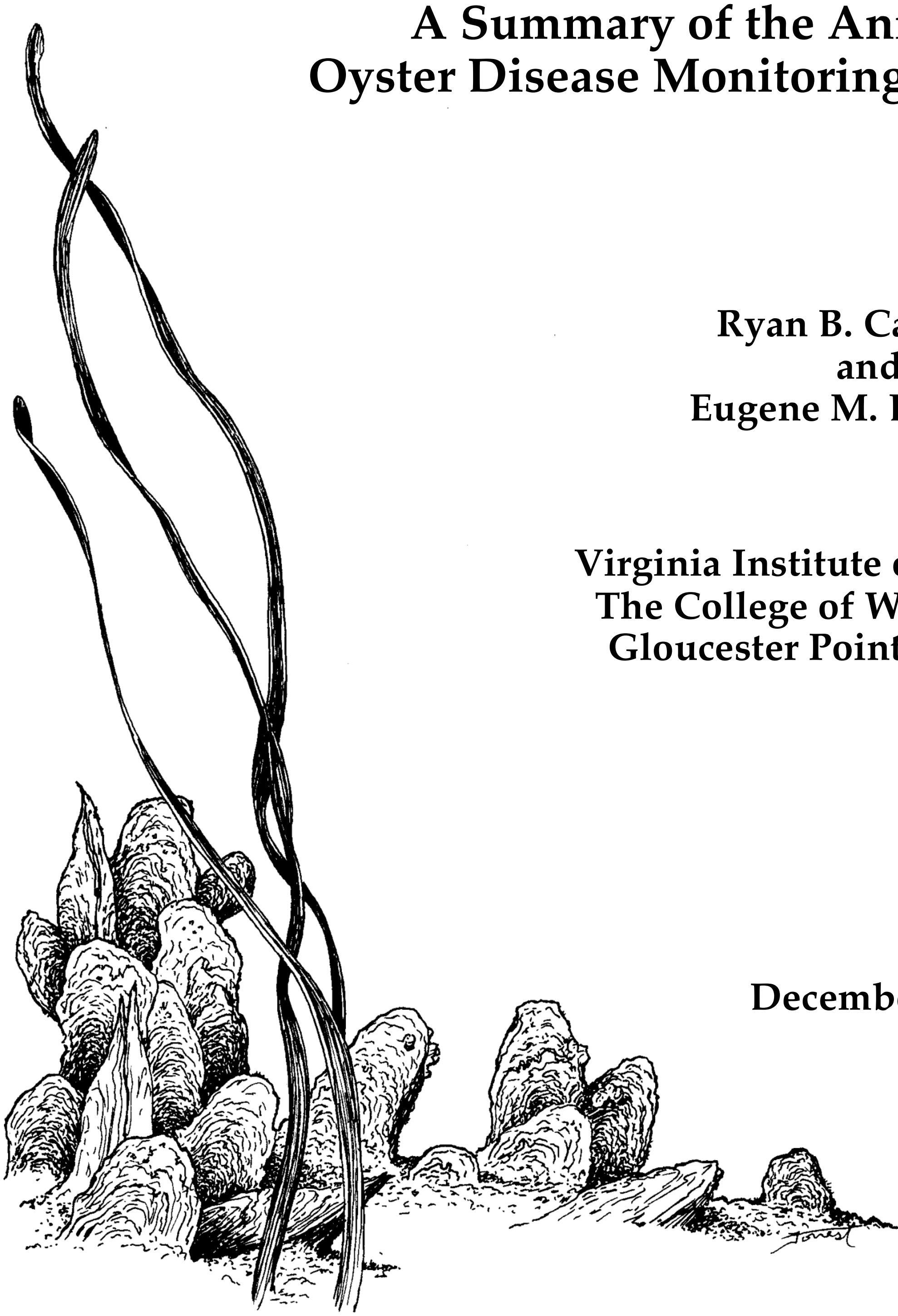
Status of the Major Oyster Diseases in Virginia 2006-2008

A Summary of the Annual Oyster Disease Monitoring Program



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Executive Summary

The years 2006-2008 brought a transition from normal to elevated water temperatures, and from normal to elevated salinities, resulting in increasing oyster disease. Water temperatures, as measured in the James River, were typical until mid-2007, from which point they were consistently above average. The winter of 2007/8 was particularly mild, with water temperatures scarcely falling below 6°C. Streamflows in the major tributaries of Chesapeake Bay were below average in most months from May 2007 through November 2008, resulting in increased Bay salinities. Influenced by these environmental factors, diseases caused by *Perkinsus marinus* (dermo disease) and *Haplosporidium nelsoni* (MSX) became more prevalent and intense through the period, continuing a trend begun in 2005.

James River Quarterly Survey sampling of four oyster reefs revealed record-high levels of *P. marinus* in the upper James River by 2008, when prevalence reached 100% and moderate to heavy infections were common at Deepwater Shoal. *Haplosporidium nelsoni* was detected at the upper three James River stations, Deepwater Shoal, Horsehead Rock, and Point of Shoal, for the first time since early 2003, although prevalence of *H. nelsoni* at these reefs was only 4%. *Haplosporidium nelsoni* was enzootic at Wreck Shoal, but its disease and mortality impacts there were probably only modest.

Fall Survey sampling revealed *P. marinus* levels to be generally normal to high in Virginia tributaries. By 2007 *P. marinus* was present on every oyster reef sampled, and by the end of the 2006-2008 period the parasite was probably causing some mortality throughout Virginia waters. Data for *H. nelsoni* are still incomplete for 2006/7 because of funding limitations, but in 2008 *H. nelsoni* was observed at 17 of 31 sampled reefs, a marked expansion in distribution since 2003/4. A significant MSX disease outbreak occurred in the Great Wicomico River in 2008, as a mild winter and a long period of elevated salinities supported increased *H. nelsoni* activity among a population of relatively susceptible oysters.

Analyses of Spring Imports deployments of susceptible upper Rappahannock River oysters to the York River revealed typically high annual levels of disease-related oyster mortality, each year exceeding 88%. *Perkinsus marinus* began to affect the deployment relatively early in 2006 and 2008, with prevalences around 50% and moderate infections emerging by early July. Infections developed more slowly in 2007, but by August of each year *P. marinus* levels were similar: 96% prevalence, with abundant moderate and some heavy infections. Late summer and fall *P. marinus* levels were above the long-term average for Spring Imports deployments. Peak *H. nelsoni* impacts on the Spring Imports deployments during 2006-2008 were typical, but the onset of serious MSX disease occurred earlier than normal in 2006, with prevalence reaching 88% and intense infections abundant by early July. Early July *H. nelsoni* levels were lower than normal in 2007 and 2008.

Long-term analysis of Spring Imports to the York River indicates that MSX disease pressure is steadily increasing, and that *P. marinus* disease levels continue to be much higher than prior to the intensification of dermo disease in the 1980s. Levels of disease in long-exposed wild oyster populations are much lower than in susceptible stocks, however, indicative of some resistance to both diseases among wild oysters. Increasingly intense parasite activity should favor the development of resistance, as susceptible oysters have fewer opportunities to reproduce before succumbing to disease. Because reproduction by adult oysters resisting serial disease challenges may promote disease resistance, protection of these oysters should be central to strategies for oyster restoration as well as fishery management.

Introduction

The protozoan parasites *Haplosporidium nelsoni* (causative agent of "MSX" disease) and *Perkinsus marinus* (causative agent of "dermo" disease) are serious pathogens of oysters in Chesapeake Bay. *Haplosporidium nelsoni* first appeared in Chesapeake Bay in 1959 and in the early 1960s killed millions of bushels of oysters on lower Chesapeake Bay oyster grounds. The continued presence of the parasite has prevented use of these once-productive areas since that time.

The infection period for *H. nelsoni* begins in early May each year with peak mortality in lower Chesapeake Bay from these early summer infections occurring during August and September. However, infections acquired during late summer and fall may overwinter if salinity remains high, and develop as soon as water temperature increases in early spring. These overwintering infections may cause oyster mortality as early as June. In the major tributaries, normal spring runoff usually causes expulsion of overwintering *H. nelsoni* infections by May, but the pathogen may reinvade an area by fall if salinity is favorable during summer. Oyster mortality is reduced under these circumstances because *H. nelsoni* is present mainly during winter when cold water temperature slows development of the parasite.

Historically, *P. marinus* in Virginia was limited to the lower river areas where salinities are highest, but the parasite increased in abundance and spread throughout all public oyster beds during the 1980s. Until that time *P. marinus* was not as serious a pathogen as *H. nelsoni* because *P. marinus* spread slowly within an oyster bed and between adjacent beds, and required three years to cause significant mortality. However, with its increase in abundance and distribution, *P. marinus* is now a more important oyster pathogen than *H. nelsoni*. Most *P. marinus*-associated mortality occurs during late summer and early fall, but it may begin as early as June following warm winters that allow more infections to persist through the winter.

The distribution and pathogenicity of both diseases are limited by salinity and, in a very general sense, neither parasite causes serious mortality in areas where the salinity remains below 12 ppt. *Haplosporidium nelsoni* is eliminated from oysters after about 10 days below 10 ppt; however, *P. marinus* may persist for years at low salinity although it is not pathogenic at salinities < 12 ppt.

Because of the detrimental effect of these diseases on the Virginia oyster industry, the Virginia Institute of Marine Science has been monitoring the prevalence of both parasites since 1960. Information on disease severity and distribution each year is provided to management agencies and the oyster industry through publications and special advisories of the Marine Advisory Program office. The results of disease monitoring for the calendar years 2006-2008 are presented in this report.

Methods

Sampling

The Oyster Disease Monitoring Program of the VIMS Shellfish Pathology Laboratory has three different components: **James River Quarterly Survey** sampling of four historic oyster reefs; yearly **Fall Survey** sampling of oyster reefs in the James, York, Piankatank, Rappahannock, and Great Wicomico Rivers as well as Mobjack Bay; and monthly monitoring of **Spring Imports** from the upper Rappahannock River (Ross Rock) to the York River.

James River Quarterly Survey and **Fall Survey.** From 1987 to the present the upper James River has been intensively monitored, though data for some sites, including Wreck Shoal, extend much earlier. In January, April, July, and October of 2006-2008, samples of 25 oysters were collected by dredge from Wreck Shoal, Point of Shoal, Horsehead Rock, and Deepwater Shoal. Around October of each year, samples of wild oysters (n = 25) were collected additionally from most major public harvesting areas in Virginia. Together, these sampling programs allow us to determine the annual distribution and severity of *H. nelsoni* and *P. marinus* activity.

Spring Imports. Oysters are collected from the upper Rappahannock River at Ross Rock late each April and held in trays in the lower York River. Ross Rock oysters are highly susceptible to diseases caused by *H. nelsoni* and *P. marinus* and serve as excellent sentinels for the assessment of annual variability in disease pressure.

Prior to deploying trays around 1 May of each year, 25 oysters from Ross Rock were screened for *H. nelsoni* and *P. marinus* to determine the level of existing infections. No *H. nelsoni* infections have ever been encountered at Ross Rock during April, but in some years *P. marinus* has been present at low (< 10%) prevalence. Each month from June through October, mortality (monthly and cumulative) was calculated and samples of 25 oysters were examined histologically for disease, with *P. marinus* detection also by RFTM (see below).

New trays are established each May to provide a record of disease prevalence and intensity for each year. Because sentinel oysters have been held at the same location each year since 1960, we have a long-term database on *H. nelsoni* and *P. marinus* abundance. It is possible to compare parasite prevalence and infection intensity between years and to relate disease abundance and distribution to various environmental parameters.

Diagnostic Techniques

Prevalence (percentage of sample infected) of *H. nelsoni* was determined by histopathological analysis of paraffin–embedded tissues sectioned at 6 μm and stained with hematoxylin and eosin; prevalence of *P. marinus* was determined by thioglycollate culture of mantle, gill and rectal tissue (the RFTM method). Infection intensity of both parasites was rated *heavy*, *moderate*, *light*, or *rare*.

The term "weighted prevalence" will be used frequently in the text. Weighted prevalence (WP) is a measure of parasite abundance that, for a given sample, integrates parasite infection prevalence and intensities. Sometimes referred to as "weighted incidence", this metric has been used since the 1950s to communicate levels of *P. marinus* parasitism. It is calculated for samples here as:

$$WP = [5*(\#\ Heavy) + 3*(\#\ Moderate) + 1*(\#Light\ and\ Rare)]\ /\ Sample\ Size.$$

As interpreted conventionally, weighted prevalence of 0.00-1.00 indicates minimal dermo disease and mortality; a WP of 1.00-2.00 indicates moderate disease and mortality; and a WP of ≥ 2.00 indicates serious disease and mortality. For the Fall Survey samples, 2006-2008 data are presented in the long-term (1989-2008) context, with annual *P. marinus* disease levels characterized as "relatively low", "normal", or "relatively high". "Relatively low" refers to a WP value falling below the first quartile for the 1989-2008 time series (i.e., in the lowest 25% of observations) for that particular site. "Relatively high" refers to a WP value above the third quartile for the 1989-2008 time series (i.e., in the highest 25% of observations) for that particular site.

Environmental Parameters

Water temperatures for the James River at Sewells Point were obtained from the NOAA Tides & Currents web site (http://tidesandcurrents.noaa.gov). Water temperature and salinity data for James River and Fall Survey sites were obtained at time of collection. River flow data for the James, Potomac, and Susquehanna Rivers were obtained from the United States Geological Survey (http://waterwatch.usgs.gov).

Results

I. Environmental Conditions

Water temperatures were generally normal in 2006, but warmer than average from mid-2007 through 2008 (Fig. 1). As measured at Sewells Point in the James River, temperatures were relatively warm in January 2007 before becoming more typical in February, and falling below 5°C for about two weeks; they remained normal through about July. Temperatures were above normal in August and remained above normal through most of 2008. Water temperature in early 2008 was very mild, falling below 6°C at Sewells Point for just hours and never falling below 5°C.

River streamflows in 2006 and early 2007 were generally normal—some months characterized by above-average and some by below-average flows—but streamflows were consistently low from May 2007 through 2008, a trend apparent in plots of streamflow anomalies (Fig. 2). The prolonged period of low streamflows was the first such period since the multi-year drought of 1999-2002. Low streamflows during this period were not limited to the James River, but extended to the other major Chesapeake Bay tributaries. Low streamflows brought elevated salinities, and in the fall of 2007 and 2008 salinities above 15 ppt, favoring serious MSX and dermo disease,

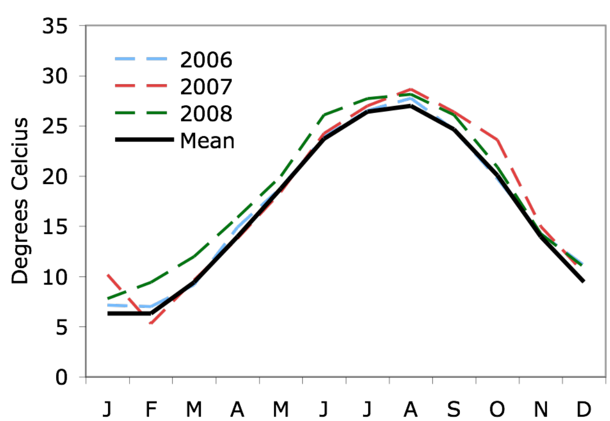

Fig. 1. Water temperatures in the James River at Sewells Point from 2006-2008, relative to the 1997-2008 mean.

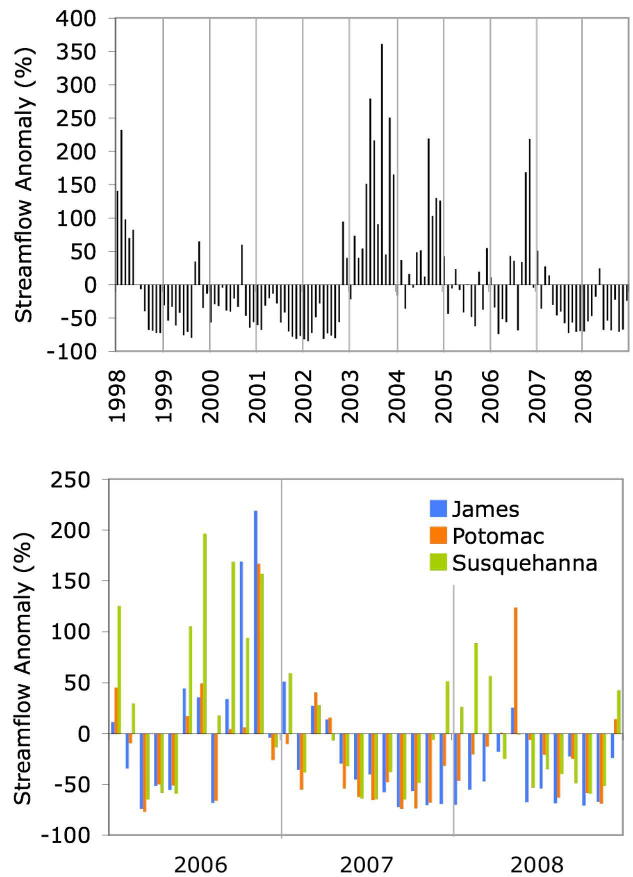

Fig. 2. Streamflow anomalies for the James River from 1998-2008 (top) and for the James, Potomac, and Susquehanna Rivers from 2006-2008 (bottom). Positive values represent months of above-average flows, and negative values months of below-average flows.

characterized most oyster-inhabiting waters of Virginia.

II. James River Survey

Infection levels of *P. marinus* at the uppermost three James River Quarterly Survey stations increased through the 2006-2008 period from relatively low levels in 2005 (Table 1A-C, Fig. 3). Fall *P. marinus* prevalence at Deepwater Shoal increased from 5% in 2005 to 100% in 2008, with infections moderate in intensity becoming very abundant by 2008. Weighted prevalence of *P. marinus* at Deepwater Shoal reached 2.84 in 2008, the highest ever recorded at that site. Fall prevalence at Horsehead Rock increased from 68% in 2005 to 100% in 2006, before decreasing to 88% in 2007 and 84% in 2008. The frequency of moderate to heavy infections increased each year, however. Prevalence of *P. marinus* at Point of Shoal increased from 56% in 2005 to a high of 100% in 2007, with the abundance of moderate-heavy infections also increasing. Both prevalence and the abundance of moderate-heavy infections decreased at Point of Shoal in 2008.

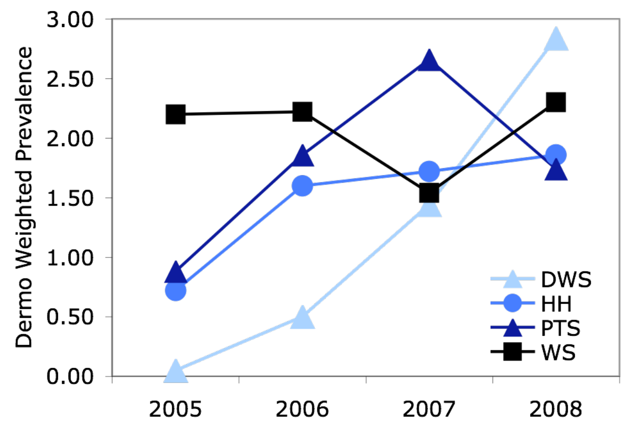

Fig. 3. Annual maximum weighted prevalence (WP) of *Perkinsus marinus* (dermo disease) at Deepwater Shoal (DWS), Horsehead Rock (HH), Point of Shoal (PTS), and Wreck Shoal (WS) in the James River, 2005-2008. The generally increasing WP trend reflects increasing parasite prevalences and intensities, thus intensifying dermo disease.

Levels of *P. marinus* at Wreck Shoal in 2008 were similar to 2005 and 2006, with prevalence approaching 100% and moderate infections abundant. *Perkinsus marinus* levels at Wreck Shoal were lowest in 2007, when prevalence was 92% but moderate infections were less abundant and heavy infections were not detected.

Haplosporidium nelsoni was detected at 4% prevalence at Point of Shoal, Horsehead Rock, and Deepwater Shoal in January 2008. These were the first observations of this parasite at these sites since early 2003. With the exception of one infection at Horsehead Rock in April 2008, *H. nelsoni* was undetected at these beds for the rest of 2008. *Haplosporidium nelsoni* was regularly detected at Wreck Shoal, with prevalence peaking at 44% in April 2006. Moderate-heavy infections were most abundant at this time. Prevalence of *H. nelsoni* at Wreck Shoal otherwise never exceeded 20%, and more advanced moderate-heavy infections were rare.

III. Fall Survey

Fall Survey sampling of Virginia oyster reefs was conducted from 29 September to 8 November 2006; 4-25 October 2007; and 6-27 October 2008. Twenty-nine oyster reefs were sampled for disease analysis in 2006, 27 in 2007, and 31 in 2008. Reefs were located in systems on the western shore of the Chesapeake Bay, including the James River, York River, Mobjack Bay, Piankatank River, Rappahannock/Corrotoman Rivers, and Great Wicomico River. Results of this survey are presented in Table 2A-C, and described for each system below.

James River

Eleven James River oyster reefs were surveyed for disease each year. *Perkinsus marinus* levels were normal to relatively high at James River sites during the 2006-2008 period. At Deepwater Shoal, *P. marinus* prevalence and intensities increased each year, as noted earlier, and a record high weighted prevalence (2.84) was reached in 2008. At Mulberry Point, record high *P. marinus* abundance was reached in 2007 (100% prevalence, with moderate infections abundant; WP = 2.52) before a return to a more normal level in 2008 (WP = 1.52). *Perkinsus marinus* levels at Horsehead and Swash were normal through the period, with prevalences of 84-100% and moderate infections common (WP = 1.64-2.00). A record high abundance was reached at Long Shoal in 2008 (WP = 2.36) after two normal years (WP: 1.00-1.16). A record-tying abundance at Point of Shoal (WP = 2.68) fell between two normal years (1.76-1.88). *Perkinsus marinus* levels were moderate in all three years at Moon Rock (WP: 1.24-1.64).

Perkinsus marinus abundance at Dry Shoal was record-high in 2006 (WP = 2.80), record-low in 2007 (WP = 0.88), and normal in 2008 (WP = 2.04). *Perkinsus marinus* abundance at Wreck Shoal was relatively normal in 2006 (WP = 2.24), relatively low in 2007 (WP = 1.44), and relatively high in 2008 (WP = 2.32). At both Thomas Rock and Nansemond Ridge, it was record-high in 2006 (WP = 2.80 and 3.08, respectively), normal in 2007 (WP = 1.40 and 1.52), and relatively high in 2008 (WP = 2.46 and 1.92).

Haplosporidium nelsoni was not detected in fall samples from Deepwater Shoal, Mulberry Point, Horsehead Rock, or Point of Shoal. Where it was present prevalence never exceeded 16%, and just a single heavy infection was observed, at Dry Shoal in 2007.

York River

Two locations were sampled in the York River from 2006-2008: Bell Rock and Aberdeen Rock. *Perkinsus marinus* levels were normal to high in the York during this period. *Perkinsus marinus* levels were normal at Bell Rock in 2006 and 2008 (WP = 2.40 and 2.08, respectively), but record-high in 2007 (WP = 3.24). Levels at Aberdeen Rock were relatively high in 2006 (WP = 3.00), but normal in 2007 and 2008 (WP = 2.04 and 1.92, respectively).

Haplosporidium nelsoni was not evaluated at these sites in 2006 and 2007. In 2008 *H. nelsoni* was observed at 8% prevalence at Aberdeen, with one infection light in intensity and the other rare.

Mobjack Bay

Two sites in Mobjack Bay, Tow Stake and Pultz Bar, are routinely monitored. Neither site was sampled in 2007, and only Tow Stake was sampled in 2006; both sites were sampled in 2008. The limited available data indicate that *P. marinus* parasitism in Mobjack Bay was normal to low during this period. *Perkinsus marinus* levels at Tow Stake were relatively low in 2006 (WP = 0.72), and normal in 2008 (WP = 2.44). The abundance of *P. marinus* at Pultz Bar in 2008 was much lower than at Tow Stake, but nonetheless normal for this particular site (WP = 0.44).

Haplosporidium nelsoni was only evaluated in 2008. It was detected at Pultz Bar at 16% prevalence, with one infection moderate in intensity, two light, and one rare. It was not observed at Tow Stake.

Piankatank River

Three Piankatank River oyster reefs were sampled: Ginney Point and Palace Bar in all three years, and Burton Point in 2006 and 2008. *Perkinsus marinus* levels were generally normal to low through the period. Levels at Ginney Point were relatively low in 2006 (WP = 1.19), and normal in 2007 and 2008 (WP = 1.92 and 1.48, respectively). Levels at Burton Point were normal in 2006 (WP = 1.80) but relatively high in 2008 (WP = 2.76). Levels at Palace Bar were normal in 2006 and 2008 (WP = 1.88 and 2.08, respectively), but relatively low in 2007 (WP = 1.36).

Haplosporidium nelsoni was evaluated only in 2008. The parasite was not observed at Ginney Point but it was present at Burton Point (8% prevalence, one light and one rare infection) and Palace Bar (12% prevalence, one infection light and two rare).

Rappahannock River

Oysters were sampled from ten Rappahannock River oyster reefs during the 2006-2008 period. Relative abundance of *P. marinus* varied by site. At Ross Rock, furthest upstream, *P. marinus* increased from a level below detection in 2006, to a typically low abundance in 2007 (WP = 0.04), to record prevalence and intensities in 2008 (WP = 0.84). Levels at Bowlers Rock were normal through the period (WP = 0.68-1.28). At Long Rock, *P. marinus* levels were relatively low in 2006 and 2007 (WP = 0.68 and 0.52, respectively), and normal in 2008 (WP = 1.16). Levels were normal throughout the period at Morattico (WP = 1.39-1.58), Smokey Point (WP = 1.16-2.04), Drumming Ground (WP = 1.96-2.54), and Hog House Rock (WP = 0.83-1.38; not sampled in 2007). *Perkinsus marinus* levels at both Parrot Rock and Broad Creek were normal in 2006 and 2007 (WP = 2.36-2.44 and 2.40-2.64, respectively), but relatively high in 2008 (WP = 2.54 and 3.04).

Fall survey samples from the Rappahannock River were not analyzed for *H. nelsoni* in 2006 and 2007. In 2008, the parasite was not detected at Ross Rock, Bowlers Rock, Long Rock, Morattico, or Drumming Ground. At other sites it was detected at 4-12% prevalence, with only one observed infection reaching moderate intensity, at Smokey Point.

Corrotoman River

Middle Ground has been the only Corrotoman River location surveyed in recent years. *Perkinsus marinus* levels were normal through the period, with weighted prevalences ranging from 1.60-2.17. *Haplosporidium nelsoni* infections were not evaluated in 2006 and 2007, but the parasite was present at Middle Ground at 16% prevalence in 2008. All four observed infections reached moderate intensity, and one of these was heavy.

Great Wicomico River

Three Great Wicomico River oyster reefs were sampled from 2006-2008: Haynie Bar, Whaley's East, and Fleet Point. *Perkinsus marinus* levels were generally high in the Great Wicomico during this period. They were relatively high at Haynie Bar in all three years (WP = 2.12-2.48), at Whaley's East in 2006 and 2008 (WP = 1.76 and 1.48, respectively), and at Fleet Point in 2006 and 2007 (WP = 1.84 and 2.00). Levels were relatively low at Whaley's East in 2007 (WP = 0.66), and normal at Fleet Point in 2008 (WP = 1.68).

Haplosporidium nelsoni was not evaluated in 2006 and 2007 Fall Survey samples, but in 2008 *H. nelsoni* levels were, on average, higher than for any other tributary in the survey. *Haplosporidium nelsoni* was observed at 28% prevalence at Haynie Bar, 12% prevalence at Whaley's East, and 12% prevalence at Fleet Point. Infections reached moderate intensity at all three sites, and heavy infections were observed at Haynie Bar and Whaley's East.

IV. Spring Imports

In order to assess inter-annual variation in disease pressure, replicate trays of Ross Rock (Rappahannock River) oysters were established in the lower York River at VIMS in late April of 2006-2008 and subsequently monitored for disease through September (2006) or October (2007, 2008)(Table 3). *Haplosporidium nelsoni* was never detected in oysters sampled at the time of transplantation; just a single *P. marinus* infection, rare in intensity, was observed in 2007. The number of live and dead oysters in each tray was assessed monthly from June into the fall; the resulting determinations of percent monthly and percent cumulative mortalities are shown in Table 3. Cumulative mortality through early July of each year was low (2.6-3.2%) similar to the long-term trend (Fig. 4, top). It was slightly above average by August and September of 2006 and 2007, and eventually exceeded 90%. The onset of serious mortality was delayed in

2008, but mortality rose sharply prior to the sampling in September 2008 and was typically high (88.3%) by October.

Samples for disease diagnoses were also taken monthly. *Perkinsus marinus* began to affect the deployment relatively early in 2006 and 2008, with prevalences around 50% and moderate infections emerging by early July. Infections developed more slowly in 2007, but by August of each year *P. marinus* levels were similar: 96% prevalence, with abundant moderate and some heavy infections. As demonstrated by the weighted prevalence trends (Fig. 4, middle), late summer and fall *P. marinus* levels were above the long-term average for Spring Imports deployments.

Peak *H. nelsoni* impacts on the Spring Imports deployments during 2006-2008 were typical, but the onset of serious MSX disease occurred earlier than normal in 2006, with prevalence reaching 88% and intense infections abundant by early July. Early July *H. nelsoni* levels were lower than normal in 2007 and 2008 (Fig. 4, bottom).

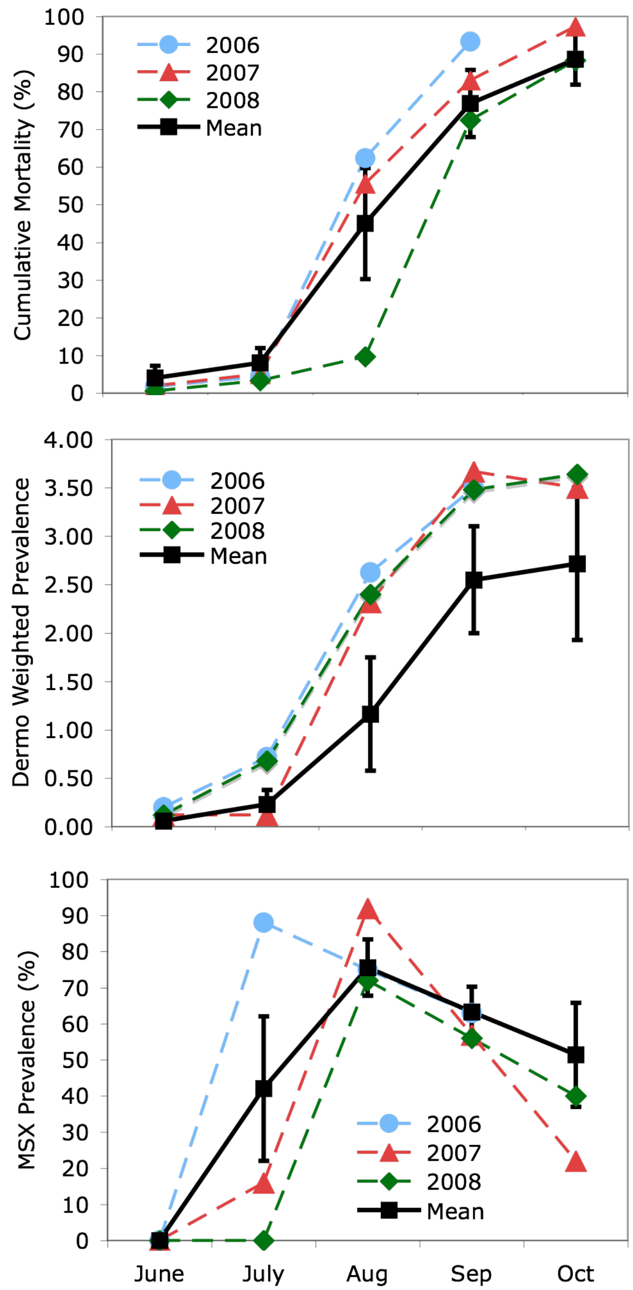

Fig. 4. Monthly cumulative mortality (top), *Perkinsus marinus* (dermo) weighted prevalence (middle), and *Haplosporidium nelsoni* (MSX) prevalence (bottom) in Spring Imports deployments to the York River, 2006-2008, relative to the 1993-2008 mean. Error bars represent 95% confidence intervals.

Discussion

The years 2006-2008 brought a return to moderately high levels of oyster disease in Virginia. The primary agent of disease, as has been the case since the 1980s, was *P. marinus*. *Perkinsus marinus* levels were among the highest observed in the past twenty years, although they fell short of those observed during the extreme epizootic of 2000-2002 (Fig. 5). By October 2008, some *P. marinus*-caused mortality was probably occurring on all oyster reefs in Virginia waters.

The increase in *P. marinus* activity was probably due to physical conditions increasingly favoring the parasite. The multi-year drought of 1999-2002 caused an extended period of decreased streamflows (see Fig. 2) and increased salinities, which brought devastating dermo (and MSX) disease. Wet years with high streamflows and reduced salinities followed in 2003 and 2004, and *P. marinus* levels fell sharply. More normal conditions of precipitation, streamflow, and salinity returned in 2005, and *P. marinus* levels once again increased. This trend continued into 2006, with *P. marinus* abundance continuing to rise.

Beginning in May 2007 and continuing through most of 2008, streamflows were depressed and salinities elevated. As in the 1999-2002 period, these conditions favored intensified *P. marinus* activity, particularly in the upper parts of the major rivers, where lower salinities normally inhibit *P. marinus*. Exacerbating the salinity effects was the extended period of elevated water temperatures, from the summer of 2007 through most of 2008. The relatively warm winter of 2007/8 in particular allowed *P. marinus* to overwinter at a relatively high level, as can be seen in the James River Quarterly Survey data (Table 2C); higher overwintering levels of *P. marinus* are thought to contribute to intensified disease the following summer.

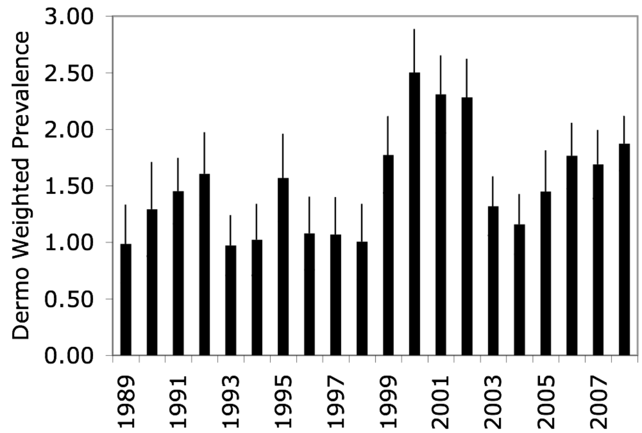

Fig. 5. Weighted prevalence of *Perkinsus marinus* (dermo disease) averaged annually across all Fall Survey samples, 1989-2008. Error bars represent 95% confidence intervals.

The recent extended period of reduced streamflows and elevated salinities favored intensification of *H. nelsoni* activity as well. *Haplosporidium nelsoni* was able to re-colonize upstream oyster beds from which it was purged in 2003/4, including those in the upper James River (Point of Shoal, Horsehead Rock, and Deepwater Shoal), the middle reaches of the Rappahannock River (Smokey Point and Hog House Rock), and the Great Wicomico River. It produced serious disease in some of these locations. Research on oyster populations in the Great Wicomico River revealed a maximum *H. nelsoni* prevalence at Sandy Point in that river in 2007 of 20% in June, with few serious infections observed. By April 2008, however, after a mild winter and months of elevated salinities, *H. nelsoni* infected 64% of oysters at this site, with many oysters displaying serious disease. Similar analyses of oysters at Broad Creek in the lower Rappahannock River revealed a 68% *H. nelsoni* prevalence in sub-market-sized oysters in May 2008, again accompanied by serious disease. Significantly, this peak in *H. nelsoni* parasitism and MSX disease was not observed in a season-long study in 2008 of oysters in the Lynnhaven River in Virginia Beach, where salinities always favor *H. nelsoni* and thus where selection for resistance to MSX disease is likely more intense. There is no refuge from MSX disease in the Lynnhaven, and oysters susceptible to MSX disease have probably been purged from that system.

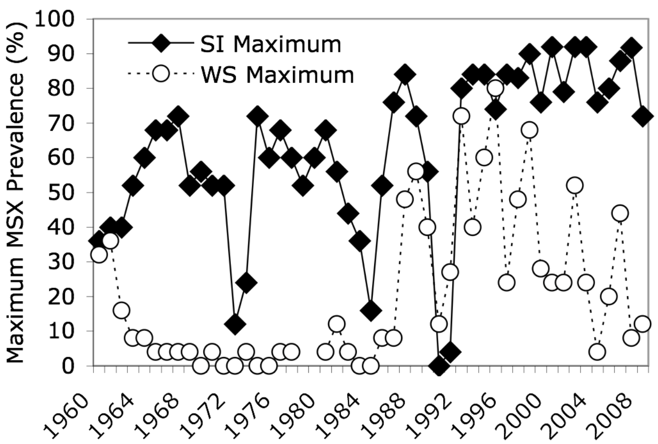

Fig. 6. Maximum annual prevalence of *Haplosporidium nelsoni* (MSX) in Spring Imports (SI) to the York River, and in wild oysters at Wreck Shoal (WS) in the James River, 1960-2008. While the annual MSX disease challenge continues to intensify, as illustrated by infection levels in the highly susceptible Spring Imports, *H. nelsoni* levels in wild oysters at Wreck Shoal continue to decline, a sign that Wreck Shoal oysters may be increasingly resistant to MSX.

It has not been widely appreciated that resistance to disease is developing among oysters in Chesapeake Bay, or that such development is even possible. Yet indications exist in the long-term data that *C.*

virginica is adapting to intense parasitism by *H. nelsoni* and *P. marinus*. The picture is most clear with respect to *H. nelsoni*. As illustrated by the general increase in maximum annual prevalence of *H. nelsoni* in Spring Imports deployments to the York River since 1960, with the exception of wet years when *H. nelsoni* parasitism subsides, MSX disease pressure has steadily increased over the last five decades (Fig. 6). By comparison, *H. nelsoni* infection levels at the now-MSX-enzootic site for which data are most complete, Wreck Shoal in the James River, have been variable but generally decreasing since the early 1990s. After causing epizootic disease at Wreck Shoal during the initial MSX disease outbreak, *H. nelsoni* was scarcely detectable at this site until 1987, when it caused serious disease in what was probably a highly susceptible oyster population. The similarity in *H. nelsoni* prevalence trends, from 1987-1992, between the clearly naïve and susceptible Spring Imports and the Wreck Shoal natives makes a compelling case for the susceptibility of the latter. Yet beginning in 1993 the trends diverged, with *H. nelsoni* prevalence persistently high in the Spring Imports (indicating the strength of the general MSX disease challenge, generated from an as-yet-unknown environmental source) yet variable but decreasing in the Wreck Shoal natives. In addition to the disparity in *H. nelsoni* prevalence, very heavy *H. nelsoni* infections are common in the Spring Imports and MSX-susceptible cultured stocks, but are rare in wild populations like Wreck Shoal. *Haplosporidium nelsoni* clearly continues to thrive in higher salinity waters of Chesapeake Bay, but oyster populations chronically exposed are displaying decreasing disease: fewer infections of any intensity, and fewer serious infections, which presumably indicates increasing disease resistance. MSX disease resistance appears to be less developed where *H. nelsoni* activity is more episodic, as in the Great Wicomico River.

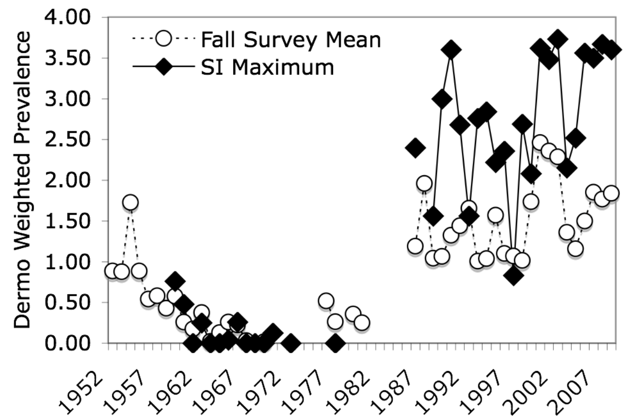

Fig. 7. Maximum annual weighted prevalence of *Perkinsus marinus* (dermo) in Spring Imports (SI) to the York River, and the average weighted prevalence among Fall Survey stations, 1952-2008. With intensification of dermo disease in the 1980s came a divergence in disease levels between susceptible oysters (e.g., the Spring Imports) and oysters from wild populations exposed for generations to *P. marinus*. Heavy systemic infections in particular are less common in wild oysters from dermo-enzootic waters, an indication that these oysters, while infected, resist the development of serious disease.

Signs of resistance to *P. marinus* have been more elusive. With regard to this parasite too, however, the long-term data provide some insight. Prior to the intensification of dermo disease in the 1980s, levels of *P. marinus* parasitism were generally low and similar in wild oysters and in Spring Imports deployments (Fig. 7), as was oyster mortality, which generally required 2-3 years of dermo disease exposure. With the mid-1980s intensification of dermo disease, *P. marinus* levels became very high annually in Spring Imports, with many oysters displaying serious disease and dying from *P. marinus* parasitism. Levels of *P. marinus* have been generally lower among wild oysters surveyed at peak season in the fall, however. Fewer wild oysters display advanced disease as determined by either RFTM or histology, despite the fact that many (if not most or all) wild oysters enter each season with existing infections that have an entire season to intensify, while additional infections are acquired during the summer. It is probably significant that dermo disease is far more acute today than it was prior to its intensification in the 1980s: becoming patent and causing serious mortality in oysters within just a few months, rather than after 2-3 years. The very high disease pressure upon initial exposure to *P. marinus* must leave susceptible oysters fewer opportunities to reproduce before being affected by disease, making dermo disease resistance more selectively advantageous today than it might have been prior to the mid-1980s.

Environmental conditions favored *H. nelsoni* and *P. marinus* during 2006-2008, and the resulting disease probably killed more oysters than in the preceding years. Initial indications are that this trend continued into 2009. Nevertheless, the divergent disease levels between long-exposed wild oyster populations and truly susceptible stocks provide evidence of developing resistance to disease, and thus a basis for optimism. Natural oyster populations in Virginia have a capacity for expansion if substrate can be managed effectively and if harvest pressure is not severe. Protection of larger adult oysters that have demonstrated an ability to survive repeated disease challenges should be central to strategies for oyster restoration as well as fishery management.

Acknowledgments

Captain Paul Oliver operated the vessels collecting quarterly James River oyster samples and the Rappahannock River spring imports; Jim Wesson (Virginia Marine Resources Commission) and Melissa Southworth (VIMS Molluscan Ecology Program) collected oysters for the Fall Survey; Rita Crockett and Susan Denny performed all the histology and RFTM diagnostics.

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Table 1A.

Quarterly survey of prevalence and intensity of *Haplosporidium nelsoni* (MSX) and *Perkinsus marinus* (dermo) in oysters from James River harvesting areas in 2006. Inf/Ex = number infected/number examined. Infection intensity was ranked heavy (H), moderate (M), light (L), or rare (R) (presented as H-M-L-R).

				Haplosporidium nelsoni			*Perkinsus marinus*		
Location	**Date**	**Temp**	**Sal**	**Inf/Ex**	**Prev**	**Intensity**	**Inf/Ex**	**Prev**	**Intensity**
Deepwater Shoal									
	2 Feb	9	5	0/25	0%	0-0-0-0	1/25	4%	0-0-0-1
	18 Apr	17	9	0/25	0%	0-0-0-0	0/25	0%	0-0-0-0
	12 Jul	29	2	0/25	0%	0-0-0-0	2/25	8%	0-0-0-2
	6 Nov	13	6	0/25	0%	0-0-0-0	8/25	32%	0-3-2-3
Horsehead Rock									
	2 Feb	8	7	0/25	0%	0-0-0-0	2/25	8%	0-0-1-1
	18 Apr	17	11	0/25	0%	0-0-0-0	0/25	0%	0-0-0-0
	12 Jul			0/25	0%	0-0-0-0	13/25	52%	0-0-8-5
	6 Nov	13	9	0/24	0%	0-0-0-0	25/25	100%	0-8-15-2
Point of Shoal									
	2 Feb	8	9	0/25	0%	0-0-0-0	3/25	12%	0-0-1-2
	18 Apr	17	12	0/25	0%	0-0-0-0	5/25	20%	0-1-0-4
	12 Jul	28	6	0/25	0%	0-0-0-0	11/25	44%	0-1-6-4
	6 Nov	13	9	0/25	0%	0-0-0-0	23/25	92%	0-12-10-1
Wreck Shoal									
	2 Feb	7	12	3/25	12%	0-0-3-0	9/25	36%	0-2-3-4
	18 Apr	16	16	11/25	44%	2-6-3-0	2/25	8%	0-0-1-1
	12 Jul	28	10	5/25	20%	0-0-4-1	25/25	100%	2-9-12-2
	2 Nov	15	15	0/25	0%	0-0-0-0	24/25	96%	2-12-9-1

Table 1B.

Quarterly survey of prevalence and intensity of *Haplosporidium nelsoni* (MSX) and *Perkinsus marinus* (dermo) in oysters from James River harvesting areas in 2007. Inf/Ex = number infected/number examined. Infection intensity was ranked heavy (H), moderate (M), light (L), or rare (R) (presented as H-M-L-R).

				Haplosporidium nelsoni			*Perkinsus marinus*		
Location	**Date**	**Temp**	**Sal**	**Inf/Ex**	**Prev**	**Intensity**	**Inf/Ex**	**Prev**	**Intensity**
Deepwater Shoal									
	21 Feb		3	0/25	0%	0-0-0-0	4/25	16%	0-0-1-3
	19 Apr	13	2	0/25	0%	0-0-0-0	0/25	0%	0-0-0-0
	17 Jul	29	6	0/25	0%	0-0-0-0	14/25	56%	0-3-4-7
	23 Oct	22	15	0/25	0%	0-0-0-0	20/25	80%	1-6-13-0
Horsehead Rock									
	21 Feb		4	0/25	0%	0-0-0-0	3/25	12%	0-0-3-0
	19 Apr	14	3	0/25	0%	0-0-0-0	1/25	4%	0-0-0-1
	17 Jul	28	7	0/25	0%	0-0-0-0	15/25	60%	0-4-5-6
	23 Oct	22	18	0/25	0%	0-0-0-0	22/25	88%	1-9-10-2
Point of Shoal									
	21 Feb		5	0/25	0%	0-0-0-0	6/25	24%	0-1-3-2
	19 Apr	14	4	0/25	0%	0-0-0-0	2/25	8%	0-0-0-2
	17 Jul	28	10	0/25	0%	0-0-0-0	18/25	72%	1-8-8-1
	23 Oct	22	18	0/25	0%	0-0-0-0	25/25	100%	4-13-7-1
Wreck Shoal									
	30 Jan	5	13	1/25	4%	0-0-1-0	13/25	52%	1-5-7-0
	19 Apr	14	7	0/25	0%	0-0-0-0	0/25	0%	0-0-0-0
	17 Jul	28	14	0/25	0%	0-0-0-0	23/25	92%	0-8-14-1
	22 Oct	22	19	2/25	8%	0-0-1-1	20/25	80%	0-8-11-1

Table 1C.

Quarterly survey of prevalence and intensity of *Haplosporidium nelsoni* (MSX) and *Perkinsus marinus* (dermo) in oysters from James River harvesting areas in 2008. Inf/Ex = number infected/number examined. Infection intensity was ranked heavy (H), moderate (M), light (L), or rare (R) (presented as H-M-L-R).

				Haplosporidium nelsoni			*Perkinsus marinus*		
Location	**Date**	**Temp**	**Sal**	**Inf/Ex**	**Prev**	**Intensity**	**Inf/Ex**	**Prev**	**Intensity**
Deepwater Shoal									
	22 Jan	5	15	1/25	4%	0-0-1-0	5/25	20%	0-0-2-3
	24 Apr			0/25	0%	0-0-0-0	1/25	4%	0-0-0-1
	17 Jul	28	10	0/25	0%	0-0-0-0	9/25	36%	0-1-5-3
	21 Oct	18	12	0/25	0%	0-0-0-0	25/25	100%	3-17-5-0
Horsehead Rock									
	22 Jan	4	17	1/25	4%	0-1-0-0	8/25	32%	0-1-3-4
	24 Apr	19	1	1/25	4%	0-0-0-1	2/25	8%	0-0-1-1
	17 Jul	27	13	0/25	0%	0-0-0-0	10/25	40%	0-0-7-3
	21 Oct	18	15	0/25	0%	0-0-0-0	21/25	84%	0-13-7-1
Point of Shoal									
	22 Jan	4	16	1/25	4%	0-0-1-0	13/25	52%	0-2-6-5
	24 Apr	19	2	0/25	0%	0-0-0-0	0/25	0%	0-0-0-0
	17 Jul	28	12	0/25	0%	0-0-0-0	14/25	56%	0-1-10-3
	21 Oct	18	14	0/25	0%	0-0-0-0	20/25	80%	0-12-7-1
Wreck Shoal									
	22 Jan	5	22	3/25	12%	0-0-3-0	7/25	28%	0-2-3-2
	24 Apr			5/25	20%	3-0-1-1	0/25	0%	0-0-0-0
	17 Jul	27	20	2/25	8%	0-1-1-0	22/25	88%	0-6-16-0
	20 Oct	18	21	0/25	0%	0-0-0-0	24/25	96%	2-13-8-1

Table 2A.

Fall survey of prevalence and intensity of *Haplosporidium nelsoni* and *Perkinsus marinus* in oysters from Virginia oyster populations in 2006. Inf/Ex = number infected/examined. Infection intensity was ranked heavy (H), moderate (M), light (L), or rare (R) (presented as H-M-L-R).

				Haplosporidium nelsoni			*Perkinsus marinus*		
Location	**Date**	**Temp**	**Sal**	**Inf/Ex**	**Prev**	**Intensity**	**Inf/Ex**	**Prev**	**Intensity**
James River									
Deepwater Shoal	6 Nov	12.9	5.8	0/25	0%	0-0-0-0	8/25	32%	0-3-2-3
Mulberry Point	6 Nov	12.8	7.4		No Data		19/25	76%	0-3-16-0
Horsehead Rock	6 Nov	12.8	8.5	0/24	0%	0-0-0-0	25/25	100%	0-8-15-2
Moon Rock	8 Nov	13.4	6.6		No Data		23/25	92%	1-7-15-0
Point of Shoal	6 Nov	13.2	9.4	0/25	0%	0-0-0-0	23/25	92%	0-12-10-1
Swash	6 Nov	13.1	12.9		No Data		22/25	88%	0-12-9-1
Long Shoal	6 Nov	12.8	10.2		No Data		24/25	100%	3-14-7-0
Dry Shoal	6 Nov	13.5	12.6		No Data		22/25	88%	8-8-3-3
Wreck Shoal	2 Nov	14.5	14.7	0/25	0%	0-0-0-0	24/25	96%	2-12-9-1
Thomas Rock	2 Nov	15.0	14.5		No Data		24/25	96%	6-11-5-2
Nansemond Ridge	2 Nov	15.4	15.5		No Data		23/25	92%	6-15-2-0
York River									
Bell Rock	29 Sept	22.3	13.0		No Data		22/24	92%	2-15-4-1
Aberdeen Rock	29 Sept	22.3	17.3		No Data		25/25	100%	3-19-3-0
Mobjack Bay									
Tow Stake	28 Sept	22.3	19.5		No Data		10/25	40%	0-4-4-2
Pultz Bar					No Sample				
Piankatank River									
Ginney Point	13 Oct	19.7	16.6		No Data		9/16	56%	0-5-3-1
Palace Bar	13 Oct	19.7	16.4		No Data		21/25	84%	1-11-8-1
Burton Point	13 Oct	19.4	16.0		No Data		19/25	76%	3-7-9-0
Rappahannock River									
Ross Rock	20 Oct	19.3	7.5		No Data		0/25	0%	0-0-0-0
Bowlers Rock	20 Oct	19.5	11.0		No Data		16/25	64%	1-6-7-2
Long Rock	20 Oct	19.6	11.3		No Data		9/25	36%	1-2-6-0
Morattico	20 Oct	19.8	13.0		No Data		16/25	64%	1-8-5-2
Smokey Point	20 Oct	19.7	14.2		No Data		15/25	60%	4-6-5-0
Hog House Rock	20 Oct	19.6	15.3		No Data		6/13	46%	1-4-0-1
Drumming Ground	20 Oct	19.4	16.3		No Data		22/25	88%	2-13-5-2
Parrot Rock	13 Oct	19.0	15.6		No Data		23/25	92%	3-13-5-2
Broad Creek	13 Oct	19.7	16.5		No Data		24/25	96%	4-10-10-0
Corrotoman River									
Middle Ground	20 Oct	19.4	15.2		No Data		9/14	64%	2-4-3-0
Great Wicomico River									
Haynie Bar	16 Oct	19.2	17.0		No Data		23/25	92%	3-12-7-1
Whaley's East/Cranes					No Sample				
Fleet Point	16 Oct	18.2	16.4		No Data		18/25	72%	5-4-9-0

Table 2B.

Fall survey of prevalence and intensity of *Haplosporidium nelsoni* and *Perkinsus marinus* in oysters from Virginia oyster populations in 2007. Inf/Ex = number infected/examined. Infection intensity was ranked heavy (H), moderate (M), light (L), or rare (R) (presented as H-M-L-R).

				Haplosporidium nelsoni			*Perkinsus marinus*		
Location	**Date**	**Temp**	**Sal**	**Inf/Ex**	**Prev**	**Intensity**	**Inf/Ex**	**Prev**	**Intensity**
James River									
Deepwater Shoal	23 Oct	22.0	15.2	0/25	0%	0-0-0-0	20/25	80%	1-6-13-0
Mulberry Point	23 Oct	21.6	16.5		No Data		25/25	100%	2-15-8-0
Horsehead Rock	23 Oct	21.8	18.0	0/25	0%	0-0-0-0	22/25	88%	1-9-10-2
Moon Rock	25 Oct	21.7	18.4	0/25	0%	0-0-0-0	17/25	68%	0-7-10-0
Point of Shoal	23 Oct	21.6	17.6	0/25	0%	0-0-0-0	25/25	100%	4-13-7-1
Swash	23 Oct	21.4	17.5		No Data		22/25	88%	0-12-10-0
Long Shoal	22 Oct	22.6	16.6		No Data		17/25	68%	0-6-11-0
Dry Shoal	22 Oct	22.0	19.0	2/25	8%	1-0-1-0	15/25	60%	0-4-8-2
Wreck Shoal	22 Oct	22.1	18.5	2/25	8%	0-0-1-1	20/25	80%	0-8-11-1
Thomas Rock	22 Oct	21.9	20.7	3/25	12%	0-0-2-1	19/25	76%	0-8-10-1
Nansemond Ridge	22 Oct	21.4	22.3	4/25	16%	0-0-2-2	18/25	72%	1-8-6-3
York River									
Bell Rock	4 Oct	25.0	16.2		No Data		25/25	100%	6-16-3-0
Aberdeen Rock	4 Oct	24.0	20.6		No Data		23/23	100%	0-12-11-0
Mobjack Bay									
Tow Stake						No Sample			
Pultz Bar						No Sample			
Piankatank River									
Ginney Point	17 Oct	21.0	19.8		No Data		20/25	80%	1-12-7-0
Palace Bar	17 Oct	21.1	20.3		No Data		18/25	72%	1-6-8-3
Burton Point						No Sample			
Rappahannock River									
Ross Rock	16 Oct	21.8	12.1		No Data		1/25	4%	0-0-0-1
Bowlers Rock	16 Oct	20.8	14.5		No Data		11/24	46%	0-8-2-1
Long Rock	16 Oct	20.9	15.2		No Data		7/25	28%	0-3-4-0
Morattico	16 Oct	20.5	17.0		No Data		15/23	65%	0-9-5-1
Smokey Point	16 Oct	21.1	18.3		No Data		17/25	68%	0-6-11-0
Hog House Rock						No Sample			
Drumming Ground	16 Oct	21.3	19.8		No Data		23/24	96%	2-15-6-0
Parrot Rock	16 Oct	21.0	19.9		No Data		18/22	82%	4-9-4-1
Broad Creek	9 Oct	25	20		No Data		48/50	96%	7-28-10-3
Corrotoman River									
Middle Ground	16 Oct	20.9	19.1		No Data		13/18	72%	3-7-2-1
Great Wicomico River									
Haynie Bar	15 Oct	20.6	19.8		No Data		23/25	92%	1-13-7-2
Whaley's East/Cranes	15 Oct	20.7	19.8		No Data		11/25	44%	0-3-7-1
Fleet Point	15 Oct	20.7	20.1		No Data		20/25	80%	5-5-8-2

Table 2C.

Fall survey of prevalence and intensity of *Haplosporidium nelsoni* and *Perkinsus marinus* in oysters from Virginia oyster populations in 2008. Inf/Ex = number infected/examined. Infection intensity was ranked heavy (H), moderate (M), light (L), or rare (R) (presented as H-M-L-R).

				Haplosporidium nelsoni			*Perkinsus marinus*		
Location	**Date**	**Temp**	**Sal**	**Inf/Ex**	**Prev**	**Intensity**	**Inf/Ex**	**Prev**	**Intensity**
James River									
Deepwater Shoal	21 Oct	17.7	11.9	0/25	0%	0-0-0-0	25/25	100%	3-17-5-0
Mulberry Point	21 Oct	17.0	13.7	0/25	0%	0-0-0-0	22/25	88%	0-8-11-3
Horsehead Rock	21 Oct	17.5	14.6	0/25	0%	0-0-0-0	21/25	84%	0-13-7-1
Moon Rock	27 Oct	15.9	14.9	0/25	0%	0-0-0-0	19/25	76%	1-7-10-1
Point of Shoal	21 Oct	17.9	13.8	0/25	0%	0-0-0-0	20/25	80%	0-12-7-1
Swash	21 Oct	17.8	14.8	2/25	8%	0-1-0-1	24/25	96%	1-11-10-2
Long Shoal	21 Oct	16.9	15.9	4/25	16%	0-2-2-0	25/25	100%	1-15-7-2
Dry Shoal	21 Oct	16.7	17.3	2/25	8%	0-1-1-0	23/25	92%	1-12-7-3
Wreck Shoal	20 Oct	17.9	20.5	0/25	0%	0-0-0-0	24/25	96%	2-13-8-1
Thomas Rock	20 Oct	18.0	21.6	2/24	8%	0-0-2-0	23/24	96%	0-18-5-0
Nansemond Ridge	20 Oct	15.8	18.8	2/25	8%	0-0-1-1	20/25	80%	3-8-7-2
York River									
Bell Rock	8 Oct	19.4	14.6	0/25	0%	0-0-0-0	22/25	88%	0-15-7-0
Aberdeen Rock	8 Oct	18.8	18.3	2/25	8%	0-0-1-1	22/25	88%	2-9-11-0
Mobjack Bay									
Tow Stake	6 Oct	20.6	20.7	0/25	0%	0-0-0-0	23/25	92%	3-13-5-2
Pultz Bar	6 Oct	20.3	21.0	4/25	16%	0-1-2-1	7/25	28%	0-2-3-2
Piankatank River									
Ginney Point	16 Oct	21.0	17.5	0/25	0%	0-0-0-0	23/25	92%	0-7-15-1
Palace Bar	16 Oct	21.0	17.5	2/25	12%	0-0-1-2	22/25	88%	1-13-7-1
Burton Point	16 Oct	20.5	18.4	2/25	8%	0-0-1-1	25/25	100%	4-14-4-3
Rappahannock River									
Ross Rock	15 Oct	21.3	10.8	0/25	0%	0-0-0-0	11/25	44%	2-1-5-3
Bowlers Rock	15 Oct	21.3	12.6	0/25	0%	0-0-0-0	13/25	52%	0-2-6-5
Long Rock	15 Oct	21.3	13.9	0/25	0%	0-0-0-0	15/25	60%	0-7-4-4
Morattico	15 Oct	21.5	15.8	0/24	0%	0-0-0-0	18/24	75%	2-6-6-4
Smokey Point	15 Oct	21.4	16.0	3/25	12%	0-1-0-2	17/25	68%	5-7-4-1
Hog House Rock	15 Oct	21.2	16.2	2/24	8%	0-0-2-0	10/24	42%	1-3-3-3
Drumming Ground	15 Oct	21.4	17.5	0/25	0%	0-0-0-0	23/25	92%	2-9-12-0
Parrot Rock	15 Oct	20.5	17.4	2/24	8%	0-0-1-1	23/24	96%	2-15-6-0
Broad Creek	15 Oct	20.5	18.0	1/25	4%	0-0-1-0	24/25	96%	5-16-3-0
Corrotoman River									
Middle Ground	15 Oct	21.5	17.0	4/25	16%	1-3-0-0	18/25	72%	1-9-7-1
Great Wicomico River									
Haynie Bar	14 Oct	21.0	17.5	7/25	28%	1-2-2-2	24/25	96%	2-15-5-2
Whaley's East/Cranes	14 Oct	20.0	17.5	3/25	12%	1-1-1-0	19/25	76%	0-9-8-2
Fleet Point	14 Oct	20.2	17.6	3/25	12%	0-1-1-1	20/25	80%	0-11-5-4

Table 3.

Mean mortality and parasite prevalence and intensity in upper Rappahannock River oysters transplanted to trays at the lower York River, Gloucester Point, VA in April of 2006, 2007, and 2008. Inf/Ex = number infected/examined. Infection intensity as heavy (H), moderate (M), light (L), and rare (R) (H-M-L).

	Monthly	Cumulative	*Haplosporidium nelsoni*			*Perkinsus marinus*		
Date	**Mortality %**	**Mortality %**	**Inf/Ex**	**Prev**	**Intensity**	**Inf/Ex**	**Prev**	**Intensity**
28 Apr 2006			0/24	0%	0-0-0-0	0/24	0%	0-0-0-0
6 June 2006	1.8	1.8	0/25	0%	0-0-0-0	5/25	20%	0-0-1-4
5 July 2006	2.6	4.4	22/25	88%	6-8-5-3	12/25	48%	0-3-4-5
2 Aug 2006	60.7	62.4	18/24	75%	5-1-10-2	23/24	96%	2-16-3-2
20 Sept 2006	82.0	93.3	10/16	63%	0-7-3-0	16/16	100%	6-8-2-0
25 Apr 2007			0/25	0%	0-0-0-0	1/25	4%	0-0-0-1
7 June 2007	2.0	2.0	0/25	0%	0-0-0-0	3/25	12%	0-0-1-2
28 June 2007	3.2	5.1	4/25	16%	0-1-3-1	3/25	12%	0-0-2-1
9 Aug 2007	53.2	55.6	22/24	92%	0-8-12-2	24/25	96%	6-5-11-2
5 Sept 2007	61.8	83.1	13/23	57%	3-4-5-1	24/24	100%	13-6-5-0
11 Oct 2007	84.8	97.4	2/9	22%	0-0-2-0	9/9	100%	2-6-1-0
30 Apr 2008			0/25	0%	0-0-0-0	0/25	0%	0-0-0-0
4 June 2008	0.6	0.6	0/25	0%	0-0-0-0	3/25	12%	0-0-0-3
2 July 2008	2.7	3.3	0/25	0%	0-0-0-0	13/25	52%	0-2-10-1
30 July 2008	6.7	9.7	18/25	72%	1-6-10-1	24/25	96%	3-12-9-0
5 Sept 2008	69.6	72.5	14/25	56%	3-5-5-1	25/25	100%	9-13-3-0
7 Oct 2008	55.1	88.3	10/25	40%	1-1-5-3	25/25	100%	8-17-0-0