Spatfall Patterns
The elevated June/July streamflows also affected the distribution of spatfall. The freshet occurred during the peak spawning period for Maryland oysters. This produced a pronounced geographic division in settlement, with little or no spatfall above the mouth of the Little Choptank River, where freshwater input from the Susquehanna River had the greatest influence. Similarly, the Potomac River, which acts as a freshwater conduit, experienced little spatfall. The exceptions were some sheltered backwaters, such as Broad Creek in the Choptank River, which have small watersheds and were not as affected by runoff. Areas that were most impacted by freshwater inputs lost an entire year class of oysters. Where the influence of freshwater flow was moderated, such as in Tangier Sound, oyster recruitment was moderately successful. Salinities in this region seem to have been finely balanced between enabling good recruitment and suppressing disease-related mortality.

Harvest Trends
During 2006, the industry experienced many gains: in harvest, dockside value, number of working watermen, and in rebounds for hand tongers, divers, and patent tongers, which had been in a serious downturn the two prior seasons. The dismal record-low harvest of 2004 is the backdrop for discussing 2006 as a stronger, better year, for when compared to other recent years, 2006 doesn’t stand out as anything other than a poor to average year. The improvement seen in 2006 doesn’t signal an actual recovery of oysters to historic levels or support an expectation for longstanding gains for the fishery. Yet, the 2006 season shows real economic gains over 2004, a benefit to the industry and working watermen.

The increase in harvest for 2005-06 was due to reduced disease levels and improved survivorship over the three preceding growing seasons. The significantly higher than average freshwater inputs during 2003 and 2004 lowered salinity, and consequently disease pressure, allowing more oysters to survive to market size into this season. Coupled with the widespread spatfall in 2002, this resulted in notable population increases in areas worked by hand tongers, divers, and patent tongers, who collectively produced 75% of the harvest in 2006. In contrast, there was a reduction in harvest by power dredgers, both in terms of the percentage of the total catch and of bushels landed. Power dredge harvest dominated the fishery during the 2004 and 2005 seasons, producing about 50% of the harvest. This trend was reversed in 2006 The decline in power dredge landings was due to persistent disease and relatively higher mortalities in Tangier Sound, a major portion of the area open to power dredging. The observed mortality rates of market oysters in Tangier Sound were 34% in 2004 and 41% in 2005, well above the Maryland-wide averages of 20% and 17%, respectively.

Good recruitment in 2002 increased the supply of seed oysters for the MDNR repletion program, which in turn supplemented the natural spatfall. Much of the harvest gain for 2006 came from areas planted by MDNR with shells and seed oysters, indicating a return on these efforts compared to if no action had been taken. The top three harvest areas of Eastern Bay, upper and mid Bay and Patuxent River have been heavily planted with shells and/or seed oysters. These Repletion Program activities, coupled with improvement in disease and survival in these areas, enabled harvests to increase.

The Chester River harvest data show how the fishery is dependent on consistent and constant seeding when natural recruitment is too low to support a fishery. Harvests from 1998 to 2002 ranged from 20K bushels to 70K bushels but plummeted after 2002, a period when no transplanting occurred in the river. With the end of the Seed Program in the Chester River, harvests collapsed and have not recovered in spite of some modest amounts of hatchery seed that have been planted on a few select Harvest Reserves (areas established for the production of harvest using hatchery seed). Since the Reserve Program has dominated the river's production, harvests have been a few thousand bushels.

2008 Fall Survey

M. Tarnowski

MDNR Publ. No. 17-4222010-448
April 2010

Factors Influencing Recruitment

One of the most critical factors for successful oyster recruitment is adequate salinity (Kimmel & Newell 2007). If salinity is below some critical threshold the likelihood of a spatfall failure is assured. The timing and volume of streamflows (which modulate salinities) are important; freshwater discharge during the March – May period appears to be a good indicator of recruitment potential. However, proper salinity is a necessary but not always sufficient condition to ensure a good spatfall. For example, 2001 and 2002 had similar spring streamflow volumes, but a twofold difference in recruitment.

Clean substrate is another important factor. Shell plantings in good recruitment areas to produce seed oysters have been the basis of the Maryland Repletion Program for many decades. The restoration activities on the Piney Island East Sanctuary illustrate the importance of clean substrate as well as the timing of the planting. This sanctuary received two distinct shell plantings separated by two years, while maintaining a portion in its natural, unimproved state. In 2000, good spat sets occurred on shells planted that year, outperforming the unimproved natural area by a factor of almost thirty to one. In contrast, the 2002 planting initially performed extremely poorly (4 spat/bu) and was bested that year by both the 2000 planting (140 spat/bu) and the natural bar (70 spat/bu), most likely because the late July planting date missed the primary spatfall. This is supported by the average size of the spat during the Fall Survey - 25 mm at both the 2000 planting and natural site vs. 10 mm at the 2002 planting, indicating the latter area missed an earlier spat set. By 2004, all three sites were roughly equivalent in term of spatfall, except in 2006 when the natural bar lagged behind the two shell plantings. The 2006 set demonstrated that even after several years, shell plantings can still receive decent spatfalls – 214 spat/bu on the 2000 planting and 293 spat/bu on the 2002 planting, in contrast to the natural bar with 95 spat/bu. These numbers are modest in comparison to a 12-year old shell planting in Eastern Bay, where in 1997 2,000 spat/bu were recorded. Thus, although clean, newly-planted shell can greatly enhance spatfall, under the right circumstances older shell plantings can continue to catch spat providing they aren’t buried or heavily fouled.

Other factors accounting for successful recruitment when salinities are adequate are a matter of conjecture. These may include, but are not limited to, broodstock densities, the physiological condition of the broodstock including the impact of diseases, adequate food in the phytoplankton assemblage, competition for settlement space with other epibenthic species (e.g. tunicates, barnacles), predator abundance, variations in physical determinants such as temperature, wind and currents, and undoubtedly other factors. Abundances of species that can impact oyster recruitment (prey, predators, competitors) and the timing of their occurrence in relation to the timing of the oyster reproductive/recruitment cycle may vary annually. This myriad of factors plays into an intricate web of interactions that is poorly understood. The multiplicity and variability of these interactions confound ready analyses.

Spring Streamflows, Disease, and Observed Mortalities
Disease levels and consequent observed mortalities in 2008 were below the 19-year average for the sixth year in a row. This extended period of reduced disease impacts has led to speculation that Maryland oysters have developed a tolerance for Dermo disease. However, our analyses suggest that there are alternative or additional reasons accounting for these observations.

The weather pattern during this period has resulted in some wetter than normal springs. Streamflows during 2003 and 2004 were exceptionally high throughout those years, knocking back record-high Dermo (Figure 17) and MSX (Figure 18) disease intensities and prevalences to current levels. Although streamflows during 2005 were near-average, they apparently were high enough that, in combination with reduced disease levels during the previous year, did not allow disease to gain traction.

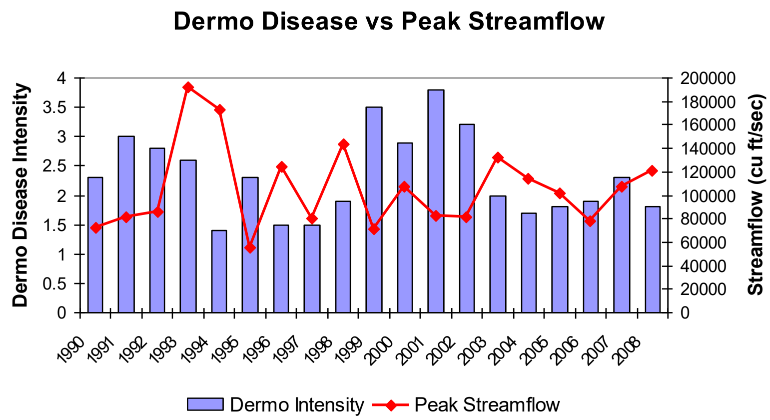

Figure 17. Dermo disease intensity (0-7 scale) compared with peak streamflow, 1990-2008. Peak streamflow is the average for March – May, except in 2006 when peak flows were delayed until June-July.

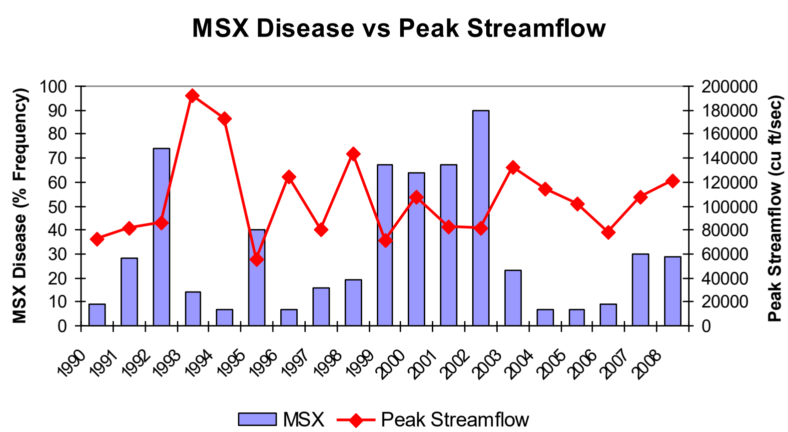

Figure 18. Frequency of bars with MSX disease compared with peak streamflows, 1990-2008. Peak streamflow is the average for March – May, except in 2006 when peak flows were delayed until June-July.

An apparent exception to this pattern was 2006, which experienced drought conditions during the spring. Actually, the wet weather was delayed until June; streamflows during June-July and September were 195% of average. The timing of this elevated flow occurred at a critical juncture of the *P. marinus* epizootiological cycle, inhibiting its proliferation at warm summer temperatures, when under favorable salinities the parasite normally begins to proliferate (Burreson & Ragone Calvo 1996).

The spike in Dermo disease intensity occurred in 2007 despite seemingly average streamflows that spring. In fact, March experienced high streamflows (133% of average), which subsequently tailed off. From May through September streamflows dried up to only 56% of the 70-year average for those months. The March-April pulse of freshwater likely was sufficient to dampen dermo to sublethal levels until the waters cooled in autumn. Another factor may have been the lower initial *P. marinus* population following four successive years of reduced Dermo disease levels. In contrast, the record high mortalities of 2002 were preceded by three years of elevated Dermo disease intensities (Figure 19) and high MSX disease levels (Figure 15). The population was essentially primed for the devastating mortalities observed in 2002.

Another wet spring occurred during 2008 which suppressed disease. June salinities were ≤ 10 ppt at 75 % of the disease bars. This is a critical threshold for Dermo disease (Ragone & Burreson 1993) and below the threshold for MSX disease (Ford & Tripp 1996). In addition, the large proportion of 2006 year-class oysters in the disease bar samples, especially those from higher salinity disease-prone areas, reduced mean Dermo disease intensities in those samples. Dermo disease-related mortality rates are somewhat influenced by the age of the oysters; older oysters are generally more likely to have higher infection intensities and mortality rates than younger oysters (Ford & Tripp 1996). The relatively young oyster population in 2008, along with the wet spring, suggests that Dermo disease did not have sufficient time to attain lethal levels before water temperatures cooled in the fall.

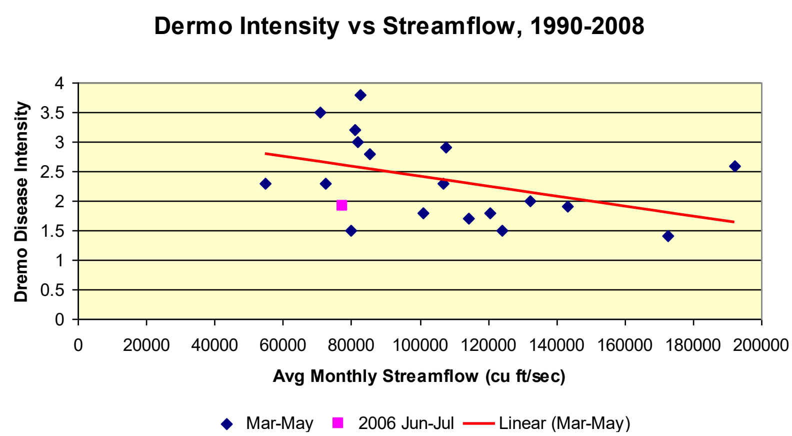

Figure 19. Relationship between Dermo disease intensity (0-7 scale) and peak streamflow, 1990 to 2008. Peak streamflow is the average for March – May, except in 2006 when peak flows were delayed until June-July.

When examining the entire disease data set from 1990 to present, a statistically significant negative relationship between streamflow and Dermo disease intensity was absent ($r^2 = 0.14$, p =

0.11), although the trend was apparent (Figure 19). The 1990's were characterized by alternating years of dry and wet conditions, including freshets in three of those years. Diseases never had the opportunity to get fully entrenched or purged during this period.
The buildup of diseases to lethal levels may require successive dry years or at least an exceptionally dry year (Figure 20). To dislodge disease takes extraordinary freshwater flows such as in 2003 and 2004, which, in combination with timely streamflow increases in succeeding years, appears to have restrained disease impacts to sub-lethal levels during the last six years.

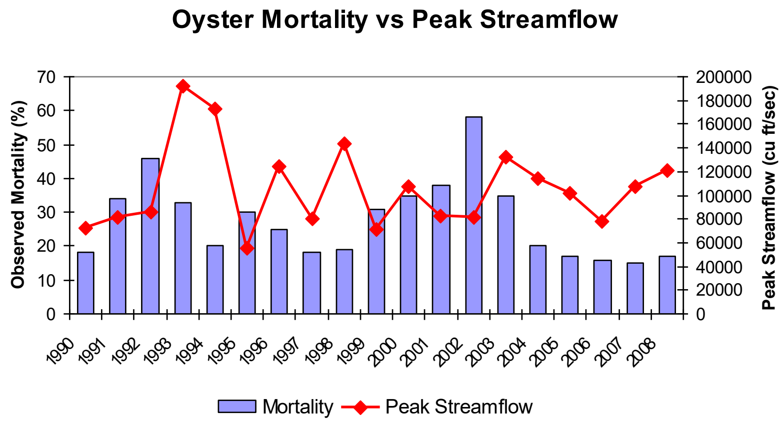

Figure 20. Observed oyster mortalities compared with peak streamflows, 1990-2008. Peak streamflow is the average for March – May, except in 2006 when peak flows were delayed until June-July.

Commercial Harvest Trends
Following the long decline from peak unsustainable harvests in the late 1800's, Maryland oyster landings enjoyed an extended period of relative stability during the middle of the 20th century. After bottoming out in the mid-1920's – in association with a typhoid outbreak attributed to eating raw oysters which shriveled up demand (Tarnowski 1999) – annual oyster harvests of between one and three million bushels were maintained for the next 60 years, despite a host of external factors impacting landings over that long time span (e.g. economic depression, world war, changes in market preferences, bad weather, etc.) (Tarnowski 1999).

The MSX epizootic and entrenchment of Dermo disease during the mid-1980's had a devastating effect on the Maryland oyster population (Figure 16). Between 1986 and 1988 landings plummeted almost 75%, with harvests dropping below the one million bushel mark for the first time in well over a century. During the late 1980's and through the 1990's the population stabilized at a new, lower level with landings in the vicinity of 400,000 bu. Even after another epizootic in the early 1990's, the population slowly built back up so that landings returned to the 400,000 bu. plateau. The four-year epizootic over the turn of the millennium knocked harvests back to two successive record lows. Although landings have rebounded somewhat they are still at less than half the peak of the previous decade, despite low observed mortalities over the past six years. Perhaps it is too early to tell, but the oyster population may have been pushed to an even lower stable state by the 1999-2002 epizootic. For a discussion of stable states in oyster populations, see Powell et al. (2009a, 2009b).

2009 Fall Survey

Mitchell Tarnowski

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September 2010

The Influence of Salinity on Oyster Populations

One of the most critical physical factors influencing oyster populations, both directly and indirectly, is salinity. Salinity, as a function of freshwater flow, varies seasonally, annually, and spatially depending on weather patterns such as rainfall and snow pack. Changes in freshwater discharges into the Bay can alter salinity regimes sufficiently to affect recruitment patterns, predation, disease pressure, and mortality rates. Even slight shifts in salinities can have profound consequences for oysters in a given area. Low salinities can inhibit recruitment and, taken to the extreme, have devastating effects on upstream oyster populations in normally marginal salinity habitats. Higher salinities enable good spatfall, but may foster oyster diseases and associated mortalities.

Oyster populations can be directly impacted by deluges of freshwater, which, depending on the timing and duration, can cause mass mortalities on vulnerable bars. A long record of oyster-killing freshets exists in Maryland, the most famous occurring in 1972 during Tropical Storm Agnes (Beaven 1947, CRC 1976). More recent freshet-related oyster mortalities were documented during 1993, 1994, and 1996 variously in the Potomac, western Wicomico, Chester and Choptank Rivers as well as the upper Bay (MDNR 2001).

Oyster recruitment is also affected by salinity, both directly and indirectly (Kimmel & Newell 2007). If salinity is below a critical threshold, a spatfall failure is assured. The timing and volume of streamflows (which modulate salinities) is important; the March – May period appears to be a good indicator of recruitment potential (Tarnowski 2010a). However, proper salinity is a necessary but not always sufficient condition to ensure a good spatfall. For example, 1999 and 2001 had similar streamflow volumes, but a twofold difference in recruitment (Figure 2a, Table 2). Factors accounting for successful recruitment when salinities are adequate may include, but are not limited to, availability of clean substrate, broodstock densities, the physiological condition of the broodstock including the impact of diseases, adequate food in the phytoplankton assemblage, competition for settlement space with other epibenthic species (e.g. tunicates, barnacles), predator abundance, variations in physical determinants such as temperature, wind and currents, and undoubtedly other factors. Species that can modify oyster recruitment have their own cycles of abundance, and the timing and magnitude of their occurrence in relation to the timing of the oyster reproductive/recruitment cycle form an intricate web of interactions. As salinity affects the physiology of oyster reproduction, it also influences those populations of species that can interfere with spat settlement.

Salinity can indirectly affect oyster populations by influencing the distribution of oyster predators and competitors. For example, in 2002, the fourth consecutive year of drought conditions, salinities had been elevated for such a prolonged period that oyster drills, which require salinities above 15 ppt, were found well up Tangier Sound in areas not normally inhabited by them. Consequently, during the spring of 2002 a large percentage of oyster spat boxes had tell-tale drill holes, indicating they had been consumed by these carnivorous gastropods (MDNR unpubl. data).

Similarly, oyster diseases are controlled by salinity. Oyster parasites are salinity sensitive, particularly *H. nelsoni* (Ford 1985, Ragone & Burreson 1993). This was dramatically illustrated in 2004, when persistently-high freshwater runoff pushed back MSX disease from its record high levels throughout much of Maryland waters during 2002 to relatively small areas in Tangier Sound and the lower mainstem (Tarnowski 2005). Since that freshet, salinities have moderated and over the past three years MSX disease has expanded geographically, but there has been no concomitant increase in the baywide average observed mortality.

Since the end of a prolonged drought in the fall of 2002 (Tarnowski 2005), a string of environmental conditions unfavorable to diseases has been documented during these seven years of below average observed mortalities. Exceptionally high annual freshwater inflows characterized 2003 and 2004 (the second and third highest over the past 25 years) (Figure 2a), and three of the subsequent five years had above average inputs. Even as annual streamflows moderated in the second half of this decade, peak spring/summer streamflows generally were still above average (Figure 2c). The timing and magnitude of these peak streamflows were such that a delicate balance may have been maintained between salinities that allowed the geographic spread of MSX disease, yet were low enough to prevent the development of lethal infections, resulting in reduced observed mortalities. Furthermore, dermo disease prevalences and infection intensities have remained below average for the past seven years. Even if the oysters were tolerant of dermo disease they would still carry infections of *P. marinus*, but the below average prevalence levels suggest that other factors are affecting dermo disease transmission and acquisition.

Disease-related oyster mortality is not the only oyster population dynamic to have been inhibited by the pattern of seasonal above-average freshwater pulses in recent years. A parallel situation exists with oyster recruitment, where high streamflows (i.e. below average salinities) result in recruitment failures (Tarnowski 2010a). Spatfall has been below the 25-year median in six of the last seven years. There are a number of other factors than can affect recruitment, but the strong numerical correlation between freshwater inputs and recruitment implicates high streamflows in the spate of recent poor spatfall years (Tarnowski 2010a).

On an annual, Baywide (Maryland and Virginia) basis, 2009 was considered a dry year by the USGS (2009). However, as in the previous four years (excluding 2003 and 2004 because of their extended high streamflows throughout the year), a timely pulse of above average freshwater flow in May and June drove down salinities. By mid-June, most of the water quality stations in Maryland were reporting surface salinities below 15 ppt, (MDNR 2009). This was followed by additional pulses of higher streamflows in August (163% of the average) and October (136% of the average), which kept salinities in most of Maryland waters below 15 ppt throughout much of the summer. The Tangier Sound region was the exception, with salinities remaining above 15 ppt, and coincidentally was one of the areas with the highest observed mortalities.

Haplosporidium nelsoni can tolerate salinities as low as 10 ppt, but MSX disease becomes substantially more pathogenic in salinities greater than 15 ppt and temperatures greater than 20°C (Ford 1985, Sprague et al. 1969), conditions which in Maryland generally develop during May. Thus, in 2009 during the critical months for the development of MSX disease infections and consequent mortalities (Ford & Tripp 1996), salinities throughout most of Maryland were within the window that allows *H. nelsoni* to survive but at sub-lethal levels.

Although the generalized picture is one of an extended period of lower observed mortalities, when localized conditions become favorable to disease, mortality events continue to occur. For example, the Paul Bailey Oyster Sanctuary in the Patuxent River received disease-free hatchery seed in 2002. These oysters experienced excellent survivorship during the first few years (MDNR unpubl. data), but by 2006 dermo disease was detected (83% prevalence, 2.8 infection intensity, 20% lethal infections), although observed mortalities were only about 7%. The following year the salinity in the area increased substantially (Fall Survey salinities were 15.7 ppt in 2007 vs. 10.7 ppt in 2006) and *P. marinus* flourished (97% prevalence, 4.6 infection intensity, 60% lethal infections), resulting in observed mortalities of 43%, despite a baywide Disease Bar average observed mortality of 15%.

The development of disease tolerance or resistance among Maryland oyster populations cannot be discounted. In higher salinity waters such as Delaware Bay and the Virginia portion of Chesapeake Bay, native oyster populations have demonstrated greater survivorship in the face of MSX disease (Ford & Tripp 1996, Burreson & Ford 2004). Furthermore, selective breeding has produced oyster strains with genetically enhanced resistance/tolerance to both MSX and dermo diseases (Ford & Tripp 1996, Ragone Calvo et al. 2003).

In Maryland, however, developing resistance or tolerance to MSX disease is problematic since most of the oyster populations are not consistently challenged by *H. nelsoni* except during dry years. Consequently, susceptible individuals are only intermittently and incompletely removed from the population. Surviving and newly recruited susceptible individuals can dilute the pool of tolerant or resistant stocks by either reproducing with them directly or by providing larvae from more remote low disease areas which may recruit, grow, and reproduce with the selected oysters. Such a scenario could have occurred in 2002, when salinities were high enough to promote recruitment throughout most of Maryland, producing the highest spat index in 12 years (Table 2). This was followed by successive years of good survivorship to reproductive age with little challenge by disease due to favorable salinity conditions. Even during an epizootic outbreak, the susceptible individuals generally would be capable of reproducing before succumbing to disease. Nonetheless, during the high freshwater flow years of 2003 and 2004, a pocket of MSX disease remained in Tangier Sound to challenge the oysters of that region. It would not be surprising if tolerant or resistant oysters developed there, although definitive, empirical evidence is not yet available to support this contention.

The host-parasite relationship as affected by salinity between oysters and *P. marinus* is considerably more involved than that described for MSX. Until the late 1980's - early 1990's, dermo disease epizootics would occur in the higher salinity Bay regions and penetrate up-Bay only during low freshwater flow periods. Since the early 1990's, however, this disease has entrenched itself in the Bay's oyster population; it is now an enzootic condition found almost everywhere oysters are present. Salinity patterns and resultant infection levels observed prior to the onset of chronic dermo disease no longer apply to oyster populations. As described here, the last seven years have seen a remarkable abatement of dermo disease, on a Baywide basis, measured by both prevalence and intensity. Although environmental conditions can adequately account for what has been observed in recent years, the apparent evolving relationship between oyster and *P. marinus* populations is not fully understood. Dermo disease appears to remain strongly influenced by salinity, but evidence for modulating effects of enhanced dermo disease resistance among oysters from chronically selected wild populations is only circumstantial to date.

2010 Fall Survey

Mitchell Tarnowski
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August 2011

A Notable Spatset

The exceptional recruitment event of 2010 was encouraging news about an oyster population still depleted a decade after being battered by disease. Its widespread distribution included the lower salinity areas that seldom receive a spatfall. Although spatfall was light in these areas, oysters historically have had good survivorship there due to reduced disease pressure. The 2010 spatfall should provide a welcome natural boost to those lower-salinity populations. Likewise, the newly-expanded system of oyster sanctuaries is off to a promising start after its populations received an opportune lift from this recruitment event.

The mechanism for enhanced oyster recruitment is still uncertain (Tarnowski 2010b). The timely increase to average salinities by May/June 2010, followed by somewhat elevated salinities thereafter, certainly enabled good recruitment to occur. This was coupled with a sharp spike in temperatures during June (Eyes on the Bay), which may have acted as a trigger for spawning. Nevertheless, while adequate salinities and favorable temperatures are necessary, they are not always sufficient conditions for enhanced recruitment (Tarnowski 2010b). It should be noted that the elevated spatfall in 2010 was a regional phenomenon, with Virginia reporting better than average spatfalls in the lower Chesapeake Bay and several of its tributaries, as well as New Jersey in Delaware Bay (Powell et al. 2011). Other molluscan species also experienced good spatsets in 2010, such as bay scallops in Massachusetts (C. MacKenzie, pers. comm.). Clearly, there were larger, broad-scale factors influencing oyster recruitment in 2010 that are only poorly understood at this time.

During the last three decades, our oyster populations have been decimated by periodic outbreaks of devastating diseases which severely eroded our oyster stocks. In this new reality, where disease mortality can and has exceeded natural background and fishing mortality, oyster recruitment has become of singular importance. Over this long period, we have seen periodic spikes in recruitment only to have hopes of population recovery crushed by the pressures of disease. What is different in recent times is a long-term abatement of disease pressure, starting in 2003, and a subsequent decrease in oyster mortality, with the latter virtually returning to pre-disease era levels. Missing in the equation, however, has been significant natural oyster recruitment. If the present trend in below average mortalities continues, the combination of the favorable 2010 spatset and high survivorship should bode well for Maryland's oyster population in the next few years.

Oyster Diseases and Recent Mortality Trends

The eight-year period of below-average observed mortalities, which in 2010 culminated in the lowest observed mortality since 1985, raises the question regarding the development of disease resistance/tolerance in Maryland oyster populations. This possibility may be examined with respect to findings discussed in a recent paper (Carnegie & Burreson 2011). The authors argue persuasively that oysters in disease-enzootic waters of the lower bay in Virginia are resistant to MSX disease, based on comparison studies and field observations among oyster populations with varying levels of exposure to the *H. nelsoni* parasite. A key point to the paper is that the less susceptible populations have been constantly challenged by disease pressure which selects for resistant individuals. As previously proposed for Delaware Bay oysters, the development of MSX disease resistance requires the elimination of most susceptible individuals and continuous challenge by *H. nelsoni* (Ford & Bushek 2006, Ford et al. 2009).

In Maryland, however, developing resistance or tolerance to MSX disease is problematic since most of the oyster populations are not challenged by *H. nelsoni* except during extremely dry years. Upstream incursions of the parasite occur when freshwater input drops, followed by retreats when flows return to normal. Consequently, susceptible individuals are only intermittently and incompletely removed from the population. The possible exception to this scenario is in Tangier Sound, where a small pocket of *H. nelsoni* with very low prevalence persisted even through the deluge years of 2003/04 (Table 5; Tarnowski 2005).

Dermo disease-related mortalities may further compromise the development of MSX disease resistance in Maryland oysters. During the first three years of the 1999-2002 drought, *H. nelsoni* was not detected from many of the upstream oyster bars. Among upstream bars where MSX disease was found during this period, prevalences were low (3-10%) and mortalities ranged from 23-60%. However, because of elevated prevalences and intensities of dermo disease at this time, many of these mortalities can likely be attributed to *P. marinus*. As the MSX epizootic intensified during 2002, only three of the disease monitoring bars remained free of *H. nelsoni*, yet observed mortalities on those bars were still as high as 61%, likely due to the high levels of dermo disease. Mortalities among oysters on MSX-affected upstream bars are also most likely the result of dermo disease because of the low prevalences of *H. nelsoni* observed there, and it cannot be ruled out that dermo disease-induced mortalities may also operate to remove some or all of the surviving potentially MSX-resistant oysters that may persist in the wake of MSX disease epizootics. Thus, dermo disease-related mortalities may have worked against the selective mechanism for MSX resistance.

The widespread spatfalls of 2002 and 2010 may have actually confounded the evolution of MSX disease resistance in the Maryland oyster populations. As a consequence of favorable salinity regimes, refugia from MSX disease persist in the upstream portion of Maryland tributaries and bay mainstem, which can act as a source of disease susceptible progeny when conditions are advantageous. Susceptible individuals can dilute the pool of tolerant or resistant stocks by either reproducing with them directly or by providing larvae from upstream lower-salinity (hence lower disease) areas which may recruit, grow, and reproduce with the selected oysters. Such a situation could have occurred in 2002 (and again in 2010), when salinities were high enough to promote recruitment throughout most of Maryland (Table 2). This may have allowed the restocking of areas decimated by disease with the progeny of susceptible individuals, which was followed by successive years of good survivorship to reproductive age with little challenge from disease due to reduced salinity conditions. Similarly, the development of highly resistant oyster in Delaware Bar was retarded by the genetic contribution of low-salinity susceptible individuals (Ford & Bushek 2006). In the lower bay of Virginia, higher *H. nelsoni* prevalences have been found in smaller oysters compared with larger individuals, suggesting that these smaller oysters are the progeny of susceptible populations from lower-salinity areas. However, these susceptibles are being selected out of the higher-salinity populations by disease (Carnegie & Burreson 2011).

Again, constant challenge from *H. nelsoni* is required to minimize reproductive interaction with more resistant stocks, a situation that usually is not found in Maryland.

Another line of evidence for resistance in higher-salinity Virginia oysters is the difference in *H. nelsoni* prevalences between susceptible and resistant populations during times of drought. As salinities increase, MSX-disease expands its range upstream into populations that are seldom regularly exposed to the disease. Consequently, the susceptible populations upstream have much higher MSX prevalences than the resistant oysters (Carnegie & Burreson 2011). However, the opposite was true in Maryland during MSX-epizootic of the past two years. In 2010, the distribution of MSX-disease was neatly divided into mid-bay and lower bay groupings (Figure 9). These same groupings were used when considering the range expansion of *H. nelsoni* in 2009. In both years, the average *H. nelsoni* prevalences were substantially lower in the upstream oyster populations, suggesting that either the mid-bay oysters were more resistant than the lower bay stocks or that salinity is exerting a controlling influence on *H. nelsoni* prevalences. The former is unlikely since selection pressure has been low in recent years: MSX-disease was not detected in the mid-bay populations until 2008 and observed mortalities have remained below average.

The steep decline in total observed mortalities in recent years from the record high levels of 2002 is associated with the abatement of MSX disease and with the decline in the annual mean intensities of dermo disease. However, the relationship between observed mortalities and MSX disease has not been as robust over the past four years, with low observed mortalities persisting despite an increased frequency of bars with MSX disease, particularly in 2009. This could be due to the timing and magnitude of peak streamflows, maintaining a delicate balance that allowed MSX disease to spread while keeping infection intensities below lethal levels (Tarnowski 2010b). The general reduction of dermo disease infection intensities, a consequence of sub-optimal salinity conditions for *P. marinus* that coincided with reduced impacts from MSX disease, became a dominant factor limiting observed mortalities over the past eight years to well below the 26-year average (Figure 11). The relative contribution of each disease to the observed mortalities varies with environmental conditions, with MSX disease intensifying during droughts (Tarnowski 2010a).

The host-parasite relationship as affected by salinity between oysters and *P. marinus* is considerably more involved than that described for MSX disease. Until the late 1980's - early 1990's, dermo disease epizootics would occur in the higher-salinity bay regions and penetrate upstream only during low freshwater flow periods. Since the early 1990's, however, this disease has entrenched itself in the Bay's oyster population; it is now an enzootic condition found almost everywhere oysters are present. Salinity patterns and resultant infection levels observed prior to the onset of chronic dermo disease no longer apply to oyster populations. Seasonal water temperatures have been demonstrated to combine with salinity to strongly influence dermo disease epizootiology on an annual basis (McCollough et al. 2007). As described here, the last eight years have seen a remarkable decline in dermo disease, on a baywide basis, measured by both prevalence and intensity. While environmental conditions can adequately account for what has been observed in recent years, the apparent evolving relationship, most likely still strongly influenced by salinity, between oyster and *P. marinus* populations is not fully understood.

The widespread and persistently low observed mortalities of the past eight years, if explained by disease resistance, would have required marked evolutionary changes to take place within two distinct species of disease-causing parasites over a very short period of time. The simpler explanation is that well-documented environmental conditions, especially timely freshwater flows, have kept diseases under control in recent years (Ford 1985, Ragone & Burreson 1993, Tarnowski 2010a,b). Nonetheless, the development of disease tolerance or resistance in Maryland's oyster populations should not be entirely ruled out. In higher salinity waters such as Delaware Bay and the Virginia portion of Chesapeake Bay, native oyster populations have demonstrated greater survivorship in the face of MSX disease pressure (Ford & Tripp 1996, Carnegie & Burreson 2011). Furthermore, selective breeding has produced animals that evidence enhanced resistance/tolerance to both MSX and dermo diseases (Ford & Tripp 1996, Ragone Calvo et al. 2003). During the high freshwater flow years of 2003 and 2004, a pocket of MSX disease remained in Tangier Sound to challenge the oysters of that region. It would not be surprising if disease tolerant or resistant oysters develop there, although definitive, scientifically-based evidence is not yet available to support this contention.

To answer the opening question of this discussion, we simply do not yet know if Maryland oyster populations are resistant/tolerant to diseases. Short of an extended drought, the way to resolve this issue is through rigorous experiments similar to those conducted in neighboring states.

2011 Fall Survey

Mitchell Tarnowski

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August 2012

A Year of Elevated Streamflows

The effect of environmental factors, particularly freshwater inflow, on oyster diseases and consequent oyster survivorship in Chesapeake Bay was again demonstrated in dramatic fashion by the near-record high streamflows of 2011. Oyster disease prevalences and infection intensities fell to their lowest levels since systematic monitoring began in 1990, resulting in the lowest average observed oyster mortality in over 25 years.

In contrast, drought conditions from 1999 through 2002 allowed diseases to attain record high levels both in prevalence and intensity. Dermo disease was pervasive throughout Maryland's oyster populations, while MSX disease experienced an unprecedented range expansion as far upbay as the Bay Bridge and lower portion of the Chester River. During this period, oyster populations experienced severe total observed mortality rates of nearly 60%.

Persistently high streamflows in 2003 and into 2004 effectively caused both oyster diseases to subside throughout the entire population range. By 2004, the extent of MSX disease was confined to limited areas in southern Maryland and dermo disease prevalences and intensities plummeted (Tarnowski 2005). The years since were characterized by a succession of average streamflow years – an unusual pattern when compared with the streamflow extremes of the 1990s and early 2000s. Disease levels began to creep back up during the late 2000s, notably dermo disease in 2007 and MSX disease in 2009, but timely pulses of freshwater inputs moderated disease levels and effects (Tarnowski 2010a, 2011). Consequently, observed mortalities remained below the 1985-present average for eight consecutive years. In a reprise of 2003-04, the strong freshwater flows of 2011 purged MSX disease from all but one of the oyster bars examined, and drove down dermo disease to newly-established lows.

One of the major dilemmas in Maryland oyster population dynamics is that some of the same factors that have a positive effect (enhanced recruitment) can also have negative impacts (disease-related mortality). Both oyster reproduction/recruitment and the life-cycles of oyster parasites may be positively influenced by higher salinities and temperatures. Following a good spat set in 2002 - the last year of the millennial drought and record high disease levels - suboptimal freshwater flows kept recruitment below or at median values for much of the same period that disease levels were below average. The exception was 2010, when recruitment occurred throughout the bay, resulting in a strong spat index. Below average streamflows for a critical period of that year along with a sharp temperature increase may have been positive factors in this recruitment, but they also helped maintain the broad geographic range of MSX disease following its expansion in 2009 (Tarnowski 2011). Note that although adequate salinities and favorable temperatures are necessary, they are not always sufficient conditions for enhanced recruitment and other factors may need to be accounted for (Tarnowski 2010b).

The timing of the high streamflows in 2011 was particularly beneficial to the strong 2010 oyster year class, reducing disease levels to record lows and interrupting a potentially threatening situation, as had been the case with the 2003 inundation for the 2002 oyster year class. A substantial number of those yearling oysters thrived as a result, which was reflected in the 44% increase in the biomass index. This strong recruitment also provided a welcome boost to the new tributary-wide sanctuary program, allowing it to get off to a propitious start.

There were downsides, however, to the elevated 2011 streamflows. Lowered salinities inhibited oyster recruitment, resulting in a 74% decline from the previous year. More striking, several oyster bars located in the Upper Bay suffered remarkably high mortality rates. Included in these were a scattering of 2010 year-class oysters in a region that receives spatsets on a decadal scale. Ordinarily, these yearlings would have been expected to have a high survival rate over a prolonged period since these lower-salinity waters ordinarily provide a refuge from the effects of oyster diseases. It should be remembered, however, that freshet-related mortalities occasionally occur in the Upper Bay. During the 20th century eight major mortality events were documented in this region – in 1908/9, 1916, 1928, 1936, 1943, 1945/46, 1972, and 1996 (Beavan 1947, Engle 1947, CRC 1976, MDNR 2001). Fortunately, the oysters lost to the 2011 freshet represent only a small percentage of the total Maryland oyster population. Regrettably, this offers small solace for the oyster harvesters who work in this region.

In summary, the results from the 2011 Fall Oyster Survey indicate that oyster populations are doing well in most parts of Maryland's Chesapeake Bay, thanks to high survivorship of yearling oysters from the good spat set of 2010. Disease levels were at their lowest since systematic monitoring began in 1990, resulting in oyster natural mortality rates comparable to the years prior to the disease epizootics of the mid-1980s. Although high freshwater flows from heavy rains in the spring and two tropical storms in late summer impacted oysters in the Upper Bay, this represented a relatively small proportion of the total oyster population. The lower salinities proved to be beneficial to the majority of oysters in Maryland by limiting disease, allowing the yearling oysters to thrive. As a result, the 2011 Oyster Biomass Index, a measure of oyster abundance and weight, increased by 44% over the previous year

2014 Fall Survey

Mitchell Tarnowski
MDNR Publ. No. 17-782015-769
July 2015

Implications of the Recent Poor Oyster Recruitment for Future Harvests

Ever since people have been observing oysters, it has been recognized that good spatsets and survivorship are needed for future bountiful harvests. This relationship was again demonstrated by the strong recruitment year of 2010, which, coupled with subsequent improved survivorship, above average growth rates, and elevated market prices, have led to the highest landings in fifteen years with a dockside value of $14.1 million for the 2013-14 season. The 2010 cohort was bolstered by another successful year class in 2012 which has not yet fully entered into the fishery. The 2012 cohort is expected to carry harvests through the next couple of years, barring a significant mortality event. Consequently, during the past four years the number of surcharges paid by watermen who wished to harvest oysters has nearly doubled to over 1,100.

The recruitment/harvest relationship is dependent on good survivorship of spat to market size. Beginning in the 1980s, disease epizootics disrupted this relationship by killing oysters before they could reach market (Krantz 1996). For example, the exceptional 1997 cohort was just entering the fishery when a four-year epizootic, the worst on record, struck Maryland's oyster populations. By 2002, almost 60% of the oysters throughout state waters were dead and landings plummeted.

Market forces and regulatory changes can also affect landings and their relationship with spatset. Despite a decrease in recruitment during the 1970s, oyster harvests actually increased, driven by higher demand and prices. This was a result of severe oyster losses to disease in Virginia and a change in law to permit Maryland watermen to fish in any county rather than just their county of residence, resulting in localized overexploitation of the resource as boats converged on a confined area from around the Bay (Krantz 1996). In recent years reduced production from the Gulf Coast states has placed a premium on Maryland oysters, leading to an increase in the number of watermen participating in the fishery and greater fishing pressure. The spike in harvests during the 2012-13 season was so abrupt that dealers could not handle the volume, resulting in industry imposed restrictions on harvesting days from five to three days a week (F. Marenghi, MDNR, pers. comm.).

The high spat-production years of 2010/2012 have been followed by two successive years of mediocre to low recruitment. This is characteristic of Maryland oyster populations, where above-median recruitment can be expected roughly once every four years. Potential factors influencing the highly variable and generally poor recruitment in Maryland were discussed in Tarnowski (2010a,b). Spat set was particularly poor in 2014, with the Spat Index at slightly over half of the 30-year median.

Past experience has proven that without successive spatsets, harvests will decline after a strong year class has played out, as evidenced by the strong recruitment years of 2002 and 2006. As a consequence of a spat set in 2002 that was double the long-term median, harvests had a slight uptick two years later, followed by a sharp increase in the 2005-06 and 2006-07 seasons. During this period, however, recruitment was well below the median. Thus, these elevated harvests were sustained by the 2002 year class for only two years before crashing in 2007-08.

Meanwhile, most of the 2006 year class reached market size in 2009, resulting in another spike in landings. However, this lasted for only one season before a sharp decline occurred in 2010-11 for lack of oysters due to depressed recruitment from 2007 to 2009.

A similar pattern is developing for the current period. A dominant recruitment event in 2010 was followed by steep increases in landings two to three years later (this year class seemed to be faster growing than usual, so began entering the fishery in larger numbers a full season earlier than expected). In this case, however, another strong year class followed in 2012. If natural mortalities remain low, the fishery should be sustained through the 2015-16 season, after which it can be expected to seriously decline due to the poor recruitment years of 2013-14, especially if the elevated fishing pressure of the past couple of years continues.

To reduce the severity of the next crash, the 2012 year class should be conserved to extend its harvest for at least another season. With the collaboration of the industry, this could be accomplished by reducing the fishing effort during the 2015-16 season using various measures such as a cap on licenses/surcharges, a reduction in the daily harvest limit and/or permitted times, and the introduction of areal management schemes such as rotational harvests.

Even with such conservation actions, the harvests should be expected to fall somewhat, then precipitously by the 2017-18 season. Should a strong year class occur in 2015, it would start entering the fishery that season, ameliorating the downslide, but recruitment levels won't be known until the 2015 Fall Survey. However, in anticipation of a decline, harvest restraints applied now would help to bridge a projected harvest gap between the 2012 year class and the next dominant recruitment event.

A key role of the Fall Survey and reports such as this is to gather and disseminate data about Maryland's oyster populations for informed and proactive management decisions. Based on the findings from the 2014 Survey, the Shellfish Division urges discussion and action on this important issue facing the harvestable stocks and the oyster industry.

2015 Fall Survey

Mitchell Tarnowski

Publication #17-5232016-823
June 2016

Present Conditions and Trends

One striking aspect of environmental conditions during 2015 was that the annual mean monthly streamflow was the lowest since the 1999-2002 drought. Consequently, salinities during 2015 have been higher than average through most of the year, since freshwater input determines salinity in Chesapeake Bay. Salinity in turn is a key factor influencing oyster reproduction and recruitment, disease, and mortality (Tarnowski 2010b).

Oyster recruitment is affected by salinity, both directly and indirectly (Kimmel & Newell 2007). If salinity is below a critical threshold the likelihood of a spatfall failure is assured. The timing and volume of streamflows (which modulate salinities) is important; the March – May period appears to be a good indicator of recruitment potential. However, favorable salinity is a necessary but not always sufficient condition to ensure a good spatfall (Tarnowski 2010b).

The elevated salinities of 2015 should have resulted in a strong recruitment year. Indeed, the 2015 Spat Index was 50% higher than the 31-year median, but the overage was due entirely to a high spatset on Chicken Cock bar in the St. Marys River. In fact, the lower Potomac River region, including the lower St. Marys River, experienced the best recruitment in 30 years, but aside from this region, spatset in Maryland was generally spotty and irregular. In Tangier Sound, the range of spatset was 0 to 518 spat/bu, with most of the results only reaching double digits at most. Further upbay some regions lacked spatsets altogether. As a result, despite the higher Spat Index, recruitment can be considered indifferent for the third year in a row, with a statistical ranking of only Tier Four (out of six) (Figure 3a). While southern waters may see an uptick in harvests in about three years, other areas, notably Eastern Bay, will continue to struggle.

The rapid and extensive range expansion of MSX disease during 2015 was likely facilitated by the elevated salinities, similar to past patterns in Maryland (Tarnowski 2010b). Oyster parasites are salinity sensitive, particularly *H. nelsoni* (Ford 1985, Ragone & Burreson 1993). *Haplosporidium nelsoni* can exist in salinities as low as 10 ppt, but it becomes substantially more pathogenic in salinities greater than 15 ppt and temperatures greater than 20°C (Ford 1985). Mid-bay locations such as monitoring buoy CB4.2C, which typically experience lower salinities, consistently had salinities above this range, enabling the spread of MSX disease as far upbay as Eastern Bay, although often at low prevalences.

The highest prevalences of MSX disease were detected in several oyster populations in southern Maryland, where salinities in certain areas approached 20 ppt, although related mortalities have been low. There are two main hypotheses as to why mortalities have remained below average, which are more fully explained in Tarnowski (2010b). Briefly, the first is that oysters have developed resistance or tolerance to the disease. Alternatively, the lower mortalities may be due to favorable environmental conditions, both short-term and extending over a decade, which have been well documented in past Fall Oyster Survey reports. The timely freshwater pulse in July 2015, which reduced mid-bay salinities to below 10 ppt, may have mitigated more serious negative impacts from MSX. Nevertheless, if the trend in elevated salinities continues well into 2016, it could test these hypotheses.

Dermo disease acquisition is influenced by thresholds of salinity and temperature, with infection prevalences and intensities typically rising with increases in these conditions (McCollough et al. 2007). While dermo disease is considered enzootic in Chesapeake Bay, not all infections are lethal or progress to lethal intensities. Environmental conditions mitigate or promote infection intensities. Increasing salinities and temperatures create favorable conditions for infection intensification, particularly in areas where otherwise typically lower salinities hold the progress of the disease in check. Both the percentage of moderate to high infection intensities and the percentage of lethal infections increased in 2015. The sample collected from Stone Rock exhibited the highest mean infection intensity on record (Table 3). Should higher salinities persist into the summer of 2016, *P. marinus* may contribute significantly to oyster mortality throughout the bay. Those populations in higher salinity areas may well experience twin stresses from both dermo and MSX disease combined.

The positive trend in the Chesapeake oyster populations over the past dozen years likely can be attributed to the generally favorable salinities during this period. The record-high disease-related mortalities at the turn of the millennium subsided during the high streamflow years of 2003-2004, dropping to pre-disease levels and has remained below the long-term average up to the present (Figure 11, Table 5). This allowed oyster stocks to rebuild, slowly during the first few years then explosively, driven by strong year classes in 2010 and 2012 (Figure 13). The resulting increase in landings is likely short-lived due to indifferent spatsets following 2012 and a downturn is expected (Tarnowski 2015).

As already mentioned, one of the most critical physical factors influencing oyster populations is salinity. But salinity is dependent on highly variable circumstances, including the frequency, intensity and timing of storm systems as well as accumulated snowpack and the rate at which it melts. Therefore, offering reliable predictions about recruitment and disease-related mortality become more difficult the further into the future a projection is made. An additional complication is the variety of other factors, some probably unknown, that can account for successful recruitment when salinities are adequate (Tarnowski 2010). The relationship between salinity and oyster diseases is more straightforward, but a random event such as a well-timed tropical storm can lower salinities over a brief duration, lessening disease pressure on the oyster populations.

Because of the highly variable nature of the conditions influencing these key population properties, the ability to predict them dwindles to nil over a relatively short period into the future.

A key role of the Fall Oyster Survey and associated reports such as this is to gather and disseminate data about Maryland's oyster populations for informed, timely, and proactive management decisions. For example, based on the findings from the 2015 Survey, the Potomac River Fisheries Commission shut down the lower Potomac fishery to protect the exceptional spatset that year from dredging-related mortality. But no survey can predict what the future may bring, whether an abundance of oysters to harvest in a few years or a disease-ravaged population. This will be left to the vagaries of nature.

2016 Fall Survey

Mitchell Tarnowski
DNR 17-582017-662
May 2017

Recent Trends and Present Conditions

By most measures, 2013 appeared to be a turning point for oysters in Maryland. Battered by devastating epizootics around the turn of the millennium and followed by a protracted recovery period, the oyster population finally was on the upswing. The Biomass Index was the highest since the index was established in 1990, boosted by strong recruitment events in 2010 and 2012 and accompanied by the lowest observed mortalities since the pre-epizootic years of the early 1980s. Dermo disease levels had remained below the long-term average for the tenth year out of the previous eleven and MSX disease was confined to two limited areas in the southern portion of the Bay. Landings during the 2012/13 season jumped two and a half-fold over the previous year, while the number of watermen purchasing surcharges to harvest oysters nearly doubled. This rebound was a welcome respite from the difficulties of the previous decade.

Not all the indices in 2013 were positive. The Spatset Index sat indifferently at the long-term median, but was not cause for concern since recruitment in Maryland has always been highly volatile on a year-to-year basis, exceeding the median about once every four years. Despite their extremely low levels, MSX disease prevalence and observed mortalities increased slightly, but well within the presumed range of sampling variability.

Oyster population indicators for 2014 were mixed. Landings during the 2013/14 harvest season surged to their highest in 15 years. The 2014 Biomass Index was close to the previous year's record-high index, as growth in the 2012 cohort balanced the removal of oysters by harvesting. Dermo disease levels fell somewhat, but MSX prevalences and observed mortalities increased for a second consecutive year. Recruitment was abysmally poor - the lowest since 2005 -with the index at only half of the long-term median, raising concerns about near-future harvests (Tarnowski 2015).

Trends within the oyster population continued to deteriorate in 2015. Oyster harvests slipped somewhat, consistent with the decline in the Biomass Index. The Spatset Index appeared to be well above the long-term median, but only because most of that increase resulted from a single bar. In most other areas, recruitment was unremarkable, with the exception of the north shore of the lower Potomac River, which experienced its best spatset in a third of a century. Other indices were even less favorable. Dermo disease prevalence and intensity both rose to their highest levels since 2007. Most troubling, MSX disease prevalence rose sharply, tripling from the previous year and expanding its geographic range all the way upbay to the Eastern Bay region. In addition, the Observed Mortality Index continued to climb, albeit modestly. These negative changes were associated with lower streamflows, hence higher salinities. The United States Geologic Survey characterized 2015 as a dry year for the Bay, with freshwater inflows below the normal range.

The negative trends persisted into 2016 to varying extent. The Dermo Intensity Index rose above the long-term average for the first time in nine years and was its highest since the drought-related epizootic in 2002. Elevated intensities were found from Pocomoke Sound north to the Wye and Miles rivers. The geographic range of MSX disease remained similar in extent as the previous year, but prevalences increased on numerous bars. The annual mean prevalence climbed more than 50% from the previous year and has multiplied 20-fold over the past three years.

The Observed Mortality Index was deceptively muted, with the index increasing only slightly from the previous year and remaining below the long-term average. However, the mortality trend continued upward; the index has doubled over the last three years. Regional and individual bar mortalities reveal a more ominous picture. The increases in the observed mortalities were uneven, with notable hotspots in the Little Choptank, lower Choptank, and lower Potomac rivers. The average observed mortality for the lower Potomac region exceeded the long-term Maryland-wide mean by over 50%. Several bars had elevated observed mortalities as high as 60%.

The exception to these negative trends was recruitment, which has been above or close to the 32-year median in six of the last seven years. In comparison, during the recovery period of 2003-09, six of seven years were below the long-term median. Spatset improved in 2016 over the previous three years with gains on a number of Key index bars. Nevertheless, the 2016 index was approximately half of the robust 2010 and 2012 indices. Only about half of the 2016 index bars received meaningful spatsets; whether this is sufficient to stabilize the population and support a robust fishery in the next few years remains to be seen.

Maryland's Oysters at a Crossroad

Referring back to 2013 in light of current trends, did that year mark an actual turning point for oyster recovery, or was it an aberrant peak, with the population now slipping back towards levels of the post-epizootic decade? Or is the recent backslide temporary, propelled by below-normal freshwater flows which elevated salinities?

Salinity is a key factor influencing oyster reproduction and recruitment, disease, and mortality (Tarnowski 2010b). There is a delicate balance between enhanced recruitment and devastating disease. Both are favored by higher salinities, although in the case of recruitment adequate salinity is necessary but not always sufficient for a strong spatset. In terms of recent salinities, disease appears to be poised at the edge of a full-blown epizootic, with salinity values that are borderline above the mean. During 2016 they averaged slightly less than 2 ppt above normal at two reference stations, enough to allow MSX and dermo disease levels to increase along with some mortalities. Diseases can be anticipated to intensify with a probable increase in mortalities if freshwater inputs are further reduced by even a modest amount. On the other hand, a slight increase in streamflows would have the opposite effect, stabilizing mortalities while allowing potential recruitment. At the extreme, a good slug of fresh water into the Bay would actually purge MSX from many upstream areas and reduce its virulence downbay. Likewise, the impacts from dermo disease would probably be reduced. Unfortunately, snowpack in the Susquehanna watershed was negligible this past winter so a potentially beneficial freshet did not occur – the 2017 streamflows were down in February and 41% below normal during March, typically a high-flow month. At this point, an extended period of heavy rains might provide relief from disease, but any impactful increase in freshwater inputs would almost certainly negate the possibility of a meaningful recruitment event. Only time - and weather - will determine which direction Maryland's oyster population will take. The ecological services and economic support to bayside communities our oysters provide are dependent on the outcome.

2017 Fall Survey

Mitchell Tarnowski
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August 2018

The Importance of Oyster Shell

The importance of shell as habitat for maintaining oyster populations and associated organisms has long been recognized. Oyster reefs and their faunal assemblages were the basis in developing the concept of an ecological community during the late nineteenth century (Möbius 1883). In 1890, the Maryland legislature passed the "cull law" requiring harvesters to return not only undersized oysters (at that time less than 2.5 inches) but also the shell that was caught incidentally to the oyster bar of origin (Laws of Maryland 1890, Ch. 602).

During the 1920s, Maryland established a routine bar replenishment program planting shells from shucking houses. This was greatly expanded in 1960 with a large-scale buried shell dredging and planting effort which lasted until 2005.

Shell adds structure and firm substrate to the estuary, contributing habitat that is in stark contrast to the otherwise soft bottom environment of the bay. These shell reefs enhance recruitment and survival of shellfish species, increase species diversity and abundance, and create vertical features on the bay bottom (Powell and Klinck 2007), which alter water circulation patterns, reduce sedimentation, and provide an elevated refuge from deeper water hypoxia. In the Chesapeake Bay the most important source of shell substrate is oyster shell.

Oysters are unique among the species in Chesapeake Bay in that they create their own habitat. Larvae of *C. virginica* require a firm, sediment-free surface upon which to settle and attach (Kennedy 1996). Also, the structural complexity that shell provides creates refuges from predation for the young oyster spat as well as other species. The larvae's gregarious settlement response produces dense aggregations of oysters coexisting with a diverse and abundant assortment of associated organisms in communities. Thus, oysters are considered a keystone species because as ecological engineers the structures they build support a vast array of species which are the foundation for complex food webs within the estuary (Mann and Powell 2007).

A shell budget is an accounting of shell accumulation balanced against shell loss, much like a bank account. Shell accretion is dependent on oyster recruitment, growth, and death (Mann and Powell 2007). Under natural conditions, shell degradation is due to a combination of taphonomic factors, where shell is lost through chemical (e.g., dissolution), physical (e.g., sedimentation, subsidence, breakage, dislodgement from the bar), and biological (e.g., shells riddled by boring sponges, polychaete worms, etc.) processes (Soniat et al. 2014). For reefs to build, the rate of shell accretion must exceed the rate of shell loss, which under natural conditions occurs by some small amount (Mann and Powell 2007). The extraordinary outbreaks of disease epizootics in recent decades and two centuries of harvesting have disrupted this balance (Soniat et al. 2014, Powell and Klinck 2007).

Recruitment is a key factor in reef accretion, in that small changes in recruitment can produce large changes in shell abundance (Powell and Klinck 2007). The issue in Maryland is that recruitment is notoriously variable, as was evident in the boost to the cultch index following the strong recruitment of 2010 and 2012 and its subsequent decline after a series of indifferent spatsets. Furthermore, there are distinct regional differences in recruitment, resulting in disparities in the cultch index between low recruitment regions such as the upper bay and higher spatset areas like the lower Eastern Shore around Tangier Sound.

Oysters must die in place in order to add shell to the bar, which in the absence of disease is a natural mortality rate of about 10% annually (Powell and Klink 2007). Although shell is added to the bar in the short term during high mortality events such as the 1999-2002 disease epizootics, unless the bar repopulates with oysters the amount of shell will eventually decline. Catastrophic mortalities are especially problematic in low recruitment regions such as the upper bay, for example, where killing freshets in 2011 resulted in mortalities of up to 100% on some bars (Tarnowski 2012). Little if any spatset has been observed in this region since then to replace the lost oysters, meaning no new shell has been added naturally to the bars. Because taphonomic processes are constantly degrading the shell base, the bar will slowly disappear unless shell is continuously replaced, either naturally or through management intervention. Over a period of time, shell either taphonomically degrades, is removed, or is incorporated into the core of the reef by the overgrowth of new oysters. For example, the half-life of shell in Delaware Bay has been estimated to be between two and ten years (Powell et al. 2006). Whatever the pathway, it eventually becomes unavailable as substrate for oyster larval settlement. Therefore, rebuilding oyster populations entails more than simply putting oysters in the water; it requires concomitantly rebuilding habitat as well (Mann and Powell 2007).

Powell and Klink (2007) assert that the decline of oysters in the Chesapeake is associated with a decline in the shell resource. Large swaths of formerly productive oyster bars in Maryland now have little if any shell. The problem is especially acute in the mainstem, but shell loss is occurring on many bars throughout the bay. Even in areas that have shown net gains recently, such as the Tangier Sound region, individual bars are degrading (e.g., Old Woman's Leg, Back Cove Lot #1). The deterioration of the oyster bars has undoubtedly had a profound effect on the Chesapeake ecosystem. In the soft bottom estuaries of the mid-Atlantic region, hard substrate for the attachment of epibenthic organisms is at a premium, provided mainly by biogenic processes. Chief among these are oyster reefs, contributing structure and substrate that sustain the rich community of organisms associated with them. The decline of the Chesapeake oyster over the past three decades has resulted in the reduction of a critical functional component of the ecosystem and the gradual disappearance of a significant structural element as well.

2018 Fall Survey

Mitchell Tarnowski

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July 2019

The Consequences of Record Streamflows

One of the most critical physical factors influencing oyster populations, both directly and indirectly, is salinity. Salinity, as a function of freshwater flow, varies seasonally, annually, and spatially depending on weather patterns such as rainfall and snow pack. Changes in freshwater discharges into the Bay can alter salinity regimes sufficiently to affect recruitment patterns, predation, disease pressure, and mortality rates. Depressed salinities can inhibit reproduction and recruitment, arrest feeding, slow growth, and elevate mortalities in marginally viable areas, but reduce disease-related mortalities by lowering disease levels. Even slight shifts in salinities can have profound consequences for oysters in a given area.

The effect of extremely elevated freshwater discharge on oyster populations and consequent oyster survivorship in Chesapeake Bay was again demonstrated in 2018, which had the highest monthly average streamflows in the 82-year record. As a result, the 2018 spat intensity index was subpar, a large pool of sublegal oysters did not grow to marketable size, oyster disease levels fell to their lowest since systematic monitoring began in 1990 (comparable to 2011), and oyster plantings suffered elevated mortalities in the upper bay and were nearly wiped out on the uppermost Potomac River bars.

Reproduction and Recruitment

Suboptimal salinities can adversely impact all phases of oyster reproduction from gametogenesis through settlement and metamorphosis. Gametogenesis is reduced or suppressed during periods of low salinity. Oysters may not be able to feed sufficiently, in which case they must draw on their glycogen reserves, inhibiting the development of gametes (Thompson et al. 1996). Gonadal development is abnormal at salinities of 5 ppt (Loosanoff 1953). Should oysters with near-ripe gonads gape open when salinity conditions are unfavorable their eggs may disintegrate (Loosanoff 1953).

The earlier developmental stages are more sensitive to low salinities; eggs and trocophore larvae cannot survive in salinities below about 10 to 12.5 ppt (Calabrese & Davis 1970). Once the swimming veliger larvae produce shells, larvae can tolerate salinities down to 7.5 ppt from the straight hinge stage through metamorphosis, although at salinities below 10 ppt development is retarded and survivorship lower (Davis 1958, Loosanoff 1965). This is a primary reason why recruitment is so low and sporadic in the low salinity regions of the upper bay and tributaries. Recruitment in these locations (<10 ppt) is likely from late-stage larvae migrating from more favorable areas when conditions are right (Davis 1958). High freshwater flow conditions can contribute to the loss of larvae in upstream regions by physically transporting oyster larvae further down the estuary, essentially flushing them out of an area well beyond the point to which the incoming tide would ordinarily return them.

Feeding and Growth

Freshets can disrupt oyster feeding behavior in different ways. Oysters may simply shut tight in response to freshwater inundation and may remain so for extended periods of time, depending on temperature (Loosanoff 1953, Andrews et al. 1959). Ciliary activity – the mechanism by which oysters feed – slows at about 5 ppt and ceases at 3 ppt (Loosanoff 1953). The food supply itself may also be affected by high streamflows and depressed salinities. Although little is known about phytoplankton population dynamics during freshets, one scenario is that the phytoplankton on which oysters feed are lost to the impacted area, either from intolerance to the lower salinities or by flushing down bay. These may be replaced by species that oysters cannot utilize. Excessive nutrients carried into the waters by runoff may result in noxious algal blooms (Heisler et al. 2008), further inhibiting feeding by adults and larvae.

Regardless of mechanism, it naturally follows that if oyster feeding is negatively impacted, growth would be slowed. Loosanoff (1953) found that growth was stunted at 7.5 ppt and limited or almost absent at 5 ppt. However, the impact of the extended 2018 freshet on oyster growth outside of the upstream areas is unclear. Anecdotally, in 2018 a sizable portion of sublegal oysters presumably failed to attain market size, but the majority of the harvest generally occurs from the Choptank region south, where salinities remained above 7.5 ppt for most of the year (Chesapeake Bay Program Data Hub). In fact, 49.1% of the oysters on the 30 Biomass Index bars were sublegals, with a peak biomass at 77 mm - barely legal (Figure 18). This had obvious implications for 2018-19 season's harvests, but this pool of sublegal oysters should be available for harvest during the following season, mitigating the downward trend in landings over the past few years. Nevertheless, baywide oyster growth in terms of biomass did not seem to be attenuated to any great extent. The Biomass Index bars within sanctuaries actually showed a robust increase in biomass, and even oysters on the harvest bars grew, albeit more modestly.

Freshet-Related Mortality

Having evolved for existence in the highly variable estuarine environment, oysters can tolerate a wide range of salinities from about 5 to 40 ppt, although the optimum range is considered to be about 14 to 28 ppt (Galtsoff 1964). Salinity tolerance values from different studies vary somewhat depending on temperature and the salinity regimes in which the experimental oysters were acclimated and lived. Because oysters can tightly close their valves (shell), they can remain alive during unfavorable salinity events for varying lengths of time depending on the ambient temperature. Oysters can survive freshets for months during the winter when they are in hibernation and can remain in a state of dormancy as late as June (Andrews et al. 1959). Even at temperatures a few degrees above quiescence, oysters have been shown to survive as long as 70 days in freshwater and 117 days at 3 ppt (Loosanoff 1953). However, if oysters have already started pumping when waters warm during the spring and summer, physiological activity increases, leaving oysters more vulnerable to adverse salinity conditions even if they consequently close up (Andrews et al. 1959). Survivorship is reduced to only a couple of weeks during the highest summer temperatures.

Devastating freshets have occurred in Maryland periodically throughout the 20th and into the 21st centuries, causing mass mortalities on vulnerable bars. During this time span ten major mortality events were documented in this region – in 1908/9, 1916, 1928, 1936, 1943, 1945/46, 1972, 1996, 2011, and now 2018 (Beaven 1947, Engle 1947, CRC 1976, MDNR 2001, Tarnowski 2012).

The previous freshwater year, 2011, was marked by a wet spring, a tropical storm, and a late-summer hurricane. However, mortalities were largely confined to the upper bay. Among the unfortunate casualties of this mortality event were the young oysters of the 2010 spatset. Although this spatset was light in the upper bay, it was widespread and was important to help sustain these populations, which receive a set once about every decade (the previous set was in 2002). Spatsets in this region usually have good survivorship, but they are vulnerable to freshets. On Man-O-War Shoal, a bar outside the mouth of the Patapsco River, 100% of the oysters had died by the time of the 2011 Fall Survey. A portion of the bar has been subsequently replanted with seed oysters in recent years. Somewhat surprisingly, mortalities were lower in 2018 (averaging 42.5%) despite the record streamflows, although they may rise if depressed salinities persist into the spring.

The Eastern Shore side of the upper bay tends to have lower mortalities during freshets due to water circulation patterns. In 2011, elevated mortalities were observed much further down bay on the western side. Although the uppermost Eastern Shore bars had a cumulative mortality of 79% that year, Swan Point oysters had much lower mortalities, averaging 17% as compared to the 74% found on the Western Shore bars at the same latitude. The same pattern held true in 2018, when observed mortalities on Swan Point averaged only 8%. In part this is because this is a deeper bar than Man-O-War Shoal (salinity tends to increase with depth). In addition, flow from the Susquehanna River at the head of the bay, the major source of freshwater input, tends to veer towards the Western Shore due to the Coriolis effect. Furthermore, the Eastern Shore bars are adjacent to the deeper shipping channel, which serves as a conduit for higher salinity water during flood tide. As an example, Deep Shoal bar, the uppermost bar sampled during the 2011 Fall Survey, had a surface salinity of 0.9 ppt but a bottom reading of 5.1 ppt. As a consequence, the observed mortality was 53%, about half that of Man-O-War Shoals located several miles down bay.

In contrast to the upper bay, in 2011 the Potomac River did not experience extraordinary oyster mortalities. Unfortunately, this was not the case in 2018, when mortalities were considerably more severe. Observed mortalities ranged from 88% to 100%, a substantial loss to the fishery since several of these bars had been planted with seed oysters. Even the unique low-salinity adapted oyster population on Beacon bar, which had survived several freshets during the 1990s and 2000s, suffered nearly total mortalities. One concept to restore that bar is to reseed it with hatchery-reared progeny of the surviving broodstock, but a source of funding must be secured to carry out the project.

Disease and Disease-Related Mortality

The influence of salinity on oyster diseases is well documented (Ford & Tripp 1996; Tarnowski 2010b, 2012). Oyster parasites are salinity sensitive, particularly *H. nelson*i. This parasite can exist in salinities as low as 10 ppt, below which it is purged from oysters. However, MSX disease becomes substantially more pathogenic in salinities greater than 15 ppt and temperatures higher than 20°C (Ford 1985).

This vulnerability of *H. nelson*i to lower salinities was dramatically illustrated in 2004, when persistently-high freshwater runoff pushed back MSX disease from its record high prevalences and extended range throughout much of Maryland waters during 2002 to relatively small areas in Tangier Sound and the lower mainstem (Tarnowski 2005). This pattern was repeated in the freshet years of 2011 and again in 2018. In 2017, the disease was found as far up bay as Hacketts bar near Annapolis. By 2018 its range had contracted to two lower Eastern Shore locations; only three out of the 1,499 oysters examined were found to have the disease.

Likewise, dermo disease, although still widespread, was at levels near or at their lowest point in 29 years, matching the record low levels of 2011. However, the host-parasite relationship as affected by salinity between oysters and *P. marinus* is considerably more involved than that described for MSX. Until the late 1980s - early 1990s, dermo disease epizootics would occur in the higher salinity bay regions and penetrate up bay only during low freshwater flow periods. Since the early 1990s, however, this disease has entrenched itself in the bay's oyster population; it is now an enzootic condition found almost everywhere oysters are present. Salinity patterns and resultant infection status observed prior to the onset of chronic dermo disease no longer apply to oyster populations. As described here, 2018 has seen a remarkable abatement of dermo disease on a baywide basis, measured by both prevalence and intensity. While environmental conditions can adequately account for what has been observed in recent years, the perceived evolving relationship, most likely still strongly influenced by salinity, between oyster and *P. marinus* populations is not fully understood.

As a consequence of reduced disease pressure, the 2018 mortality index was stable despite the freshet-related losses in the upper bay and Potomac River. Nonetheless, the index was almost double that of the previous freshet year of 2011, suggesting that some disease-related mortalities occurred in the earlier part of the year before salinities began to decline. The highest MSX disease prevalences of 2017 were detected in Tangier Sound and the adjacent lower mainstem, coinciding with the highest regional mortalities of 2018. Since the surface salinity in southern Tangier Sound remained intermittently above 15 ppt into September, it is possible that these mortalities were MSX-related. The only residual pockets of *H. nelson*i were found in this region, including at one of the deepest stations adjacent to the main channel in southern Maryland, the one most likely to maintain the higher salinities conducive to MSX disease.

2019 Fall Survey

Mitchell Tarnowski

DNR 17-050420-232

July 2020

Streamflow – Timing is Everything

The consequences of the elevated streamflows over the first half of 2019 and the timing of its return to normal during that summer were mixed. The most dramatic of the adverse effects were the catastrophic mortalities suffered by the oyster populations on the most upriver bars of the Potomac River. What few oysters remained during the 2018 Fall Survey succumbed to the continued onslaught of freshwater afterwards. Observed mortalities were 100% on the seven farthest upstream Potomac River sites surveyed in 2019.

Recruitment was also impacted throughout large swaths of Maryland waters. The abatement of streamflows and return to normal salinities occurred too late in many areas to allow for spawning and/or spatset, which ordinarily begins in June/early July, but can be inhibited by depressed salinities (see Tarnowski 2019 for a review of the effects of low salinities on oysters). The broodstock oysters may have been in poor condition due to sustained exposure to these low salinity conditions. Another possibility is the phytoplankton that they feed on may have been sparse or of a different community composition more suited to lower salinities, which the oysters were unable to fully utilize. Either situation would affect their ability to store the energy reserves needed for gametogenesis. Further exacerbating the problem, the inability to feed sufficiently also causes oysters to draw on whatever glycogen reserves they have remaining from overwintering (Thompson et al. 1996). This could account for the poor spatfall in normally productive areas such as Broad Creek. This tributary actually had higher recruitment in 2018, probably because of spring salinities favorable to oyster condition and gametogenesis before the summer deluge began.

Further downbay, the situation was quite different. The surface salinity in southern Tangier Sound remained at or above 10 ppt through the winter and into spring, sufficient to allow the initiation of the gametogenic process (Loosanoff 1953, Calabrese & Davis 1970), even though it was below average for that time of year in that region. The elevation in salinity during May and into mid-summer was well timed for successful spawning and spatfall (Thompson et al. 1996). The result was a geographic band of elevated spatfalls from middle and lower Tangier Sound across the bay to Pt. Lookout, with counts ranging from about 100 spat/bu to 350 spat/bu.

The influence of salinity on oyster diseases is well documented (Ford & Tripp 1996; Tarnowski 2010b, 2012). Oyster parasites are salinity sensitive, particularly *H. nelson*i. The below average spring/early summer salinities, coupled with low salinities of the previous year, suppressed the development of diseases to striking effect – disease levels were the lowest in the 30-year time series. Although MSX disease can exist in salinities as low as 10 ppt, below which it is purged from oysters, it becomes substantially more pathogenic in salinities greater than 15 ppt and temperatures higher than 20°C (Ford 1985). But by the time salinities returned to normal, it was too late in the year for diseases to progress to any great extent. As a consequence of reduced disease pressure, the 2019 observed mortality index remained below the long-term average despite the freshet-related losses in the upper bay and Potomac River.

The timing of the reduced freshwater flow also benefited oyster growth, which had been depressed from the prolonged freshet. With salinities returning to normal in the late summer and early fall, at least two year classes of sublegal oysters began attaining market size simultaneously, just in time for the 2019-20 harvest season.

The Status of Tangier Sound Oysters

Several notable metrics call attention to the current status of the oyster population in Tangier Sound. As one of the most productive regions in Maryland, Tangier Sound historically has been the center of the oyster industry in the state. Although this productivity is in part due to its higher salinity regime, for the same reason it is also an area that has been battered by diseases, and has been especially vulnerable to MSX disease. During the 2000-01 season, in the middle of the millennial epizootics, soaring mortalities as high as 61% were observed on some bars and harvests sank to a scant 1,550 bu, or only 4% of the total Maryland landings. And yet, despite this devastation, by the 2013-14 season landings had rebounded to 103,000 bu, the highest since the 1985-86 season and three times the 34-year average, which speaks to the resiliency of this population. Landings continued to be above the long-term average until this past (2018-19) season.

The disease results of the 2019 survey in Tangier Sound have turned long-term patterns of geographic distribution on its head. Expected increased levels of disease with increased salinity did not occur and were below the baywide average; despite the near ubiquity of dermo disease in Maryland oysters, it was not detected in three of the five disease monitoring stations within Tangier Sound (Holland Straits bar is included in this group). The average prevalence was 16% compared with the 2019 baywide average of 27% and the 30-year average in Tangier Sound of 73.8%. Likewise, the average infection intensity was 0.58 versus 0.97 baywide and 2.6 for the 30-year average. To give an idea of how exceptional the Tangier Sound dermo disease levels were, note that the 2019 baywide averages for both prevalence and intensity were the lowest in the long-term time series. Furthermore, MSX disease, a past scourge of Tangier Sound oysters, was not detected in oysters at any of the five standard monitoring sites.

The exceptionally low disease levels consequently inverted the spatial model for mortality. Observed mortality for all Tangier Sound bars was 4.2% and 3.3% for the subset of the five disease/mortality index bars, compared with 13% for the 2019 baywide mortality index and 28.7% for the long-term average of those five Tangier Sound bars. This is in contrast with the upper reaches of the bay and tributaries, where elevated 2019 observed mortalities ran as high as 100% at some locations due to prolonged high freshwater flows.

Equally noteworthy was the good spatset experienced in Tangier Sound, in particular the middle and lower portions of the sound. For example, Great Rock near the Virginia line had spat counts that were four times its long-term average. Bars in this region had the highest counts since the strong 2010 and 2012 year classes. This same portion of the sound also had an above average spatset in 2018, though the counts were not nearly as high as in 2019.

This strong recruitment event brings to focus two issues in particular. First is the question of the source of the larvae that generated this spatset. Given the present state of scientific expertise, the source of these larvae is unknowable, so this topic is largely speculative. What brought attention to this issue was the low average density of oysters in Tangier Sound relative to nearby tributaries. Two of these tributaries, both with oyster sanctuaries within them, have substantial numbers of broodstock oysters that could very well have provided the larvae. As noted in Table S-1 of the Sanctuary section of this report, the Manokin Sanctuary averaged over eight times the number of broodstock oysters in a bushel sample as did the adjacent high recruitment area of mid-Tangier Sound. In addition, the Nanticoke River Sanctuary, with its substantial natural oyster population (averaging 172 adult oysters/bu sample), augmented by numerous oyster aquaculture operations, sits atop Tangier Sound. This difference is even starker when looking at oyster densities over a fixed tow distance, using the same methodology as was used to determine the Cultch Index. On average, a nearly threefold longer tow distance was required to obtain a sample in Tangier Sound than in these two tributaries. The mean number of adult oysters per 100 ft. tow distance in Tangier Sound was 17 oysters/100 ft., compared with 490 oysters/100 ft. in the Manokin Sanctuary and 271 oysters/100 ft. in the Nanticoke Sanctuary. Since oysters release their gametes into the water column when reproducing, the higher the oyster density the greater the probability of fertilization success (Thompson et al. 1996).

Other possible sources of larvae are suggested by the widespread nature of the southern Maryland recruitment event. This spatset, stretching from Tangier Sound across the bay to Point Lookout, may have resulted from a larval swarm from Virginia, riding saltier tidal currents upstream. Alternatively, there could have been two or more independent sources, benefitting from the mid-year increase in salinity. And, of course, the Tangier Sound oysters could have produced the larvae, but as noted, the broodstock/bu and densities/100 ft. in the sound proper were much lower than those of adjacent areas. But to repeat, the actual source of larvae producing the strong Tangier Sound spatset is unknown.

These findings lead to the second issue of concern. The longer tow distances required to obtain a sample in Tangier Sound compared to adjacent tributaries implies not only a lower density of oysters but also a lower quantity of cultch habitat. Although the Tangier Sound region ranked highest in the Cultch Index comparisons, the higher cultch densities were actually found in the surrounding tributaries. Combined, these tributaries (including the Manokin, Wicomico, Nanticoke, and Honga rivers, Pocomoke Sound, and Fishing Bay) averaged more than twice the quantity of cultch per 100 ft. tow distance than Tangier Sound proper (tributaries = 1.33 bu/100 ft. vs. Tangier Sound = 0.60 bu/100 ft.). Therefore, the high volumetrically assessed spatset (spat/bu) was actually found on a lower abundance of cultch scattered over a larger area, requiring a longer tow. Consequently, the density of spat (spat/area) was much lower than suggested by the volumetric measure. In other words, had the cultch density of Tangier Sound been as high as those in the surrounding tributaries, there likely would have been more spat.

The importance of cultch and maintaining a balance of shell for oyster habitat cannot be overemphasized. Larvae of *C. virginica* require a firm, sediment-free surface upon which to settle and attach, and their gregarious settlement response can produce dense aggregations of oysters. Additionally, oysters are unique among the species in Chesapeake Bay in that they create their own habitat. The shell cultch adds structure and firm substrate to the estuary, contributing habitat that is in stark contrast to the otherwise soft bottom environment of the bay. In addition to enhancing recruitment, the structural complexity the shell provides refuges from predation for the young oyster spat as well as other species. Therefore, rebuilding and maintaining oyster populations entails more than simply putting oysters in the water; it requires concomitantly rebuilding habitat as well (Mann and Powell 2007). Options include planting more shells, excavating buried shell in the region, and planting an alternate substrate suitable for harvest areas. **C**reative solutions may be required to effectively improve the availability of cultch.

In the near term, there is cause for optimism for the Tangier Sound fishery. Following the strong spatsets of 2010 and 2012 there was an uptick in harvests which lasted four years before winding down in the 2016-17 season. During this period landings averaged 88,000 bu/year; since then, they have averaged about 36,000 bu/year. Meanwhile, a sizable proportion of the 2015/16 year classes have transitioned to market-size oysters, which could mean an increase in harvests in the upcoming season. The 2019 spatset, which was comparable in magnitude to that of 2012, should provide a further boost to the landings, supplemented by the 2018 set. This is contingent on whether nothing untoward happens during that time frame, such as a disease epizootic. However, disease levels and consequent mortalities have generally remained below average for the past 15 years. If this trend continues Tangier Sound could see respectable harvest levels in upcoming seasons. Given the poor recruitment in the Choptank region this past year, there may be a falling off of landings there, leaving Tangier Sound all the more important to sustaining the oyster fishery in Maryland over the next few years.

2020 Fall Survey

Mitchell Tarnowski
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Trends in Oyster Population Indicators Improve

The past decade was marked by advances and setbacks for oysters in Maryland. Battered by devastating epizootics around the turn of the millennium, followed by a protracted recovery period, the oyster population finally was on the upswing, beginning with a strong recruitment event in 2010. By most measures, 2013 appeared to be a turning point for oysters in Maryland, including the highest Biomass Index in the time series. But by 2016, with the Chesapeake region in the grip of a two-year drought, conditions had begun to deteriorate. Indifferent spatsets in 2013 and 2014, followed by rising disease and mortality levels and harvesting on the abundant 2010 and 2012 year classes, contributed to a 33% drop in the Biomass Index from its 2013 peak. Oysters appeared to be at a crossroad. Would the downward trajectory continue or would environmental conditions improve and reverse the trend? Then came the record high streamflows in 2018 that devastated some regions and stunted growth in others, and resulted in a below-median spatset. At the same time, other metrics improved. Disease levels plummeted and the Biomass Index actually increased due to the 2015/16 year classes. With freshwater flows returning to normal by mid-2019, oyster populations in many parts of Maryland appear to be rebounding. The last two years have been particularly favorable to oysters, as reflected in the primary population indicators:

- Strong recruitment
- Good growth
- Record low disease levels
- Well below average mortalities
- Third-highest biomass index

Although impossible to predict what the future holds, the recent positive direction the oyster population has taken recently is a welcomed turn that is cause for cautious optimism.

Strong Recruitment

Broad Creek, historically a commercially productive tributary of the Choptank River, experienced the highest average spat count for any region since 1997, when Eastern Bay and its tributaries had among the highest average regional spatsets on record. In 2020, several bars had spat counts of over 1,000 spat/bu; Deep Neck, a Key Spat Index Bar, led with over 1,800 spat/bu, the second highest in the 82-year time series for that bar.

Equally encouraging are the two successive years of strong recruitment in the commercially important Tangier Sound region, centered in mid-Tangier Sound, with even higher counts in 2020 than the previous year. The actual source of larvae producing this robust spatset is unknown. This area is immediately outside of the Manokin River Sanctuary, which may have provided the larvae from the substantial number of broodstock oysters found there. In addition, the Nanticoke River Sanctuary, with its sizeable natural oyster population (averaging 303 adult oysters/100 ft. sample), augmented by numerous oyster aquaculture operations, sits atop Tangier Sound, an ideal location for suppling larvae to the northern reaches of the region. Other possible sources of larvae may have been Virginia, which has more consistent spatsets associated with a higher salinity regime. Alternatively, there could have been two or more independent larval sources. And, of course, the Tangier Sound oysters could have produced the larvae, although the average broodstock density (small and market oysters) standardized to a 100 ft. tow was four to five times lower in Tangier Sound proper than in the adjacent sanctuaries. Whatever the source of the larvae, the back-to-back years of successful recruitment bodes well for these oyster populations in the near term.

Adequate salinity is a necessary though not always sufficient requirement for strong recruitment. The return to normal salinities in 2020 set the stage but it is unknown what other factors, if any, contributed to such good spatsets in some areas, or conversely, why other regions such as on the lower Western Shore underperformed.

Good Growth

Like recruitment, somatic growth depends on proper salinity, as well as an adequate supply of proper nutritional sources, among other requirements. The depressed salinities during 2018/2019 inhibited growth, especially among the sublegal oysters (Tarnowski 2020). After salinities returned to normal during the second half of 2019, the average shell height of oysters on the biomass index bars in the commercial areas jumped from 69 mm in 2018 to 76 mm in 2019. As a result, many of the small oysters from the 2015/16 year classes attained the minimum legal size limit, which contributed to the 86% increase in landings during the 2019-20 season.

In 2020, growth rates in the previously established populations slowed naturally as the oysters aged. What was striking, however, was the exceptional growth of the hatchery-reared spat planted in commercial areas (Appendix 1). Although variable due to environmental conditions, the general rule of thumb for oyster growth rates in Maryland during their first three years is 1 in. (~25 mm) per year (Beavans 1952). With a mean shell height of 3 mm at time of planting, many of these seed oyster plantings averaged between 40 to 59 mm in their first year, with about a month left in their growing season at the time they were sampled. The average daily growth rate for all plantings was 0.31 mm/day. In comparison, previous studies separated by four decades reported average growth rates of 0.16-0.22 mm/day (Beavans 1952, Paynter and DeMichele 1990, Kraeuter et al. 2007).[1] The oysters in these studies had initial sizes of 5-9 mm.

Two of the samples with the largest average spat sizes as well as the biggest individuals were observed on the triploid plantings at Well Cove in Eastern Bay and Nanticoke Middleground (Appendix 1). Triploidy confers an advantage to growth as these oysters have reduced reproductive activity; less energy is diverted to gonad development, so that more goes into somatic growth (Longwell and Stiles 1996, Thompson et al. 1996). Therefore, after their first year higher growth rates would be expected to be seen in the triploids compared with the sexually maturing diploid oysters, but not necessarily in spat. In fact, the Well Cove triploid planting had only a slightly above average growth rate of the 2020 plantings; these oysters went in earlier in the year. Nevertheless, some individual oysters exhibited phenomenal growth, with the largest oyster measured at this site reaching a shell height of 85 mm, comparable to a three-year-old oyster. In contrast, the Nanticoke Middleground triploid planting had one of the highest average growth rates, similar to the diploid plantings at Howells Point and nearby Dickinson, both in the middle Choptank River. Aside from overall environmental conditions that vary annually, location as well as time of planting also play a role in spat size at time of sampling. Despite having the largest average sizes, the verdict on the growth rates of the triploid oysters is still out, pending sampling in the upcoming years.

A fundamental question arises as to whether planting triploid oysters on public oyster grounds is appropriate. A potential faster growth rate attributed with triploidy is advantageous in a mariculture setting, where the oyster growers could benefit from a rapid turnover of stock, thereby maximizing production on their investment. In contrast, growth rate is not necessarily as critical for the public fishery, where other locations are available for harvest until the planted oysters reach legal size. Faster growth in the public fishery would be desirable if disease was an issue – the oysters could be harvested before they succumb to disease. However, disease levels and related mortalities have been low for an extended number of years, so there is little to gain in this regard at the present time. The trade-off to planting triploids for possibly quicker growth is their greater cost – about 25% higher than diploid oysters. Perhaps more importantly for a public bar is the inability of triploids to functionally reproduce, whereas diploids potentially could have two or more spawnings before being harvested, serving as broodstock for their surrounding areas. Since oysters reproduce by external fertilization, broadcasting their gametes into the water column, the often higher densities of the seed plantings compared with natural populations also help promote fertilization success. The degree to which the benefit of faster growth offsets the added expense of triploid oysters and their lack of reproductive potential merits further consideration.

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[1] Growth rates in the Beavans (1952) study were derived from a graph for the first four months of growth (July-October).

Record-Low Disease Levels
Over the last three years, oyster disease levels have trended downward to record lows. Although still widespread, the geographic range of dermo disease continues to contract – in 2020, dermo was found on the fewest number of bars of the time series. Furthermore, MSX disease has been limited to small, discrete locations in the lower bay, where it was detected in only one or two oysters per year of the over 1,500 oysters examined annually during the past three years. These reduced infections are associated with the freshwater deluges of 2018 and early 2019, which likely were beneficial in suppressing disease (Ford 1985, Tarnowski 2019).

In the longer term, disease levels have generally been below average since 2003. In the case of dermo disease, it is uncertain whether this is due to resistance or tolerance developing in the oyster population, generally unfavorable environmental conditions for dermo, or a change in the parasitic organism that causes the disease. The latter possibility is not unprecedented: Carnegie et al. (2020) showed that *P. marinus* underwent a rapid phenotypic change in the 1980s and became more virulent, as evidenced by escalating mortality rates during that time. With respect to MSX disease, resistance in oysters has been amply demonstrated over the years in many regions, such as in Delaware Bay, where the first outbreaks of this disease occurred in the 1950s (Ford and Tripp 1996). The caveat is that in order to develop resistance to MSX, oyster populations must be constantly challenged by the disease, which is not always the case in the lower salinity waters of Maryland. Nonetheless, it would have been difficult to imagine during the height of the millennial epizootics that disease metrics would drop to such low levels shortly afterwards and remain consistently below average for such an extended period of time, to the point that they are the lowest in 31 years.

Below Average Mortalities
As a consequence of low disease levels, the Observed Mortality Index has also been below the long-term average for the last 17 years, with 2020 tied for the fourth lowest mortality rate in the 36-year time series. This has resulted in enhanced survivorship of the strong recruitment events such as occurred in 2010 and 2012, leading to increased harvests and allowing the sanctuaries to thrive, especially where natural spatset or restoration efforts have taken place. While dermo disease levels tend to be higher in the sanctuaries, that is because those oysters are older. Also, there is little real difference in disease-related mortalities with nearby harvest areas. These low mortality rates are a remarkable turnaround considering the devastation to the oyster populations due to disease during the early 2000s, when the baywide observed mortality index was 58% and some tributaries such as the Little Choptank River suffered mortalities of over 90%. Non-disease-related natural mortality events continue to take place, but while they can be locally devastating, they are limited in extent.

Third-Highest Biomass Index
The outcome from the improvements in all these factors – robust recruitment, good growth, low disease levels, below average mortalities – is the third-highest Biomass Index in the 28-year

record. As expected, the biomass in the sanctuaries remained higher, though the commercial areas showed substantial gains. Consequently, an increase in landings can be anticipated for the 2020-21 season and beyond – further sustained by the strong 2020 year class as it attains market size should conditions remain stable.

Persistent Issues

The paucity of spatset over large areas of the bay is the result of the convergence of three problems: a salinity regime that is often too low for gametogenesis and recruitment, the dearth of substrate for larval attachment, and a shortage of broodstock in those areas. The first is in the hands of nature with little of the physical environment that can be controlled. One possible approach might be a selective breeding program to develop oysters that can reproduce and recruit in lower salinity conditions. Then again, even areas that have suitable salinity during some years are lacking either or both of the other two factors, resulting in recruitment failure. The broodstock issue can be somewhat mitigated with plantings in sanctuaries, but in places such as the upper bay it becomes perhaps a decadal-scale wait for a drought to elevate salinities. Adequate habitat is another issue for successful recruitment. Even if competent oyster larvae are present – whether during a dry period or transported from outside the area or by means of genetic selection – the lack of substrate is a major obstacle to recruitment (Tarnowski 2018). These low recruitment regions, in particular the mainstem of the bay, had the lowest Cultch Index of the bay (Figure 16). Essentially a negative feedback loop has been established:

no cultch = no recruitment = no oysters = no cultch.

Localized non-disease-related natural mortality events, especially due to freshets, have always been a fact of oyster life in low salinity regions (Beavan 1947, Tarnowski 2010b, 2012, 2019). The results can be extreme, such as the total loss of oysters from several of the uppermost bars in the Potomac River during the record freshwater streamflows in 2018/19. As with reproduction, perhaps a selective breeding program can develop an oyster that tolerates lower salinities. This would be of benefit not only to restoring oyster populations in these lower salinity regions, but could expand the potential areas for raising oysters in an aquaculture setting.

Anoxic or hypoxic conditions fueled by algal blooms can also result in oyster mortality events. The tighter confines of many tributaries, which often have limited tidal flushing as well as higher ratios of impervious surfaces that can result in greater runoff and nutrient input, are particularly vulnerable to the development of low dissolved oxygen situations.

The upper St. Marys River is an example of a region with recurring elevated oyster mortalities, usually of a highly localized nature centered on Gravelly Run bar. Little if any evidence exists as to the cause(s) of these deaths. This past year, however, there was a much larger mortality event that spread upriver into the oyster sanctuary – Horseshoe bar lost 95% of its oysters. Anecdotal reports indicated that a mahogany tide bloom had occurred, coincident with a hypoxic event that had been documented with a dissolved oxygen meter. The St. Marys River historically has been a productive oyster recruitment tributary. It is considered a trap estuary, where the configuration of the river and associated water currents tend to hold the free-swimming oyster larvae within the system (Manning and Whaley 1954, Kennedy 1996). It seems reasonable that these same water circulation patterns could also retain an algal bloom, with fatal consequences as was evident in 2020. This is not to say that the mortality events in previous years were the result of anoxic conditions – there simply is no information to determine causality – but a low dissolved oxygen issue and/or toxic algal blooms are certainly candidates (Wolny et al. 2020).

"Whereto Tends All This"[2]

With the positive direction in oyster population indexes over the last two years, the immediate future in general looks promising for both the commercial fishery and sanctuaries. These improvements continue a trend that started in 2010 with the most substantial spatset since the onset of the millennial epizootics and continued with another strong spatset in 2012, resulting in the highest recorded biomass indexes in 2013 and 2014. These advances were set back for a few years in the middle of the decade by often indifferent spatsets that could not adequately support subsequent harvests, as well as rising disease and mortality levels, all leading to declining biomass. Nevertheless, the past 11 years has seen a net gain for oysters in Maryland, especially when compared with the devastated post-epizootics populations of the previous decade. Five of the last 11 years had spat indexes well above the long-term median, four to six years (depending on the metric) during this period had the lowest disease levels of the 31-year time series, the average observed mortality for this period was lower than any but one year[3] of the 25 mortality index years prior to 2010, and the five highest annual biomass indexes of the 28-year time series occurred during this decade. Whether these trends will continue remains to be seen. Given the vagaries of environmental conditions, which control so many aspects of oyster population dynamics, it is impossible to predict what the long-range prospects will be for oysters, but all present indicators clearly point to an increasing and sustainable oyster population, albeit incrementally.

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[2] Shakespeare, Wm. – *A Midsummer's Night Dream*

[3] 1985 – the last pre-epizootics year

2021 Fall Survey

Mitchell Tarnowski
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Resiliency and the Road to Recovery
The Eastern Oyster *Crassostrea virginica* is a resilient species, living as it does in the harsh and highly variable environment of coastal estuaries. There it is subjected to seasonal variations if temperature ranging from -2°C to 30°C. It can inhabit a wide range of salinities down to as low as 5 ppt and can survive extended bouts of freshwater input. Another key to this species' success is its method of reproduction. It is a broadcast spawner, releasing vast quantities of gametes into the environment. Once fertilized, the resulting larvae reside in the water column for about two weeks, carried along by the vagaries of wind and current. This potentially allows them to recolonize bars where oysters have been devastated by freshets or disease, or occupy new areas such as directed shell plantings.
Beginning in the mid-1980s through 2002, the resiliency of Maryland's oyster population was tested by successive waves of disease epizootics, culminating in record high levels of dermo disease and MSX at the turn of the millennium. The result was catastrophic – in 2002 the Maryland-wide oyster observed mortality index was 58%, with populations in some tributaries such as the Little Choptank River suffering mortalities of over 90%. Harvests plummeted to their lowest point in 150 years of oystering due to these extreme disease impacts.

The extended drought that fueled these epizootics finally came to an end in 2003 with higher than normal freshwater input dropping disease levels and lowering mortalities. But recovery was stagnant for the remainder of that decade, with the Biomass Index remaining below the baseline of 1.0 established by the previous low point in 1993. The strong recruitment event in 2010, marked a turning point – the start of recovery for at least some segments of the population. Since then the parameters used to assess the status of the population have generally trended in a positive direction over the past 12 years, continuing with notable markers in 2021.

Recruitment as the First Step to Recovery
The first positive indicator to discuss is the Spat Index, which measures annual recruitment or spatset at fixed stations throughout the bay. The 2021 Spat Index was almost double the 37-year time series, continuing a trend that began in 2010. Six of the last 12 years have had above-median spat indexes, three of which can be considered exceptional (i.e., three to five times higher than the long-term median). Only two years during this period were substantially (>25%) below the long-term median, both during periods of high freshwater inputs.

Resilience and recovery is predicated on recruitment to build the population and survival to sustain it. A sustainable recovery cannot be expected without recruitment. Conditions for different regions can vary considerably, enhancing or impeding recovery. The upper bay is an area with severely depleted oyster populations due to consistently poor to non-existent spatsets, but in reality this example can be extended down the mainstem and Western Shore tributaries almost to the Patuxent River.

Over the past two decades, Eastern Bay has been in a similar situation of poor spatsets. At one time this was a highly productive region where the state had even established seed production areas, which routinely produced millions of oyster spat. The record high Spat Index in 1997 was driven by the Eastern Bay region, where spat counts on many bars were in the thousands per bushel. Consequent harvest in the region rose to as high as 152,000 bu. But the disease outbreak began, with observed mortalities averaging up to 50% in 2002 and as high as 85% on individual bars. Annual landings since then have been well below the long-term average. Recovery has stalled, and the Eastern Bay remains a vestige of its former productive self. That said, the 2021 spatset in this region, including the Miles and Wye rivers, offers a glimmer of hope that the situation can turn around. Although the spatset is modest in scope, it is a considerable improvement for the once-thriving area that has endured repeated recruitment failures in recent years.

In contrast to Eastern Bay, a prime example of resiliency and recovery is the oyster population in the St. Marys River. Observed mortalities were even higher than in Eastern Bay in 2001, averaging 80%, yet harvests, which had been nonexistent in 2003 and 2004, exceeded the long-term average by 2013. A rapid start to recovery from another high mortality event was also observed in 2021. During 2020, what is believed to have been an extended hypoxic event in the sanctuary portion of the river resulted in an average observed mortality of 66.6%. Pagan bar, one of the index sentinel sites, had 49% mortality. Yet in 2021, the St. Marys River had the highest average spatset of any region and Pagan bar had the highest spat count of the Index bars and second highest for all bars.

While success or failure of recruitment have many known factors and likely some unknown, certain differences in the course and timing of recovery stand out between Eastern Bay and the St. Marys River:

- In Eastern Bay, the epizootics were widespread and devastating, severely depleting broodstock necessary for spawning. On the other hand, the heaviest losses in the St. Marys were largely confined to the sanctuary portion of the upper river. Adequate numbers of broodstock oysters remained in the lower harvest portion of the river, as well as on Pagan bar in the sanctuary despite the high mortality at that location.

-An insidious problem in many parts of the bay including the Eastern Bay region is the disappearance of hard surface substrate or cultch –primarily oyster shell - for the oyster larvae to attach to. This paucity of cultch is well documented by the Fall Survey, and by the simple fact that it requires longer tow distances to obtain a sample. Taphonomic processes such as burial, settling into the bottom, displacement from the bar, etc. resulting in shell loss are exacerbated by the long open wind fetch from western points into Eastern Bay. In contrast, the St. Marys River has good quantities of cultch. And because the high mortalities of the previous year occurred in the sanctuary, additional shell was retained within the system rather than if the oysters had been harvested. This part of the river is relatively sheltered from severe wave action, reducing some taphonomic processes.

-Hydrodynamics also play an important role in how the larvae are distributed and where the ultimately settle out. The smaller and more confined St. Marys River is considered a trap estuary, one which retains larvae and consistently produces good spat sets. Eastern Bay obviously must have had favorable hydrodynamics to be so productive in the past, but it is a much more open system than the St. Marys River. Whether flow patterns have changed is unknown. More likely, broodstock that had been strategically located as sources of larvae within those currents have disappeared, which, along with the loss of cultch, have led to repeated recruitment failures.

Cultch is Critical to Recruitment

A key factor for successful recruitment is adequate hard surface such as clean oyster shells on which the oyster larvae can attach. This was illustrated by a series of demonstration shell plantings made in recent years just outside the restored Harris Creek and Little Choptank sanctuaries. Spatset on the plantings outperformed samples from the unplanted part of the same bars by factors ranging from 1.6 to 3.7. The one exception when the spatset was about the same low count for both planted and unplanted samples was during a poor recruitment year overall. The location of these plantings just outside of the sanctuaries suggest that the sanctuaries may be the source of the larvae, although it is impossible to ascertain where the spat originated.

Unfortunately, the cultch situation on unrestored or unplanted bars appears to be deteriorating. For example, in 2021 it took an average tow of 507 ft to obtain a sample from Tilghman Wharf, an index bar in the open harvest portion of Harris Creek. In 2006, it took an average tow of 180 ft to obtain a sample at that same location. For comparison, the average tow distance for the sanctuary samples was 104 ft in 2021. Similar examples can be found throughout the bay.

Improved Survivorship

The second necessary ingredient for recovery of oyster populations is good survivorship to first reproduction and beyond. In a year of positive oyster population metrics, one of the most significant was the Maryland-wide Observed Mortality Index. At 6.0%, the 2021 index was the lowest of the 37-year time series and well below the long-term mean of 21.5%, continuing an 18-year period of below average mortalities as a consequence of low to moderate disease pressure. The average observed mortality of 13.1% over these last 18 years approaches the background mortality levels of 10% or less found prior to the mid-1980s disease epizootics (MDNR, unpubl. data). This is in remarkable contrast to 2002 when record-high disease levels devastated Maryland populations, resulting in a 58% observed mortality rate.

This trend in improved survivorship has been driven by the subsidence of diseases over the past two decades, with record low levels of both dermo disease and MSX following the freshwater deluge of 2018/19. Although still low, the measures of both diseases crept up slightly in 2021 with the return of normal salinities.

Record High Biomass Index
The Biomass Index is a relative measure of how the oyster population is growing or shrinking over time, integrating several population metrics into a single value. As a consequence of the good recruitment, low disease, and high survivorship in recent years, another significant oyster population milestone was attained in 2021, when the Maryland Oyster Biomass Index reached 2.69, the highest index of the 29-year record and double the long-term average of indexes. This represents a gain of 36% from the previous year and 92% over the last four years. Consequently, another increase in landings can be anticipated for the 2021-22 season and beyond – further sustained in the future by the strong 2020 and 2021 year classes as they attain market size should conditions remain stable.

Conclusion
Two decades after the devastation from the last of the great epizootics, the oyster population in Maryland remains a long way from its pre-disease status of the early 1980s. Even with reduced disease pressure, recovery has been slow and uneven, and some recruitment-poor areas may never return to historical levels. But the positive trends in population indicators that began 12 years ago and have substantially improved over the past three years offer encouragement that a corner has been turned. Three years is a relatively short period of time for predicting trends, and it remains to be seen whether the oyster population continues to grow. Nevertheless, the past dozen years has seen a net gain for oysters in Maryland, especially when compared with the devastated post-epizootics populations of the previous decade:

- Six of the last 12 years had spat indexes well above the long-term median. Only two indexes during this time frame were substantially below the median, both in high streamflow years.

- Four to six years (depending on the metric) during this period had the lowest disease levels of the 32-year time series.

- The average observed mortality for this period was lower than any but one year[4] of the 25 mortality index years prior to 2010.

- The six highest annual biomass indexes of the 29-year time series occurred during the past decade.

Whether these trends will continue remains to be seen. But barring the resurgence of disease or some yet unknown threat, there is every reason to believe that oysters can continue to flourish in Maryland. They are a resilient species.

[4] 1985 – the last pre-epizootics year

2022 Fall Survey

Mitchell Tarnowski
DNR 17-071723-4
September 2023

Highest Landings in Thirty-Five Years

The highlight of the year was the final harvest figures for the 2021-22 oyster season. Landings jumped by almost 200,000 bu, or 58% from the previous year, exceeding the half-million bushel mark for the first time since the 1986-87 season, the span of a generation of watermen. The dockside value of $21.5 million was the highest on record (not accounting for inflation), and double the value of landings from the previous season.

Over 70% of the harvest came from the Tangier Sound region, which included Tangier Sound proper, Honga River, Fishing Bay, parts of the Nanticoke and Manokin rivers, and Pocomoke Sound. Upper Tangier Sound alone accounted for nearly 40% of the landings. Notably, the harvest from this region increased tenfold over a short period of time. In only four years, from the 2018-19 through the 2021-22 seasons, landings from the Tangier Sound region went from 39,735 bu to 394,884 bu, which was by far the largest increase of any region in Maryland. The statewide harvest tripled over this same time period.

This robust growth in landings was not entirely unexpected. The Biomass Index, which is compiled at the start of the harvest season, is generally correlated with subsequent landings in that season. Since the most recent nadir in 2017, the Biomass Index almost doubled to a record high in 2021. After including the 2021 Biomass Index, a regression model predicted the harvest for the upcoming season would be 547,490 bu, which was less than 2,000 bu above the final tally for the 2021-22 season (Figure 17a). The overall 12% decline in the 2022 Biomass Index was likely attributable to the substantial increase in harvest, since the Index bars in open harvest areas showed a biomass loss of 14% from the previous year.

The resiliency of Maryland's oyster populations over the last decade is discussed at length in Tarnowski (2023). In order for this trend in enhanced harvest to continue, two population requirements – good recruitment and low disease-related mortalities – must be balanced against appropriate removal rates. The slow initial rebound immediately following the record-high mortalities due to the millennial epizootics of 1999-2002 was marked by a period of lower disease levels but poor recruitment. From 2003 to 2005 the average spatfall was 6.1 spat/bu, a quarter of the long-term median, while through 2009 the average was still subpar at 14.1 spat/bu. This period of low spatsets coincided with years of below baseline Biomass Indexes, suggesting that recruitment was at least in part broodstock limited as a result of the devastating epizootics. The strong recruitment event in 2010 set in motion the buildup of the population that we see today, albeit still a long way from where it could be or has been in the past..

In contrast to the 2003-2009 time frame, the recent trend in increased harvests coincides with the growth of broodstock biomass in nearby priority sanctuaries and improved spatset. The Manokin Sanctuary is immediately east of upper Tangier Sound, where much of the recent higher recruitment and subsequent harvesting has taken place. Although not a priority restoration sanctuary, the Nanticoke Sanctuary on the upper end of Tangier Sound also has a considerable number of oysters, both on the natural oyster bars and on the numerous oyster aquaculture farms that may serve as a source of larvae. Landings in the Little Choptank River just outside of another priority restoration sanctuary have grown from 222 bu in 2018-19 to 12,786 bu during the 2021-22 season. In the St. Marys River, the four sampled harvest bars closest to the sanctuary averaged over 400 spat/bu in 2022, possibly spillover from the sanctuary where the average spatset was more than double those counts. Although suggestive, a direct connection between broodstock sources in the sanctuaries and spatset in nearby fishing areas has yet to be confirmed.

While broodstock abundance is an important element in recruitment, there are several other factors as well. Cultch, the substrate on which larval oysters attach, is in short supply and diminishing in many areas. Even when cultch is present it may be compromised by silt or attached organisms. Environmental conditions, in particular salinity, are critical for successful recruitment. However, adequate salinity, although a necessary requirement, is not always sufficient to produce good spatsets, as there are certainly other factors, some that have yet to be determined. These topics have been discussed extensively in previous reports of this series (e.g., Tarnowski 2022, 2020, 2019, 2018, and earlier).

The Broad Creek Paradox

When analyzing the data for the section of this report comparing sanctuaries and adjacent public fishery areas, Broad Creek stood out as the exception to the general rule that the restoration sanctuary metrics were higher than in their corresponding harvest regions.

Deep Neck bar, a Key and Disease sentinel bar representative of Broad Creek, has the second-highest spatset average of the 53 bar suite that comprises the Spat Index over the 38-year time series. Historically, Deep Neck has consistently outperformed Key Bars in nearby tributaries, by nearly fourfold at Eagle Pt./Mill Pt. in Harris Creek and more than eight times higher than Double Mills in the Tred Avon River, even before they became sanctuaries. In recent years Deep Neck has experienced good to exceptional spatsets – seven of the last eight years exceeded the long-term median. The climax of this period was in 2020, when spatset was the second highest in the 81-year record at that bar, the 1,838 spat/bu was the highest count of any Index bar since 1997. Broad Creek overall averaged 1,032 spat/bu in 2020, with six of eleven bars having counts of over 1,000 spat/bu. In 2022, of all comparison areas, both sanctuaries and public harvest bars, Broad Creek bars had the highest average number of adult (small and market) oysters/100 ft dredge tow, a reflection of these spatsets.

Other metrics are also favorable in Broad Creek. Disease levels remain low, accompanied by single digit observed mortalities. MSX disease has been detected in only two of the past twenty years, the last time in 2015 with a meager 3% prevalence (one oyster). Deep Neck had the highest biomass standardized to a 100 ft tow of the sentinel bars in the comparison areas. Lastly, Broad Creek had the highest amount of cultch/100 ft tow. In this regard, Deep Neck had the shortest sampling tow distances of the entire survey, averaging 26 ft for 1.2 bu of material, an indication of abundant cultch. In comparison, the average tow distance for all surveyed bars was substantially longer - 139 ft for 1.3 bu.

Despite these positive indicators, one metric – landings – has remained flatlined for the past six seasons at about half of the harvests immediately prior to that. Harvests in these prior years received a boost from the strong 2010 and 2012 spatsets, increasing by over sixfold between the 2011-12 and 2012-13 seasons. Even with low disease-related mortalities, these greatly improved harvests lasted only four years before collapsing due to poor spatsets in 2011, 2013, and 2014, which couldn't support that level of fishing activity. Landings have fallen by about 50% from their peak in 2013-14. Over this past decade, the contribution of Broad Creek to total Maryland landings dropped from 21.3% in 2013 to 6.9% in 2022.

Paradoxically, another reason for the reduced harvests in Broad Creek over the last three years was the extraordinary spatset in 2020. Anecdotally, market oysters were so covered in spat and subsequent sublegal oysters that culling or removing them was extremely difficult, slowing down harvesting or leading some watermen to avoid the tributary. In 2022, the average size of oysters at Deep Neck was 65.6 mm, or still 10 mm below the legal market size, with market oysters comprising only 26.8% of the total adult oysters; for all sampled Broad Creek bars, the fraction of market oysters was even lower at 21.0%. These proportions further increased the time and tedium of culling.

In comparison to the 2020/21 year classes, the 2010/11 cohorts of Broad Creek oysters appear to have grown faster. Over the same 2+ years length of time at Deep Neck, by 2012 the average size of adult oysters was 74.2 mm or almost legal size, and the proportion of markets was 47.8%, leading to the substantial increase in landings during the 2012-13 season. Note that these average sizes include two year classes. The apparent slower growth of the 2020 year class may be attributable to continued good recruitment in 2021, which may have skewed the average size downward by adding more small oysters to the population, although the proportion of the 2021 cohort was only 8.8% of the 2020 cohort. In contrast, 2011 was a very poor recruitment year, which would have little effect on the average size of the combined 2010/11 cohorts. Other possible reasons for the apparent slower growth could be overcrowding (the 2020 spatset was ten times as high as the 2010 set) - competing with neighbors for space and food, or perhaps some environmental condition. Nevertheless, although lagging behind their predecessors in time to legal size, landings from Broad Creek can be expected to increase considerably over the next few years as this large population attains market size, which will also make culling easier.

Intensifying Disease a Potential Threat

Although disease levels and observed mortalities have remained below the long-term average over the past five years, the increases in dermo and MSX seen this year may be cause for concern in 2023, depending on environmental conditions, especially salinity. With favorable salinities over the past two years, MSX has spread rapidly, from one oyster at each of two locations in 2020 to occurring throughout much of the waters of the lower Eastern Shore and establishing a toehold on the Western Shore.

Persistent elevated salinities over the next year or so may allow for an unintended and perhaps unwelcome experiment. MSX becomes lethal at salinities above about 15 ppt (Appendix 2). A prolonged period of higher salinities could test the hypothesis that the lower observed mortalities of the last two decades are the result of disease resistance/tolerance in oysters (Appendix 3).

A counter hypothesis is that oyster survival is due to favorable salinities, not genetic improvements. Interannual streamflow and salinity patterns differed markedly between the high disease-related mortality period (mortality averaging 31%) from 1987 to 2002 (Period 1) and 2003 to 2022 (Period 2), with less favorable conditions for disease during the latter years (mortality averaging 14%). There has not been an extended high-salinity period and associated epizootics since the four-year millennial drought (1999-2002), which decimated oyster populations in Maryland. Streamflows have been much less volatile over the past two decades - the variance of below average flow years during Period 2 was only 57% of the variance in Period 1 - with elevated salinities in Period 2 lasting for shorter durations and at greater annual intervals. For example, at Ragged Point bar in the Little Choptank River, 62% of the years in Period 1 averaged more than 15 ppt during August through November, while only 21% of the years during Period 2 were above 15 ppt. The average length of time between years when the August-November salinity averaged more than 15 ppt in Period 1 was 1.6 years (and not more than two years), while for Period 2 it was 4.0 years (maximum six years). Does the shorter periodicity of low-flow years in Period 1 have any effect on the virulence of disease or susceptibility of oysters (weakened physiological state)? Perhaps the oysters in Period 1 didn't have enough time to recover from one bout of disease before the next assault.

Low flow years in Period 1 were also more acute. Five of 16 years (31%) had flows below 75% of the time-series mean, with an average of 69.4% of the mean (range 64% - 73% of the mean). In contrast, the 20 years of the post-epizootic period (Period 2) had only one year (5%) when flows were below 75% of the time-series mean (74% of the mean). Comparing all below-average flow years between the two periods, Period 1 had significantly lower flows (t-test, $p=0.004$).

A well-timed pulse of freshwater can mitigate the impacts of MSX. MSX had been creeping up in 2016, a dry year. Alerts were sent out to growers by VIMS in early 2017 anticipating a worsening condition, especially with March flows being well below average. But above average streamflows for the next few months reduced the impact of MSX. For example, in southern Tangier Sound the salinity dropped from 19.59 ppt in Feb. to 15.47 ppt in June.

MSX is easier to comprehend than dermo disease, given its known salinity thresholds and evidence of resistance in other regions such as in Virginia and Delaware Bay (Carnegie & Burreson 2011, Ford & Bushek 2012). In Maryland, MSX resistance may have developed at Sharkfin Shoal in Tangier Sound, as suggested by lower prevalences in Period 2 compared to Period 1 at salinities over 15 ppt. Observed mortalities on that bar were significantly lower in Period 2 (t-test, p=0.001).

While an argument for MSX resistance may be made down bay, it cannot be invoked baywide. If environmental conditions are not factors, MSX should occur further upbay in Period 2 as it did previously. But MSX has largely been confined to southern Maryland in Period 2, with brief flareups upbay when conditions permitted. Through natural selection, the level and frequency of disease-related mortality on a bar may determine whether disease resistance or tolerance develops. However, the low-salinity bars were either never exposed to MSX or were challenged at such low frequencies (and possibly low intensities) that natural selection could not come into play. These lower-salinity oysters likely remain susceptible to MSX disease.

Dermo disease is more of a conundrum. There are unresolved questions of salinity thresholds for mortality, the relationship between intensity and mortality, the effect of temperature on lethality, whether there was a hypervirulent strain in Period 1 (Carnegie et al. 2021) that has run its course, whether the duality of MSX and dermo infections increased the lethality, and the possible development of resistance/tolerance.

In the case of both diseases, their impact on past oyster populations was greatly intensified by an extended period of elevated salinities. Should such a prolonged period occur again, it would test whether and to what extent disease resistance/tolerance has developed in the current populations. The outcome of this "experiment" with persistently elevated salinities could determine whether the recent trend in population growth can maintain its momentum.

Conclusion

Two decades after the devastation from the last of the great epizootics, the oyster population in Maryland remains a long way from its pre-disease status of the early 1980s. Even with reduced disease pressure, recovery has been slow and uneven, and some recruitment-poor areas may never return to historical levels. But the positive trends in population indicators that began 12 years ago and have substantially improved over the past three years offer encouragement that a corner has been turned. Three years is a relatively short period of time for predicting trends, and it remains to be seen whether the oyster population continues to grow. Nevertheless, the past dozen or so years has seen a net gain for oysters in Maryland, especially when compared with the devastated post-epizootics populations of the previous decade. Seven of the last 13 years had spat indexes well above the long-term median, five to seven years (depending on the metric) during this period had the lowest disease levels of the 32-year time series, the average observed mortality for this period was lower than any but one year[5] of the 25 mortality index years prior to 2010, and the seven highest annual biomass indexes of the 30-year time series occurred during this decade – all leading to the highest harvest total in 35 years. Whether these trends will continue remains to be seen. But barring the resurgence of disease or some yet unknown threat, there is every reason to believe that oysters can continue to flourish in Maryland.

[5] 1985 – the last pre-epizootics year

2023 Fall Survey

Mitchell Tarnowski
DNR 17-062524-1
August 2024

The findings of the 2023 Fall Oyster Survey and two ancillary surveys illustrated the profound influence salinity has on oyster population dynamics. An extended drought and consequent elevated salinities enabled an exceptional spatset while allowing for the rapid and extensive spread of MSX disease. A dramatic reversal in salinity levels during the late winter and spring of 2024 resulted in a sharp decline and even disappearance of MSX at selected sites.

This Discussion deals with these two opposing factors: population growth through recruitment and regression through disease-mediated mortality. The first section describes the strong and widespread recruitment that occurred in 2023, focusing on the Potomac River as an example of how important this event was for repopulating depleted, normally low-recruitment areas. The second section incorporates the results of a directed spring survey in 2024 that was conducted in large part as a follow-up to the fall MSX disease and observed mortality findings. The Spring Dredge Survey results are presented in Appendix 1 of this report.

An Outstanding Spatset

The 2023 Spatfall Intensity Index, a measure of reproductive success and potential population growth, was the fifth highest of the 39-year time series and nearly four times the index median over that time period. It also marks the fourth consecutive year of above-median recruitment, rebounding from the extended freshets of 2018-19.

Equally important, and what made this recruitment year exceptional, was the widespread distribution of the spatset. Spat were even observed in the upper reaches of tributaries that are normally too brackish to receive a spatset. Fifty of the 53 Key (Spat Index) Bars had spat, the most bars since 1985 - the first year of this time series. The only regions where spat were not found were the upper bay above the Bay Bridge and the Chester River. Spat numbers were well distributed within the Key Bar data set, with ten stations accounting for 50% of the spat index. No one station dominated the 2023 index, in contrast to 2020, which had a higher spat index but was heavily skewed by the extraordinary spatset on one bar – Deep Neck in Broad Creek – which alone accounted for 32% of that year's index.

Salinity is a primary environmental driver of oyster recruitment. Adequate salinity is necessary for gametogenesis, spawning, larval survivorship, and settlement (Loosanoff 1953, Davis 1958, Calabrese & Davis 1970, Thompson et al. 1996, Kimmel & Newell 2007, Tarnowski 2019). Salinity is regulated by freshwater streamflow into the bay. When the Chesapeake watershed entered a drought period beginning towards the latter portion of 2022 and throughout 2023, the reduction in streamflows caused salinities to rise to suitable levels for spatset in most corners of Maryland's oyster grounds.

Suitable salinity for spatset is influenced by this streamflow-salinity dynamic in two ways: dilution and tidal transport (Pritchard 1952, 1967). Higher salinity originates from the Atlantic Ocean, which is carried up the estuary by tidal currents and is increasingly diluted by freshwater input along the way. With lower streamflow entering the bay such as in 2023, there was less fresh water mixing with the incoming tidal flow, raising salinities further upstream. But in addition to dilution there is a second factor influencing salinity. Lower streamflows mean less volume and force of freshwater to push against the tidal surge, allowing saltier water to penetrate further up the estuary. This transport mechanism also allows the pelagic oyster larvae to be carried further into the upper reaches of tributaries where broodstock might be limited or nonexistent. Flushing time is also regulated by streamflow. Lower freshwater flows mean longer flushing times and longer retention of larvae, enhancing the possibility of settlement in a given area (Gaines and Bertness 1992).

Adequate salinity is necessary but not always sufficient for a strong recruitment event. A combination of other physical parameters including temperature, dissolved oxygen, water chemistry, wind-driven currents, ill-timed storms, siltation, and suitable substrate to set on interplay with biological factors such as sufficient broodstock, predation, competition for space and food with other epibenthic organisms, adequate and appropriate phytoplankton food, harmful algal blooms, and likely other unknown factors to determine whether an outstanding recruitment event occurs. Oftentimes these are dependent on extremely localized conditions, such as the 2020 Broad Creek spatset. So, to have such an extensive recruitment event as in 2023 is rare, given the host of variables that can negatively impact spatset even under optimal salinity conditions. The significance of this event is illustrated by a case study of the Potomac region, which experienced a once in a generation spatset.

The Potomac Region

The Potomac oyster populations have been struggling ever since Tropical Storm Agnes inundated the river with freshwater and silt in 1972, causing extensive mortalities (Krantz and Carpenter 1981, Haven et al. 1976). This was followed by high MSX disease-related mortalities that periodically ravaged the populations in the lower portion of the river beginning in the mid-1980s through the millennial epizootics which ended after 2002 (Tables 4, 5). Oysters further up the river, at least as far as Lower Cedar Point and the western Wicomico River, were not spared from disease, succumbing to high levels of dermo disease (Tables 3, 5). Even Beacon bar, the furthermost bar upriver to be surveyed in a normally low salinity regime, had a dermo prevalence of 43% in 2002 (MDNR, unpubl. data). Compounding the problem on these uppermost bars were three killing freshets during the mid-1990s (MDNR 2001).

Coincident with these events was the collapse of recruitment, possibly a consequence of the loss of broodstock coupled with often unfavorable environmental conditions. There was a brief reversal in this trend during the early 1980s when a series of strong recruitment years lasting through 1986 occurred in the lower portion of the Potomac, though not on the upper bars. This was followed by decades of persistently poor spatsets, save for an occasional modest event in the lower north shore (Figure 22). The Potomac's Maryland tributaries of the Wicomico River and Breton Bay also endured long-term recruitment failures. The only bright spot in this region was the St. Marys River, which has produced above average spatsets fairly consistently through the years.

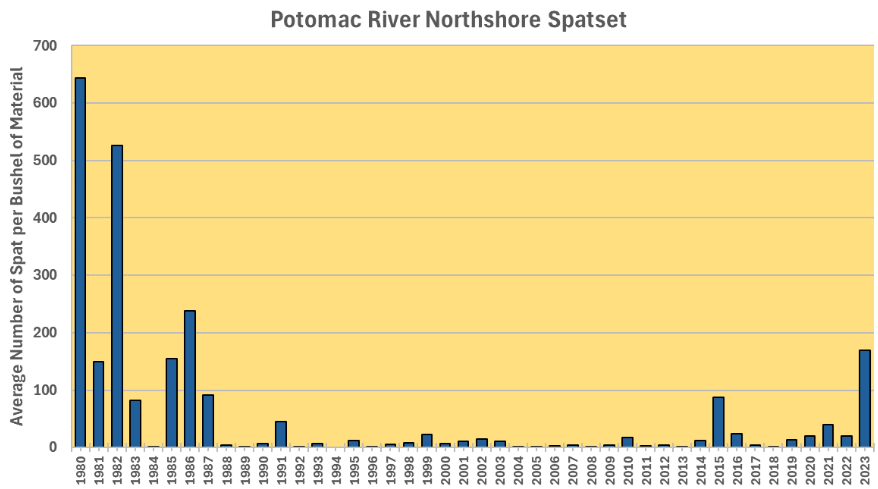

Figure 22. Average annual natural spatset in the north shore of the Potomac River.

In more recent years, the latest freshet event persisted for an extended period overlapping 2018 into 2019, and was the most devastating. The freshet completely extirpated oyster populations over a distance of approximately 15 km, from Beacon bar, at the first bend in the river, all the way below the Route 301 bridge to Colonial Beach, where mortalities began to ease somewhat. Gum bar, directly in front of Colonial Beach, had an observed mortality rate of 86%, while across the river, 64% of the oysters were dead on Swan Point (Tarnowski 2019). Thus, there was an extensive stretch of the upper oyster grounds, normally an extremely poor recruitment region to begin with, that had lost the entirety of its broodstock (Figure 23). In particular, Beacon bar oysters were unique in that they were adapted to living in lower salinities and had withstood the mid-1990s freshets. Being so far upriver with no immediate source of broodstock, the likelihood of a recovery seemed remote without management actions such as oyster seed plantings, but this area above the bridge has a history of low harvest activity. Given the logistical and monetary constraints, as well as the high-risk factor of such an option with marginal returns for the funds-limited Potomac River Fisheries Commission (PRFC), this seemed unlikely to happen. The area would probably remain one of relict shell bars without living oysters.

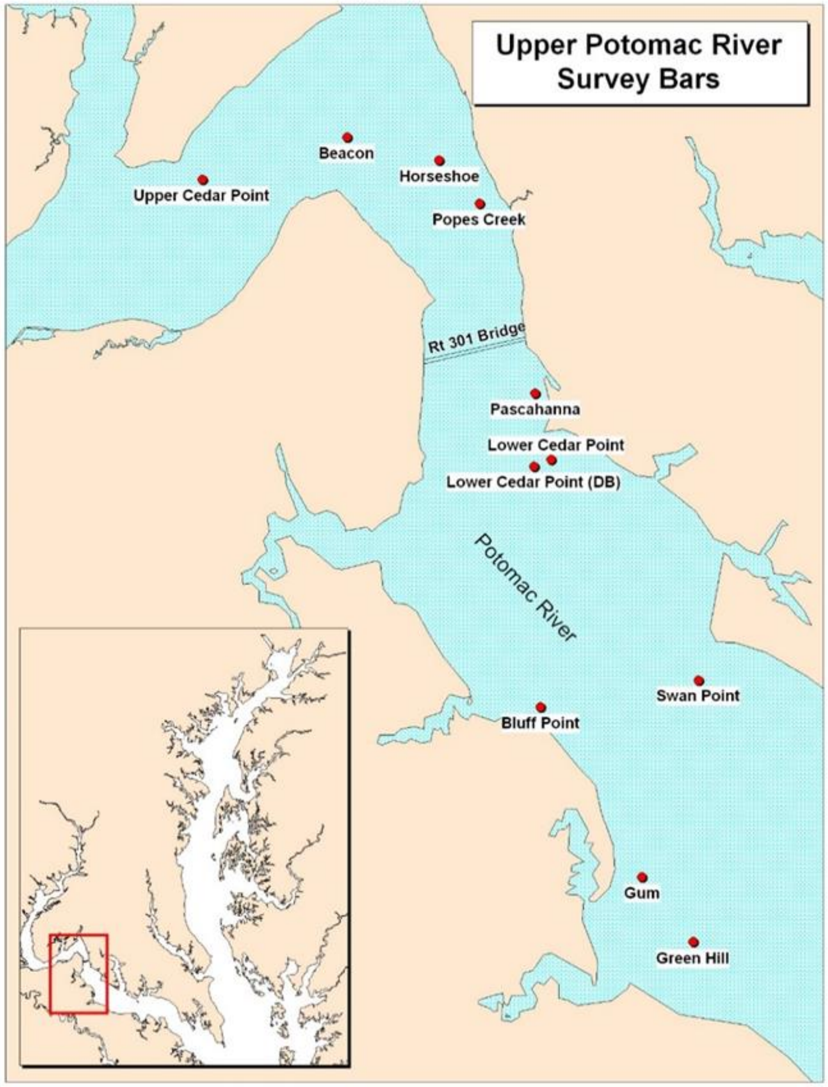

Figure 23. Location of upper Potomac bars referred to in the text.

Because of the absence of oysters on the bars above the Route 301 bridge and the considerable additional travel time to get to those bars, this area had not been included in the Fall survey since 2020. However, in 2023 spat were found throughout the Potomac as far upriver as Pascahanna bar, just below the bridge. The Wicomico River and Breton Bay also had welcome spatsets after three decades of recruitment failures (Figure 24). Notably, the north shore of the Potomac River experienced the highest average spat count of any region in Maryland – the best recruitment in the river in almost 40 years. It was a salient event for a river that had faired so poorly for so many years. But the tantalizing question remained: What if any spatset occurred above the bridge?

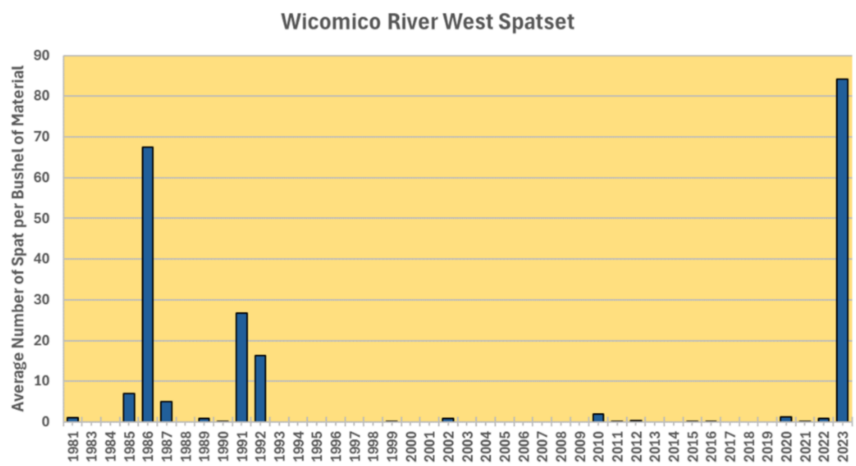

Figure 24. Average annual natural spatset in the western Wicomico River.

On 25 November 2023, an informal survey of four bars in this area using a local waterman's boat found excellent spatsets not only on Beacon bar (250 spat/bu) but even about 6.5 km further upstream on Upper Cedar Point (115 spat/bu), which has never been sampled on the Fall Survey. Lesser, but still important, spat counts were observed on Horseshoe and Popes Creek bars. The significance of this spatset in repopulating this area cannot be understated - recruitment had essentially ceased in this upper zone since 1969 (Krantz and Carpenter 1981; MDNR, unpubl. data). The only spatset of importance on Beacon bar since then had been 46 spat/bu in 1986 (MDNR, unpubl. data). Given the rarity of such occurrences and absence of oysters in this region, the 2023 spatset was a serendipitous event.

Adequate broodstock is a primary biological consideration for successful recruitment. The source of the oyster larvae that settled on the upper Potomac bars is a matter of conjecture. A larval transport model specific to the Potomac River projected a median dispersal distance of 12 km, with a range of estimates from 2 km at the 25th percentile and 22 km at the 75th percentile (North et al. 2008). The nearest known broodstock reservoir was on Lower Cedar Point bar, approximately 8.4 km downriver from Beacon bar and 15 km from Upper Cedar Point bar. The population on Lower Cedar Point bar had suffered 100% mortality during the latest freshet. Despite the losses, under ordinary conditions this bar is notable for the growth rates and quality of its oysters. Consequently, PRFC has been planting seed oysters for eventual harvest every year since 2020, while unintentionally providing a concentration of broodstock waiting for proper conditions to reproduce.

Larvae could possibly have travelled from further down river but this does not seem as likely. The next closest bar is Swan Point, about 15 km below Beacon bar. But the freshet mortality on this bar was heavy, leaving a relatively sparse population of oysters (34/bu scattered over a 304 ft tow). On the south shore, the nearest known location with oysters was on Green Hill, some 20 km from Beacon bar, but oysters were extremely scarce (6/bu) when the bar was last sampled in 2022. The paucity of oysters and distance from the bridge would seem to preclude these areas as sources of larvae. There are also some bars in the deeper portion of the river where oysters may have survived the freshet, but these are in the firing range of Dahlgren Naval Station and have not been surveyed since an artillery shell was dredged up several years ago.

An increase in broodstock through management actions involving planting and harvesting on a rotational basis among bars may have benefitted the western Wicomico River, a tributary of the Potomac River. Recruitment in this river has basically been non-existent since 1986, but in 2023 there was a fair spatset, averaging 67 spat/bu. Numerous seed oyster plantings for eventual harvest have been made here in recent years, which could have contributed to this spatset. There may have even been some spillover effect from the Wicomico River into the Breton Bay area, which averaged 92 spat/bu despite a paucity of broodstock oysters there.

As described previously, reduced streamflows in 2023 allowed for the strong recruitment event on the upper Potomac bars in two ways. First was the dilution factor, where there was less freshwater to dilute the incoming tidal flow, raising salinities to suitable levels for recruitment. The surface salinity during the Beacon bar sampling was 13 ppt, more than adequate for recruitment and survival (Davis 1958, Calabrese and Davis 1970). Second was the transport mechanism. Lower freshwater flow means the saltier flood tide can penetrate further upstream, carrying oyster larvae along with it. The high spat count on Beacon bar may also be attributable to its location at the first sharp bend in the river (Figure 23), with the tidal current running into and over the shoal bar. Similarly, larvae travelled against the net downstream flow even further upriver to Upper Cedar Point.

Cultch is oyster habitat consisting of hard substrate, usually oyster shell, and is crucial for larval oysters to set or attach to (Tarnowski 2018). Field notes from the November 2023 upper bars survey reported that there was an abundance of brown surface shell on these sites. Previous Fall Surveys needed only short tow distances to obtain a sample on Beacon bar, indicating abundant cultch. With good habitat and suitable salinity, Beacon bar was primed and ready to receive the oyster larvae in 2023.

Beacon bar also provides an example that adequate salinity is not always sufficient for successful spatsets. Being so far upriver, Beacon was thought to be a refuge from oyster diseases. In fact, dermo disease was not detected in 1999 downstream on Lower Cedar Point bar, the closest disease monitoring bar prior to 2002. But by 2002, the fourth year of drought-level streamflows, the dermo prevalence was 97% on Lower Cedar Point, and a supplemental sample taken on Beacon bar found 43% prevalence. The point is that *Perkinsis marinus*, the organism that causes dermo disease, could travel upstream and infect remote oyster bars in normally low-salinity areas during elevated salinity periods, likely utilizing the same transport mechanism as oyster larvae. Fall Survey salinities over this drought period ranged from 8.7 to 11.0 ppt, sufficient for a spat set. Yet Beacon bar received no spat during this time span.

In conclusion, elevated salinities enabled a once in a generation spatfall, perhaps assisted by management actions that boosted broodstock numbers, in a region that desperately needed it. This epic recruitment event bodes well for the Potomac oyster populations, along with the ecological benefits they afford and watermen they help support. As they grow, the oysters will provide additional habitat and reproduction potential in a positive feedback loop, allowing the possibility for the population to expand even further. But as always with oysters, there is a caveat: providing they survive in this hostile environment. They must grow and reproduce without facing freshwater deluges and the ravages of diseases on either end of the historically notorious Potomac.

Spring Survey Observed Mortalities and MSX Disease

The effect of streamflow and consequent salinity on *Haplosporidium nelsoni* - the causative agent of MSX disease - and associated oyster mortalities was graphically demonstrated in the half-year span separating the Fall and Spring (Appendix 1) surveys. As discussed in the 2022 Fall Survey report (Tarnowski 2023):

Persistent elevated salinities over the next year or so may allow for an unintended and perhaps unwelcome experiment. MSX becomes lethal at salinities above about 15 ppt (Appendix 3). A prolonged period of higher salinities could test the hypothesis that the lower observed mortalities of the last two decades are the result of disease resistance/tolerance in oysters (Appendix 4). A counter hypothesis is that oyster survival is due to favorable salinities, not genetic improvements.

With elevated salinities continuing throughout 2023, the spread of MSX disease was anticipated, but not to the geographic extent or extraordinary prevalence levels acquired by oyster populations on certain bars. MSX range and prevalences were already expanding in 2022, increasing from one oyster at each of two locations in 2020 to eight sites throughout much of the waters of the lower Eastern Shore and establishing a toehold on the Western Shore. Thus, the system was primed for the 2023 MSX epizootic, as streamflows remained reduced and salinities increased. By the 2023 Fall Survey, MSX disease was found at 27 disease sentinel sites (65% of total) as far upbay as Hacketts bar outside of Annapolis. The Patuxent River is not included in the following discussion since the nearest disease sentinel bar was outside of the study area and had a lower MSX prevalence than the other sites.

As the MSX pathogens infiltrated the middle reaches of the bay, they encountered oyster populations that were relatively naïve to them. Prior to 2023, the two Choptank region disease bars in this study had experienced *H. nelsoni* infections only a limited number of times in the 21 years since the millennial epizootics: Lighthouse – three years; Royston – two years. With so few challenges combined with light mortalities, there was little opportunity for these populations to develop resistance or tolerance to the disease, with little selection taking place. Consequently, the results in the fall of 2023 were a hefty 67% prevalence on Royston and an astonishing 93% prevalence on Lighthouse. In contrast, the Piney Island East oysters were challenged by MSX disease in 16 of the past 21 years. Considering that the salinity regime in Tangier Sound is the highest in Maryland, and by extension has the greatest disease prospects, the highest fall *H. nelsoni* prevalence in that region was only 40% (at Piney Island East), well below the lower Choptank bars – a strong indication that this population has evolved a tolerance or resistance to MSX infection.

Another feature of the *H. nelsoni* prevalences during the fall 2023 was the patchy distribution. It appears there was a sharp demarcation between high and low disease levels. While Lighthouse bar, just outside of the mouth of the Tred Avon River, established a record high MSX prevalence, the pathogens were not detected about 10 km away on Double Mills within the Tred Avon oyster sanctuary. Also, the next Choptank disease bar upstream from Lighthouse (also about 10 km) – Sandy Hill – had a much lower prevalence (17%). This pattern was observed in other tributaries as well, such as Harris Creek, Little Choptank River, and Manokin River (Table 4).

Observed mortalities in the fall were not as accordant with disease levels as might been expected. Regionally, the Tangier area had the highest observed mortality averaging 26%, although it was somewhat lower on Piney Island East (18.9%). Observed mortalities in the naïve Choptank populations were even lower, averaging 21%. Despite their extremely high *H. nelsoni* prevalences, observed mortalities were only slightly elevated at Royston (17.5%) and Lighthouse (20.9%).

Lower Choptank Region

In the Choptank oysters, two possibilities for this incongruity between MSX prevalence and mortality during the fall are that either they had only recently acquired the disease or environmental conditions had suppressed its impact. Although oysters usually become infected in May, parasite acquisition can occur as late as October (Ford and Tripp 1996). Given the distance of the Choptank bars from the presumed initial source of infection in the Tangier region, it would not be surprising for infections to have been acquired later in the year as the parasites expanded their range up the bay, but there is no way of knowing for sure.

Considering the second possibility, salinities at the Outer Choptank monitoring station were above 10-12 ppt for the entire year, allowing infection by the MSX pathogen without inflicting mortalities (Ford 1985, Sprague et al. 1969). During the period of potential infection, salinities did not exceed the 15 ppt threshold for increased MSX-related mortalities until in October 2023 and remained above it through December. Salinities fell below 15 ppt in January, concomitant with temperatures below 5°C, and continued to drop to 8 ppt by May.

It may be that either or both possibilities were at work. If *H. nelsoni* parasites were acquired earlier in the season, salinities appeared to be in the range to allow infections but not result in mortality. In both cases, there was still at least two months of suitable environmental conditions after the Fall Survey for the pathogens to proliferate before water temperatures below 5°C inhibited their activity (Ford and Haskin 1982). A second mortality period in late winter and spring can occur when water temperatures rise above the pathogen's activity threshold (Ford and Tripp 1996). Stressed oysters may continue to die as metabolic demands for host response remain high in the face of declining energy reserves and food availability. As it turned out, in the Choptank region the temperature dropped below the 5°C threshold only during January (Figure A1-3). This suggests that at least in the Choptank region the combination of low temperatures and dropping salinities caused pathogenic activity to be suppressed during the first half of 2024. By the time of the Spring Survey in late May the parasites had essentially been purged from the two study populations, with 7% prevalence on Royston and 0% prevalence on Lighthouse. This is consistent with findings that *H. nelsoni* was purged from oysters when salinities were 10 ppt or less (Haskin and Ford 1982, Andrews 1983).

Because of unsuitable environmental conditions for *H. nelsoni* in late winter/spring, it would be expected that the increased mortalities occurred soon after the Fall Survey. However, the Spring Survey results found the number of recently dead small oysters in the Choptank region was double that of older small boxes, indicating a spring mortality event. And although market boxes tended to be older, about a third of them were recent. We can only speculate that the oysters were so physiologically weakened in the spring that they eventually succumbed despite the absence of the parasite. The final result was that post-Fall Survey observed mortalities doubled regionally and more than doubled by the time of the Spring Survey at the two study bars with the highest fall *H. nelsoni* prevalences of the Choptank region.

Tangier Sound Region

Piney Island East presented a different situation from the Choptank region. Salinities remained above 15 ppt throughout 2023 into 2024 before falling below that mark in March (Figure A1-2) and temperatures never dropped below 5°C, presumably allowing the pathogens to remain active through the winter. With salinities hovering at the lower tolerance threshold for *H. nelsoni* (Figure A1-2), the prevalence declined in the spring, but was still a substantial 26%. Yet the mortalities were actually lower in the spring. This conundrum raises three questions: Why was the average MSX prevalence in the fall about half of the Choptank region? Why did observed mortalities not go up as they did in the Choptank region? Instead, why did mortalities go down?

Despite environmental conditions at Piney Island East that were conducive to MSX acquisition and pathogenic activity, prevalences and related mortalities were relatively moderate in the fall, and post-Fall Survey observed mortalities failed to rise as they did at the Choptank bars. Also, the Tangier region likely was the epicenter of the disease outbreak, as the oyster populations there were already infected from the previous year. Yet there was not a similar impact as seen in the Choptank region. The most parsimonious answer is that the Tangier region populations had developed resistance/tolerance to MSX disease after years of being challenged by it, as opposed to the infrequent exposure of the Choptank region to *H. nelsoni*. Resistance is suggested in the Tangier region oysters as prevalences never got very high, averaging 19.9% in the fall, compared to 50.7% in the more susceptible Choptank region populations.

The possibility of MSX disease tolerance and/or resistance among Maryland oyster populations in the Tangier Sound regions is supported by findings in neighboring localities. In higher salinity waters such as Delaware Bay and the Virginia portion of Chesapeake Bay, native oyster populations have demonstrated greater survivorship in the face of MSX disease (Ford & Tripp 1996, Burreson & Ford 2004). Furthermore, selective breeding has produced oyster strains with genetically enhanced resistance/tolerance to both MSX and dermo diseases (Ford & Tripp 1996, Ragone Calvo et al. 2003).

Observed mortalities did not increase by the spring, even though the prevalence on Piney Island East, for example, was still 26%, perhaps because the infected oysters were able to tolerate the pathogens, again because of the frequent MSX challenges over the decades that this population has endured. This idea might be confounded by the drop in salinities in March 2024 to below the 15 ppt lethal threshold, which would allow the parasites to exist without killing the oysters, and may have reduced the prevalence from the fall value. Nevertheless, salinities remained above 15 ppt for an extended period through the winter while water temperatures remained above 5°C, which should have allowed pathogenic activity to continue.

One possible explanation for the decline of observed mortalities in the Tangier region between fall and spring is the impact of heavy fishing activity on boxes. Most of the bars selected for the spring survey were in commercial areas and had the highest reported landings for each region. In the Tangier region, approximately 20% of the boxes were categorized as recent with the remainder as old. Old boxes could be anywhere from a few weeks to almost a year old, so there was no telling when the Tangier oysters died. In the Choptank region, about 40% of the boxes were considered recent in the fall. Added to that was the fresh wave of mortalities after the Fall Survey. Recent boxes would be much less likely to disarticulate from fishing activity than old boxes. So, although the Choptank region also experienced a good amount of harvesting, the large proportion of recent boxes likely remained intact through the harvest season, while there was a higher degree of disarticulation in the older Tangier boxes due to fishing and possibly other taphonomic processes associated with their age.

The unintended and unwelcome experiment mentioned in the quote at the beginning of this discussion came to pass in 2023. Which of the two hypotheses explaining the lower observed mortalities over the past two decades is correct – the development of resistance/tolerance to the disease or favorable salinities which inhibited *H. nelsoni*? The answer appears to be both are correct, depending on the salinity regime and frequency of exposure to MSX disease pathogens.

2024 Fall Survey

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Timing is (Almost) Everything

The findings of the 2023 and 2024 Fall Oyster Surveys and an ancillary survey in the spring of 2024 illustrated the profound influence that salinity, both in terms of magnitude and timing, has on oyster population dynamics. An extended drought and consequent elevated salinities during 2023 enabled an exceptional recruitment event while allowing for the rapid and extensive spread of MSX disease and increase in dermo disease intensity. Previous experience with a similar situation was not encouraging. The millennial epizootics beginning in 1999 decimated the promising 1997 year class, which was the product of a record-high spatset, before most of those oysters attained market size. The average MSX prevalence in 2023 was the highest since the 2002 peak of that devastating epizootic, causing deep concern for the 2023 cohort. Was history going to repeat in 2024?

Serendipitously, the drought broke with heavy rains and freshets during the late winter and spring of 2024, causing a dramatic reversal in salinity levels. The result was a sharp decline and even disappearance of MSX from all but a few disease monitoring sites. For example, in the fall of 2023, the highest MSX prevalence ever recorded (93%) was on Lighthouse bar in the Choptank River, but by the spring of 2024, MSX disease was completely absent after the salinity had fallen to half of its fall peak. The remaining pockets of MSX disease were at low prevalences no higher than 7%.

While the abatement of MSX brought relief to the general oyster population, there was concern that streamflows had gone too far in the other direction, possibly dropping salinities on the upstream bars of tributaries to the extent that the rare spatsets that had occurred at those locations were in jeopardy. In particular, the portion of the Potomac River oyster grounds above the Route 301 bridge, which received an extraordinary spatset in 2023, was especially vulnerable to high freshwater flows and had previously suffered 100% mortality of oysters due to the prolonged 2018/19 freshets. Fortunately, the pre-existing elevated salinities initially buffered the effect of the 2024 freshets. Also, the freshets occurred during the cold winter months, when oysters are in a physiologically quiescent state and less susceptible to depressed salinities. Lastly, the 2024 freshets were relatively short-lived, subsiding as temperatures began to rise in the spring and the oysters became more active; by June salinities had returned to normal. The 2024 Fall Survey found that the upriver oysters survived the freshets, although their growth was stunted by the lower salinities. In comparison, the record-high streamflows of 2018 persisted for an extended period through the warmest months of the year and into the spring of 2019, resulting in the extensive loss of oysters in the upstream portion of the Potomac River population.

The timing of reduced freshwater input to the bay and return of salinity levels back to normal fortunately coincided with the spawning period of oysters. Subsequently, recruitment was above the long-term median. Also, spat were extensively distributed, occurring on 51 of 53 Spat Index bars. Spatset was observed as far upbay as Mountain Point bar above the Bay Bridge for the first time since 2002 and only the fifth time on record – a rare finding. In contrast, recruitment in the high flow year of 2018 was only 60% of the long-term median with a limited distribution – spat were found on only 31 Spat Index bars; 16 of those had single-digit counts.

The Importance of Salinity to Oyster Recruitment
Salinity is a primary environmental driver of oyster recruitment. Adequate salinity is necessary for gametogenesis, spawning, larval survivorship, and settlement (Loosanoff 1953, Davis 1958, Calabrese & Davis 1970, Thompson et al. 1996, Kimmel & Newell 2007, Tarnowski 2019). Salinity is regulated by freshwater streamflow into the bay. When the Chesapeake watershed entered a drought period towards the latter portion of 2022 and throughout 2023, and again during the summer of 2024, the reduction in streamflows caused salinities to rise to suitable levels for spatset in most corners of Maryland's oyster grounds.

Suitable salinity for spatset is influenced by this streamflow-salinity dynamic in two ways: dilution and tidal transport (Pritchard 1952, 1967). Higher salinity originates from the Atlantic Ocean, which is carried up the estuary by tidal currents and is increasingly diluted by freshwater input along the way. With lower streamflow entering the bay as in 2023, there was less fresh water mixing with the incoming tidal flow, raising salinities further upstream. But in addition to dilution there is a second factor influencing salinity. Lower streamflows mean less volume and force of freshwater to push against the tidal surge, allowing saltier water to penetrate further up the estuary. This transport mechanism also allows the pelagic oyster larvae to be carried further into the upper reaches of tributaries where broodstock might be limited or nonexistent. Flushing time is also regulated by streamflow. Lower freshwater flows mean lengthier flushing times and longer retention of larvae, enhancing the possibility of settlement in a given area (Gaines and Bertness 1992).

Adequate salinity is necessary but not always sufficient for a strong recruitment event. A combination of other physical parameters including temperature, dissolved oxygen, water chemistry, wind-driven currents, ill-timed storms, siltation, and suitable substrate for larvae to set on interplay with biological factors such as sufficient broodstock, predation, competition for space and food with other epibenthic organisms, adequate and appropriate phytoplankton food, harmful algal blooms, and likely other unknown factors to determine whether a strong recruitment event occurs. Oftentimes these depend on synergies of extremely localized conditions, such as the exceptional 2020 Broad Creek spatset. So, having successive widespread recruitment events such as in 2023 and 2024 is uncommon, given the host of variables that can negatively impact spatset even under optimal salinity conditions.

An Abundance of Small Oysters

As a result of the abatement of diseases and related lower mortalities, as well as good survivorship despite the freshets in the upper reaches of tributaries, abundant 2023 year class oysters were observed throughout the Chesapeake region during the 2024 Fall Survey. Referring back to the Potomac River, which in 2023 had the highest regional recruitment in Maryland, the average number of sublegal adult oysters in 2024 was two and a half times greater than in 2023. The change in the average number of small oysters in the western Wicomico River, a tributary of the Potomac, was even more pronounced, increasing from 27/bu in 2023 to 184/bu in 2024. Similarly, increases in small oysters to varying degrees were found in almost every region save for areas where spatsets were not observed in 2023, such as the upper bay and Chester River.

The notable 2023 spatset and subsequent high survivorship benefited several major sanctuaries, especially those in areas that usually have lower recruitment. The number of sublegal adult oysters in the Tred Avon Sanctuary quadrupled in 2024 following a strong spatset in the previous year. Other sanctuaries, including Breton Bay, Manokin, Nanticoke, Upper Choptank, Harris Creek, Lower Patuxent, and St. Marys also showed increased numbers of small oysters in 2024.

The net result from the advantageous salinity conditions that have existed over the past two years has been natural population growth and an increase in biomass in the sanctuaries, reducing the need and considerable expense of planting spat-on-shell for restoration purposes. For example, timely stone plantings in the Manokin Sanctuary produced a considerable spatset in 2024, curtailing the need for spat plantings at a substantial cost savings. Noteworthy is the population expansion in the complex of sanctuaries in the upper Choptank River above Cambridge, where no recent restoration efforts have taken place. Ordinarily a lower salinity area with poor recruitment, the oyster population has tripled since 2021 coincident with higher salinities. On two bars in the upper reaches of the sanctuary that experience the lowest average salinities, the mean number of small oysters jumped from 7/bu in 2022 to 127/bu in 2024. In addition, this area usually is not affected by disease (Oyster Shell Point, the Disease Bar within this area, encountered MSX in two out of 35 years, and long-term average dermo levels are among the lowest of the Disease Bar set). The episodic spatsets and good survivorship due to low disease pressure should help assure a sustaining population, provided there is not another extreme freshet such as occurred in 2018/19, which heavily impacted these sanctuaries.

The main commercial harvest areas also benefited from the 2023 spatset and now have abundant sublegal oysters. The addition of these to the population compensated for the removals of market oysters to the extent that the Biomass Index in these areas increased somewhat in 2024. This bodes well for the fishery in the near term, especially with the lower disease levels observed in 2024 and the possibility of disease resistance/tolerance developing in populations that are consistently challenged by disease, where much of the harvesting takes place.

Salinity/Disease Dynamics
In addition to recruitment, salinity plays a determining role in oyster disease dynamics. The effect of streamflow and consequent salinity on *Haplosporidium nelsoni* - the causative agent of MSX disease - and associated oyster mortalities was graphically demonstrated in the year-long span separating the 2023 and 2024 Fall surveys. There was considerable uneasiness following the 2023 Fall Survey regarding the direction MSX disease would take during the upcoming year. The average disease prevalence was the highest since the 2002 peak of the four-year millennial epizootic and was widely distributed – almost to the Bay Bridge. However, these elevated prevalences were not yet reflected in the observed mortality index, which although having increased to 15% was still below the long-term average. In contrast, nearly 60% of the Mortality Index oysters were observed to be dead during the 2002 Fall Survey.

An inkling of what to expect was seen in the spring 2024 survey. The drought had broken and salinities plummeted, in some cases to half of what they were during the previous fall and below the 15 ppt threshold where MSX becomes lethal. Admittedly, the Spring Survey provided a mere glimpse of the situation as only three sites were assayed for MSX disease, but the results were encouraging. MSX prevalence was either greatly reduced or completely purged from those bars, particularly in the Choptank River. The full extent of the impact of the elevated winter/spring streamflows on *H. nelsoni* was still unknown, or if there would be a resurgence of the parasite after the freshets slowed and salinities began to climb again – in fact, drought conditions returned through the summer and into the fall of 2024. Also, dermo disease, whose levels exceeded the long-term averages for both prevalence and intensity in 2023, is undetectable in the spring using standard methods, so its status was unknown going into the 2024 Fall Survey.

Despite rising salinities, by the fall of 2024 there was no indication of a resurgence of disease – in fact, the results of the survey showed just the opposite. MSX disease had been purged from most of the disease sentinel sites and the few locations where it remained had low prevalences, no higher than 7%. This once again demonstrated the sensitivity of MSX disease to lower salinities, as reported at the conclusion of earlier epizootics. Dermo disease levels also declined, though not to the dramatic extent as MSX disease.

Disease-Related Mortality
The drought of 2023 provided a natural experiment. The prolonged period of elevated salinities baywide tested the hypothesis that the lower observed mortalities of the last two decades were the result of disease resistance/tolerance in oysters (Appendix 4). A counter hypothesis is that oyster survival was due to favorable salinity conditions, not genetic improvements. There had been no extended or severe periods of drought during this span of time comparable to the four-year drought that enabled the 1999-2002 millennial epizootics so devastating to the Chesapeake oyster populations.

The degree and geographic extent that MSX disease was able to proliferate in 2023 was unexpected, though the system was already primed in 2022, when 19% of the assayed bars had MSX infections, all in southern Maryland. The disease spread a substantial distance upbay and reached a record-high prevalence in the lower Choptank River where it had not been detected in the previous year, accompanied by a heavy loss of oysters. In the opposite direction, the rapid purging of *H. nelsoni* from all but a few bars in 2024 was equally dramatic.

A striking aspect of the 2023 MSX epizootic was the lower prevalences in the normally disease-prone, higher salinity region of Tangier Sound compared with the elevated prevalences of areas further upbay. The disease-naïve oysters on bars where salinities are rarely above the lethal threshold for MSX disease (e.g., in the lower Choptank River) experienced higher prevalences and mortalities when salinities exceeded that threshold. Despite environmental conditions in the Tangier Sound region that were conducive to MSX acquisition and pathogenic activity, prevalences and related mortalities were relatively moderate in the fall of 2023. Also, the Tangier region likely was the epicenter of the disease outbreak, as most of the highest prevalences were found there in 2022. Yet there was not as severe an impact as was seen in the Choptank region. The most parsimonious answer is that the Tangier region population has developed resistance/tolerance to MSX disease after years of being challenged by it, as opposed to the infrequent exposure of the Choptank region oysters to *H. nelsoni*. Resistance is suggested in the Tangier region oysters as prevalences never got very high, averaging 19.9% in the fall of 2023, compared to a regional average 50.7% in the more susceptible Choptank populations.

The possibility of MSX disease tolerance and/or resistance among Maryland oyster populations in the Tangier Sound regions is supported by findings in neighboring localities. In higher salinity waters such as Delaware Bay and the Virginia portion of Chesapeake Bay, native oyster populations have demonstrated greater survivorship in the face of MSX disease (Ford & Tripp 1996, Burreson & Ford 2004, Ford & Bushek 2012). Furthermore, selective breeding has produced oyster strains with genetically enhanced resistance/tolerance to MSX disease (Ford & Tripp 1996). Yet given that most of Maryland waters rarely or only intermittently experience elevated MSX levels, resistance/tolerance is less likely to develop there with the expectation of higher mortalities when MSX spikes.

Observed Mortalities

Observed mortalities in fall 2023 were not as accordant with disease levels as might been expected. Regionally, the Tangier area had the highest observed mortality, averaging 26%, although it was somewhat lower on Piney Island East bar (18.9%). Surprisingly, observed mortalities in the naïve Choptank populations were even lower, averaging 21%. Despite their extremely high *H. nelsoni* prevalences, observed mortalities were only slightly elevated at

Royston (17.5%) and Lighthouse (20.9%). These were the three bars assayed for MSX disease in the following spring.

This situation reversed in the following spring, as the anticipated mortalities that were not observed in the Choptank during the 2023 Fall Survey became evident. By the time of the 2024 Spring Survey, post-Fall Survey observed mortalities had doubled regionally and more than doubled at the two study bars with the highest fall *H. nelsoni* prevalences of the Choptank region. Because of unsuitable environmental conditions for *H. nelsoni* in late winter/spring that reduced its prevalence, it would be expected that the increased mortalities occurred soon after the 2023 Fall Survey while the parasite was still active. However, the 2024 Spring Survey results found the number of recently dead small oysters in the Choptank region was double that of older small boxes, indicating a spring mortality event. And although market boxes tended to be older, about a third of them were recent. We can only speculate that the oysters were so physiologically weakened in the spring that they eventually succumbed even though the parasite was purged.

In the Choptank oysters, two possibilities for this incongruity between MSX prevalence and mortality during the fall of 2023 are that either they had only recently acquired the disease or environmental conditions had suppressed its impact. In both cases, there was still at least two months of suitable environmental conditions after the 2023 Fall Survey for the pathogens to proliferate before water temperatures below 5°C inhibited their activity (Ford and Haskin 1982). It may be that either or both possibilities were at work. If *H. nelsoni* parasites were acquired earlier in the season, salinities appeared to be in the range to allow infections but not result in mortality. A second mortality period in late winter and spring can occur when water temperatures rise above the pathogen's activity threshold (Ford and Tripp 1996). Disease-stressed oysters may continue to die as metabolic demands remain high in the face of declining energy reserves and food availability. As it turned out, in the Choptank region the temperature dropped below the 5°C threshold during January, but only for one month (Figure A1-3). This suggests that at least in the Choptank region the combination of low temperatures and dropping salinities was able to suppress pathogenic activity during the first half of 2024.

In contrast, observed mortalities in the Tangier region did not increase by the spring of 2024, even though the MSX prevalence on Piney Island East, for example, was still 26%. Perhaps the infected oysters were able to tolerate the pathogens because of the frequent MSX challenges over the decades that this population has endured. This idea might be confounded by the drop in salinities in March 2024 to below the 15 ppt lethal threshold, which would allow the parasites to exist without killing the oysters, and may have reduced the prevalence from the fall value. Nevertheless, salinities remained above 15 ppt for an extended period through the winter while water temperatures remained above 5°C, which would have allowed pathogenic activity to continue.

In estimating the timing of observed mortalities from the Fall Survey data, it is assumed that the mortalities occurred during the intervening time between surveys and that boxes remain articulated for about a year (Doering et al. 2021). This second assumption was not the case on four high mortality bars in the spring of 2024. Between the fall of 2023 and spring 2024, the number of boxes at these sites had increased by an average of 71%. However, that increase in boxes in the spring did not persist into the fall, dropping 64% on average. This decrease in boxes is reflected in the observed mortalities at these bars. By the 2024 Fall Survey, the elevated mortalities observed during the spring on Royston and Lighthouse bars had dropped up to fourfold. Similarly, the observed mortality on Southeast Middleground in the Patuxent River fell from 65% in the spring to 16% the following fall, and Cook Pt. bar mortalities went from 68% in the spring to 17% six months later. In contrast to the shorter disarticulation rates on these high-mortality bars in 2024, the observed mortalities back in 2003 seem to be an overestimate due to residual boxes from the 2002 epizootic that were over one year old. A comparison of the box-count method used in this report and a Bayesian model for estimating oyster mortality is discussed in Doering et al. (2021).

The 2024 spring mortality event would have been missed if that survey had not been conducted, just leaving a comparison between the two Fall Surveys. The only clue would have been to examine the change in oyster numbers between 2023 and 2024, but this is fraught with ambiguity. The decrease in the number of market oysters that was recorded at all of the aforementioned sites could also be attributed to seasonal harvesting. In addition, sublegal oysters could not be considered since their numbers increased due to the strong 2023 spatset, a percentage of which transitioned to the sublegal oyster stage. A regular small-scale spring survey may be warranted moving forward, especially during years with abnormal freshwater flows or high fall MSX disease prevalences, with sampling locations targeted annually based on salinity and disease conditions.

Which of the two hypotheses explaining the lower observed mortalities over the past two decades is correct – the development of resistance/tolerance to the disease or favorable salinities which inhibited *H. nelsoni*? The alternation and timing of drought and freshets during the period of the last two Fall Surveys and the Spring Survey between the two provided considerable insight into this question. The answer appears to be both are correct, depending on the salinity regime and frequency of previous exposures to MSX disease pathogens.

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