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OYSTER (Crassostrea virginica) RECRUITMENT STUDIES IN THE GREAT BAY ESTUARY, NEW HAMPSHIRE

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OYSTER (*Crassostrea virginica*) RECRUITMENT STUDIES IN THE GREAT BAY ESTUARY, NEW HAMPSHIRE

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THESIS

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ABSTRACT

OYSTER (*Crassostrea virginica*) RECRUITMENT STUDIES IN THE GREAT BAY ESTUARY, NEW HAMPSHIRE

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Oyster populations in New Hampshire's Great Bay Estuary have experienced dramatic declines similar to populations along the east coast. These declines have caused ecosystem degradation in estuaries and prompted a focus on oyster reef restoration. Despite the large use of procured funds dedicated for oyster reef restoration, few quantifiable successes have occurred. Currently, there is no rigorous method for determining where a restored reef would have the highest probability for long-term success. However, consistent and substantial natural recruitment is a major factor to consider.

In this research, I identify historic trends in oyster populations, quantify the success and failures of restored reefs, and examine how proximity to a native oyster reef affects recruitment. Oyster populations throughout the Great Bay Estuary declined significantly after the introduction of two diseases, MSX and Dermo, in 1995. Although, populations rebounded after large spatfall events, three to four years after these events population levels declined, probably mainly a result of disease.

My results suggest oyster recruitment is significantly greater on natural oyster reefs compared to restored reefs. There was also a significant increase in recruitment on restoration reefs less than 1 km from a native reef compared to restoration reefs greater than 1 km from a native reef.   Furthermore, recruitment decreased significantly as proximity from a native reef increased. Results suggest that restoration efforts should consider extending the natural boundary of native oyster reefs to provide the greatest potential for natural recruitment and thus long-term reef development.

INTRODUCTION

Oyster Life History

Eastern oysters, *Crassostrea virginica* (Gmelin, 1791), inhabit coastal marine and estuarine waters from the St. Lawrence in Canada to the Gulf of Mexico, Caribbean, and coasts of Brazil and Argentina (Galtsoff 1964). Oysters inhabit intertidal and subtidal zones throughout this range but predominantly live subtidally in the northeast US, though some have been reported intertidally in New England (Capone et al. (2008). Oysters have a bipartite life cycle with pelagic larvae and sessile adults (Galtsoff 1964). They are broadcast spawning, protandric hermaphrodites (Coe 1943), meaning young oysters generally function as males and older oysters as female (Andrews 1979).

Oysters can tolerate a wide range of environmental conditions. Specifically, adult oysters can live in water temperatures ranging from $-2^{o}C$ to $36^{o}C$ (Galtsoff 1964). However, their growth ceases below $8^{o}C$ (Price et al. 1975). Growth rates vary with temperature (Butler 1953), with the highest growth rates occurring around $25^{o}C$ (Galtsoff 1964). Oysters also tolerate a wide range of salinities, from about 5 ppt to 40 ppt (Davis 1958; Galtsoff 1964), with 14 to 28 ppt being the optimum salinity range (Galtsoff 1964). As salinity decreases, the tolerated range of temperatures narrows (Davis and Calabrese 1964). Flood events can temporarily reduce salinity and cause reductions in oyster abundance, larval settlement, and filtration rates (Pollack et al. 2011). Moreover, flood disturbances can also cause reductions in predation and disease, allowing for rapid reestablishment of oyster populations (Pollack et al. 2011).

Spawning is triggered by a variety of factors including temperature (Nelson 1928a; Nelson 1928b), phytoplankton abundance (Nelson 1955; Nelson 1957), and to a lesser degree, salinity (Butler 1949). While a sudden rise in water temperature is more critical to spawning than a certain threshold being attained (Medcof 1939; Butler 1956), a phytoplankton bloom can also initiate spawning and may be a more reliable spawning cue than variability in water temperature (Nelson 1955; Starr et al. 1990). Once spawning conditions occur, male oysters release sperm into the water column, inducing mass spawning by the rest of the population (Galtsoff 1938). However, a critical density of oyster broodstock is necessary for a coordinated spawning response and successful fertilization.

Oyster eggs are fertilized externally in the water column and develop into larvae. The larval period decreases as temperatures increases (Kennedy 1996) and in northern waters, the larval period ranges from 30 days at 18^{o}C to 24 days at 21^{o}C (Needler 1940). The larval stage ends with settlement of oysters onto substrate. During settlement the larvae cement their left valve to the substrate and become permanently attached (Harper 1992). Numerous factors affect oyster settlement, including: temperature (Ryder 1885; Loosanoff and Engle 1940), mechanical disturbance, oxygen supply, food supply, light, cultch type, and waterborne chemicals (Lutz et al. 1970). A recent study conducted by Lillis et al. (2013) found the sounds produced from oyster reefs apparently attract and cause settlement of oyster larvae. Bacterial films on the surface of substrates can also enhance settlement (Weiner et al. 1985; Weiner et al. 1989).

Through the process of repeated settlement of oysters in an area, oysters create complex matrices of structured habitats, referred to as reefs or beds. Ecologically, these aggregations of live oysters and associated organisms can provide important ecosystem services, including habitat provision, water filtration, food for other invertebrates and fish and benthic-pelagic coupling of material and energy (Wells 1961; Bahr and Lanier 1981; Lenihan and Peterson 1998; Coen et al. 1999, 2007; Grabowski et al. 2007). In addition to the ecosystem services provided by oysters, they also provide a valuable commercial and recreational resource.

<u>Declines in Oyster Populations</u>

Wild oyster populations in the northeastern US dramatically declined over the past century due to multiple factors including past exploitation, pollution, and diseases. More than 99% of natural oyster reefs are considered functionally extinct (Beck et al. 2011). Habitat loss associated with overfishing is considered the major cause of the initial declines in oyster populations along the east coast (Rothschild et al. 1994; Jackson et al. 2001). Estuaries along the east coast have also experienced a decreasing trend in spat fall since the 1940's which is driven by the loss of adult oysters in the spawning stock (Kimmel and Newell 2007).

In the late 1800's, land clearing for agriculture caused heavy siltation events in coastal estuaries which led to decreases in oyster populations (MacKenzie Jr 2007). The accumulation of silt deposits on oyster reefs can prevent oyster larvae settlement and degrade oyster habitat. Oysters buried under 20 mm of sediment can clear the overlying silt, but if the silt layer exceeds 40 mm the oyster will die within two weeks (Comeau 2014).

In addition to over harvesting and siltation events, multiple diseases have drastically affected oyster populations along the east coast. Although many different diseases can affect oysters, MSX (*Haplosporidium nelsoni*) and Dermo (*Perkinsus marinus*) have been the greatest causes of oyster mortality. Dermo was initially discovered in the Gulf of Mexico in the late 1940’s and prior to the 1990’s was rarely found north of the Chesapeake Bay. Increasing water temperatures during the 1990’s is thought to have led to outbreaks of *P. marinus* in the northeast (Cook et al. 1998). Warmer winter temperatures correlate with increased survival of *P. marinus* (Ford and Tripp 1996). Pollutants also enhance preexisting *P. marinus* infections in oysters (Chu and Hale 1994). Oysters infected by *P. marinus* experience slower shell growth and soft tissue growth (Menzel and Hopkins 1955; Ray et al. 1953). These Infections can also impair adductor muscle strength, leaving oysters prone to gape (Gauthier and Fisher 1990). Dermo is transmitted directly from oyster to oyster and proliferates rapidly at temperatures between 25 ^{o}C and 30^{o}C and salinities greater than 15 ppt (Ford and Tripp 1996).

The protistan parasite *H. nelson*, or MSX, was first introduced from populations of *C. gigas* in the Pacific Ocean to *C. virginica* on the east coast in the 1950’s (Burreson et al. 2000). MSX is active in temperatures above 10^{o}C and intolerant of salinities below 10 ppt (Ford and Tripp 1996). The cause of oyster death by MSX is not completely understood, but Ford and Tripp (1996) suggest a toxin may induce rapid death after infection, while slower death is associated with loss of metabolic condition.

Repercussions of climate change, especially ocean acidification and warming water temperatures, has and will also continue to impact oyster populations. Ocean acidification leads to lower pH that weakens the oyster larvae shells, diminishing their growth and lowering survival rates (Miller et al. 2009). Acidification can also decrease calcification rates of juveniles and adults (Beniash et al. 2010; Dickinson et al. 2012; Waldbusser et al. 2011). Moreover, warming water temperatures can lead to increased incidences of infectious diseases (Burge et al. 2014) while also increasing the ranges of these diseases which will contribute to species declines (Harvell et al. 2002).

Site Selection and Restoration Success

The causes for oyster declines in New Hampshire also reflect trends in other areas and include disease, sedimentation, and human harvest (Langan 1997; Odell et al. 2006; Grizzle et al. 2006; Konisky et al. 2014). Management agencies in the state initiated oyster restoration programs in the early 2000s, and substantial progress has been made. However, much remains to be learned, particularly with respect to long-term success and the factors affecting success. The bulk of the research on eastern oyster reef restoration has occurred in the mid-Atlantic and southeastern US. In general, the amount of hard substrate suitable for oyster reef development in these areas has declined but natural oyster populations are still sufficient in many areas to consistently produce a substantial annual recruitment of young oysters (spat set). Thus, the major focus in many areas has been on determining the types and spatial arrangements of substrate material suitable for natural recruitment and subsequent reef development (Soniat et al. 1991; Luckenbach et al. 1999; Coen and Luckenbach 2000; O'Beirn et al. 2000; Luckenbach and Ross 2003; Piazza et al. 2005; Nestlerode et al. 2007; Powers et al. 2009; Brown et al. 2013; La Peyre et al. 2014). However, oyster populations in the northeastern US, including New Hampshire, are typically substrate and recruitment limited so more complex restoration methods must be developed (Grizzle et al. 2013; Lodge et al. 2015).

More than 20 oyster restoration projects involving a diversity of objectives, sizes, and methods have been completed in the state since 2000. Most of the early projects were experimental in nature and conducted by scientists at the University of New Hampshire (UNH). Total bottom area involved in each of the early projects was typically <1 acre and each was focused on particular research topics. Since the mid-2000s, the emphasis has been on full restoration-scale projects, most of which have been collaborative efforts between UNH and The Nature Conservancy (TNC), and building on what was learned from earlier work in the state and elsewhere. The current oyster restoration process in New Hampshire includes the methods used in many areas where the oyster populations are substrate and recruitment limited (Brumbaugh and Coen 2009): construction of a hard substrate reef base followed by deposition of remotely set oyster spat-on-shell onto the reef base. One of the major unknowns in the overall process is how to choose sites that have good potential for consistent natural recruitment, and thus long-term success. The overall goal of my research was to assess how natural oyster recruitment varied spatially in the estuary and how this variation might affect oyster reef restoration success.

In recent years, oyster reef restoration site selection received increased attention (Kennedy and Sanford 1999) with establishment of site planning criteria (Brumbaugh et al. 2006) and monitoring standards (Baggett et al. 2014). Currently, restoration sites are selected based on factors such as: historic distributions of oysters, source/sink areas for larvae, current velocity, sedimentation, and predation (Lipcius et al. 2015). To limit the impacts of harvest on oyster populations, sites are placed on privately leased or owned lands that are closed to shellfish harvest. The cost incurred from restoration projects located in non-harvest areas will be recovered by the economic value of oyster reef ecosystem services (e.g. shoreline stabilization, water quality improvement) in 2 to 14 years, while sites that allow harvest will not recover the cost of restoration (Grabowski et al. 2012). Improvements in site selection have been made in reef restoration because of restoration guidelines, but there is still no comprehensive understanding of the factors affecting long-term success.

The most common way for restoring oysters are with remote setting and shell planting. Remote setting involves hatchery produced oyster larvae settled onto cultch material, referred to as spat-on-shell, which are transferred to the restoration sites (Castagna et al. 1996). Shell planting, which is relatively inexpensive compared to remote setting, involves placing shell in an area and allowing native spat to settle onto it (Coen and Luckenbach 2000; O'Beirn et al. 2000). Oyster larvae prefer to settle onto oyster shell (Ayer et al. 1970), but they will also settle on cement, limestone, granite, plastic, algae, and various trash objects (Soniat and Burton 2005; Nalesso et al. 2008).

Oyster shell has become a limited resource due to its use as construction material. Therefore, it is critical for managers to restore sites that will have the greatest likelihood for success.

Despite the large use of procured funds dedicated for oyster reef restoration, few quantifiable successes have occurred (Hargis Jr and Haven 1988). As previously mentioned, lack of sufficient shell material for setting oyster larvae limits oyster production on reefs (Mackenzie 1970; Hargis Jr and Haven 1988). In addition, oyster reefs can fail to accrete reef material via natural recruitment at sufficient rates to compensate for losses due to shell degradation and sedimentation (Powell et al. 2006; Mann and Powell 2007). Although there is no rigorous method for determining where a restored reef would have the highest probability for long-term success, consistent and substantial natural recruitment is a major factor to consider. Therefore, it is critical to collect oyster recruitment data to properly assess the spatial distribution of spat within an estuarine system.

Great Bay Estuary

The Great Bay Estuary located in southeastern New Hampshire is a tidal system that supports diverse habitats, including eelgrass meadows, salt marshes, oyster reefs, mudflats and rocky intertidal zones. Seven rivers discharge into this estuary: Winnicut, Squamscott, Lamprey, Oyster, Bellamy, Cocheco, and Salmon Falls rivers. The estuarine tidal waters cover approximately 17 square miles (10,900 acres) and, tidal height ranges from 2.7 m at the mouth of the estuary to 2.1 m at the mouth of the Squamscott River. Strong tidal currents and mixing limit vertical stratification during most of the year throughout the estuary. The flushing time for the whole estuary is 28.5 days (Brown and Arellano 1980; Bilgili et al. 2005). The average salinity ranges from 10 ppt in the Squamscott River to 26 ppt in the Piscataqua River (Brown and Arellano 1980).

The Great Bay Estuary has seven major oyster reefs (Figure 1), three in recreational harvest areas and four in non-harvest areas. All of the native oyster reefs in non-harvest areas are located at the mouth or along a tributary of Great Bay Estuary; Squamscott (3.9 acres), Piscataqua (19.9 acres), Oyster (1.7 acres), and Lamprey Rivers (Smith 2002; Grizzle et al. 2008a). The three harvestable reefs are all located within Great Bay proper; Adams Point (13.1 acres), Nannie Island (24.7 acres), and Woodman Point (7.3 acres) (Smith 2002; Grizzle et al. 2008a). Although oyster reefs in the Great Bay Estuary are primarily subtidal, oysters live among *Ascophyllum nodosum* in intertidal regions with rocky substrata throughout the estuary (Capone et al. 2008).

Figure 1. Major oyster reefs in the Great Bay Estuary, NH.

Organization of Thesis

The thesis is organized to reflect the chronology of my research, proceeding from an assessment of historic oyster population data to field experiments. The objective of Chapter 1 is to examine historic oyster population data collected in the Great Bay Estuary for trends in population dynamics. This assessment quantified the impact MSX and Dermo, as well as other negative factors have had on the oyster populations. The data also indicated when annual oyster recruitment peaked and the relationship these peaks have with oyster adult densities.

The objective of Chapter 2 is to assess the success of oyster restoration projects in the Great Bay Estuary. The major finding was that natural recruitment onto restored oyster reefs was negatively related to distance from a natural reef. The data also provided information on the size distribution of oysters on both natural and restored reefs.

The objective of Chapter 3 is to test the hypothetical negative relation between natural recruitment and distance from a natural reef. Field experiments on three reefs over two years (2014 and 2015) quantified the relationship, and provided information on the size distribution of oysters and the factors that influence their growth rates. Collectively, these data are relevant to restoration site selection and could assist restoration managers in selecting restoration sites with the greatest potential for success.

CHAPTER 1

HISTORIC OYSTER POPULATIONS IN THE GREAT BAY ESTUARY

Introduction

The Great Bay Estuary has a long history of exploitation, especially oyster harvesting. In the 17th and 18th centuries, oysters were plentiful in the Great Bay Estuary (Jackson 1944). In 1874, during a coastal mapping survey, surveyors described a flourishing oyster population from one end of the bay to the other (approximately 900 acres of oyster reefs). At that time, no oyster reefs were found in Little Bay. Historically, vast quantities of oysters settled at the mouths of the Squamscott and Lamprey rivers, evidenced by the shell-heaps along the southeastern shore of the Great Bay (Goode 1887). Adult oysters were large relative to today, with a length of 230 mm to 255 mm and some specimens reaching 380 mm. Shortly after the 1874 survey, intense oyster harvesting began with the use of tongs and dredges. During the winter, horses pulled the dredges through holes cut in the ice to access the reefs. Regulations were enacted to forbid the use of oyster dredges and limit oyster-harvesting days, but the laws came too late and within five years the flourishing oyster reefs were severally deteriorated (Goode 1887).

Even with the previously enacted laws, over harvesting continued into the next century. In the early 1980s, the oyster populations in the Great Bay Estuary were significantly reduced to approximately 148 acres of major oyster beds (Short 1992). Populations declined further in the mid-1990's due to outbreaks of the diseases MSX (*Haplosporidium nelsoni*) and Dermo (*Perkinsus marinus*) (Barber et al. 1997). During this period, the number of adult oysters dropped from over 25 million in 1993 to 1.2 million in 2000 (Piscataqua Region Estuaries Partnership 2013). The loss of large adult oysters was followed by observed declines of annual recruitment as well as available substrate on which oyster larvae typically settle.

Currently, recreational harvest of oysters is limited to New Hampshire residents who possess an oyster-harvesting license. Harvesters can only collect oysters by hand, hand rake or tongs from September through June, sunrise to sunset and oysters cannot be collected through the ice. In 2008, oyster harvest limits were reduced from one bushel to one-half bushel per day. Currently, oysters from natural reefs are only harvested recreationally in Great Bay proper and all commercial activity is limited to the newly expanding aquaculture industry in Little Bay.

This chapter gives an overview of recent trends in oyster populations in the Great Bay Estuary. I used data collected by the New Hampshire Fish and Game Department to describe the impacts of harvest and diseases on oyster populations. The historic data set also provides insight into oyster recruitment and population dynamics in this estuary. Monitoring of oyster reefs in the Great Bay Estuary provides valuable information on how oyster populations are changing and what could be causing those changes.

Methods and Materials

Since 1991, the New Hampshire Fish and Game Department has monitored oyster recruitment and population composition on natural oyster reefs in the Great Bay Estuary. Oysters are collected from six oyster reefs during the fall at the following locations: Adams Point, Woodman Point, Nannie Island, Oyster River, Piscataqua River, and Squamscott River. Consistent annual data was collected from all sites except the Squamscott River.

During fall, divers collect approximately five replicative 0.25 m^2 quadrat samples at each oyster reef by excavating by hand all of the shell material within the quadrat. All shell materials are rinsed with seawater and all live oysters are measured (shell height in mm) and counted. Approximately ten oysters, greater than 60 mm from each surveyed site, are tested for prevalence of MSX and Dermo.

Oyster recruitment and adult densities were analyzed for all surveyed sites. Mean oyster density was calculated for both oyster spat and adult oysters by averaging the numbers of oysters collected from all quadrat samples at each site. Oyster spat was defined as oysters with shell height less than 40 mm and adult oysters are defined as having shell height greater than 60 mm. The maximum shell height was determined each year by the largest oyster at the Adams Point, Nannie Island, and Woodman Point oyster reefs. A quadratic trend line was used to fit the maximum shell height data. The percent prevalence of MSX and Dermo was calculated only for oysters sampled at the Adams Point, Nannie Island, and Woodman Point oyster reefs. Temperature and salinity data, collected from the Great Bay National Estuarine Research Reserve water quality monitoring stations, was averaged by month (May through October). Data are not collected during the winter when the estuary typically freezes over.

Results

Temperature and salinity has consistently increased during the spring and summer, before decreasing in the fall (Figure 2, Table A3, and Table A4). The monthly temperatures have been warmer since 2007 (Table A3). The number of NH residents permitted to recreationally harvest oysters has drastically decreased since the mid-1990s (Figure 3). Maximum shell height of oysters collected during the surveys has continued to decrease since the mid-1990s (R^2 = 0.6901) (Figures 3 and 4). The prevalence of MSX in oysters in Great Bay has fluctuated between 10% and 50% since it was first found in 1995 (Figure 4). The percentage of oysters infected with Dermo drastically increased in the mid-2000s to approximately 90% and has stayed above 50% since (Figure 4).

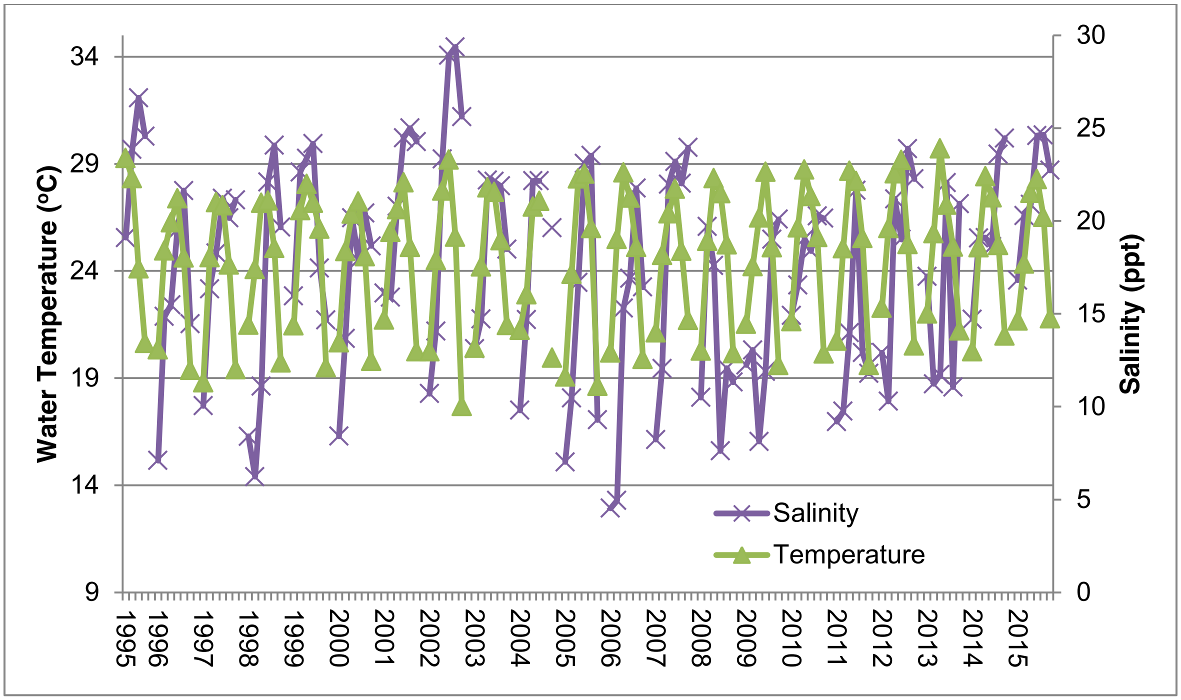

Figure 2. Mean monthly temperature and salinity data for Great Bay from May through October for 1995 – 2015.

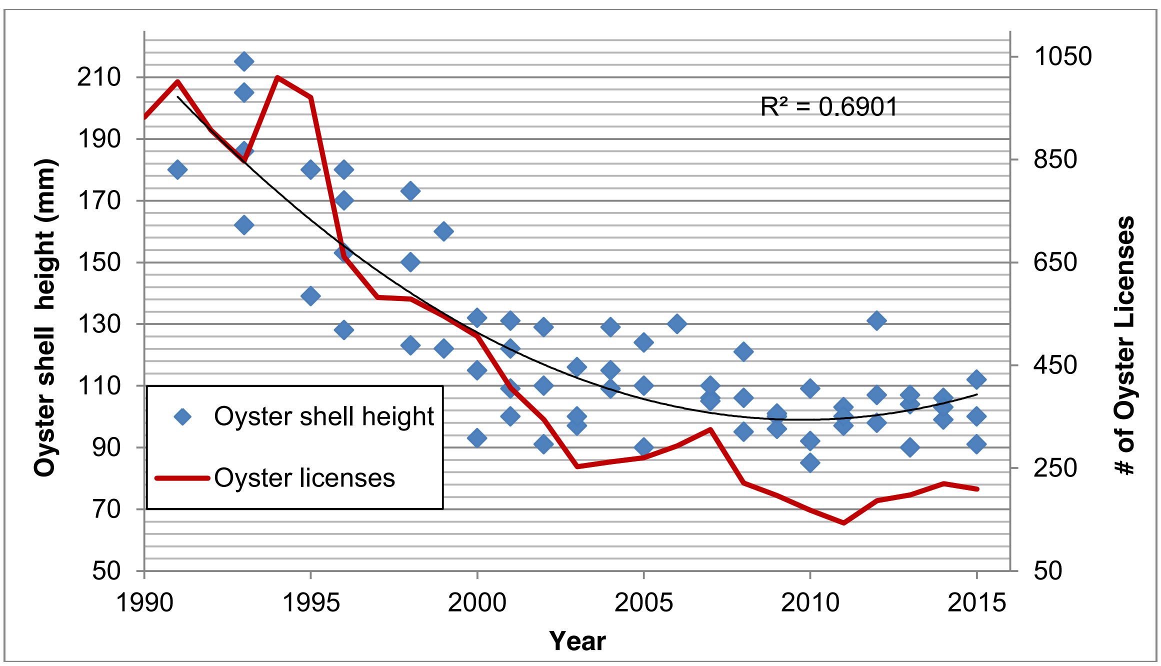

Figure 3. Maximum shell height for oysters collected using quadrats (0.25 m^2) on oyster reefs (Adams Point, Nannie Island, and Woodman Point) in Great Bay and the number of oyster licenses issued per year (NH Fish & Game data).

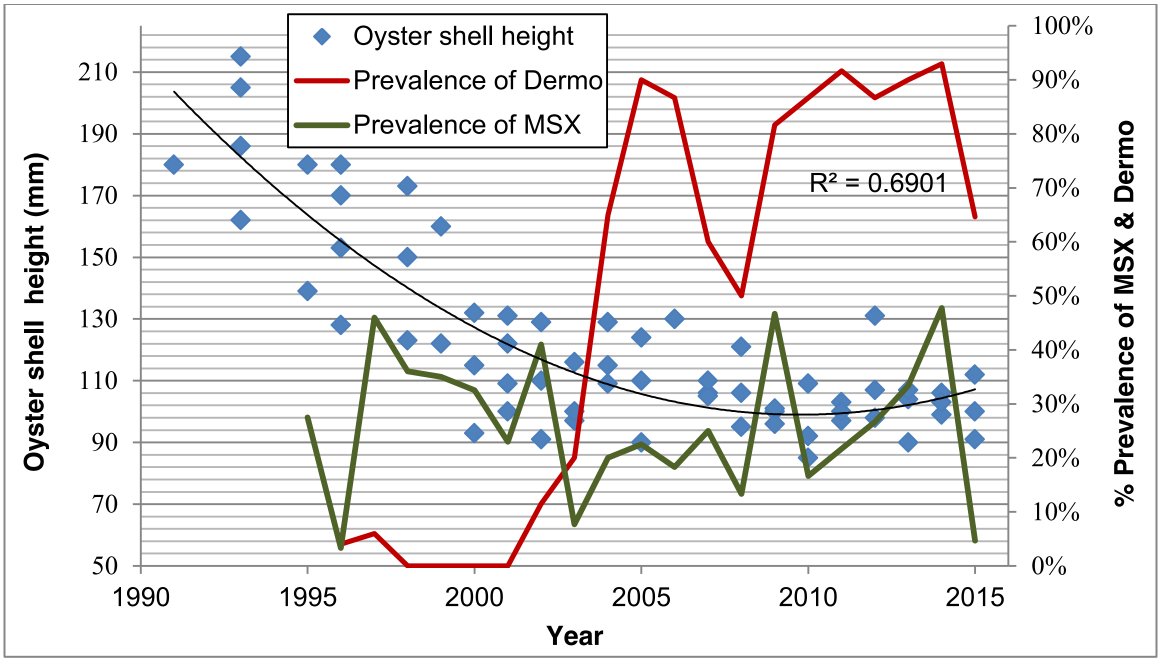

Figure 4. Maximum shell height for oysters collected using quadrats (0.25 m^2) on oyster reefs (Adams Point, Nannie Island, and Woodman Point) in Great Bay and the percent prevalence of Dermo and MSX in oysters (NH Fish & Game data).

Oyster recruitment has varied both spatially and temporally throughout the Great Bay Estuary since the NH Fish and Game Department started monitoring oyster reefs in 1991 (Table 1 and 2, Figure 5). Complete failure in recruitment was observed at the Nannie Island oyster reef in 2004, 2005, 2014, and 2015 (Table 1). The highest recruitment events throughout the estuary occurred in 2006 and 2007 (Table 1). The abundance of oysters greater than 60 mm has also varied among all locations between 1991 and 2015 (Table 2). The greatest abundance of adult oysters was at the Squamscott River oyster reef in 2005 with 401.2 oysters per square meter (Table 2).

Table 1. Mean density (# oysters/m^2) ± 1 SE for oyster spat (shell height <40 mm) on oyster reefs in the Great Bay Estuary (NH Fish & Game SCUBA quadrat data).

	Harvestable Reefs			Non-Harvestable Reefs		
Year	**Adams Point**	**Nannie Island**	**Woodman Point**	**Oyster River**	**Squamscott River**	**Piscataqua River**
1991	NS	182.0 ± 74.1	65.0 ± 17.3	NS	NS	NS
1992	NS	NS	NS	NS	NS	NS
1993	14.0 ± 1.4	12.7 ± 5.0	1.7 ± 0.8	2.9 ± 0.8	NS	23.4 ± 12.0
1994	NS	NS	NS	NS	NS	NS
1995	NS	4.4 ± 2.2	58.9 ± 16.5	12.7 ± 3.9	NS	NS
1996	4.7 ± 3.2	13.0 ± 4.1	21.0 ± 5.3	6.4 ± 1.6	NS	NS
1997	NS	NS	NS	NS	NS	36.0 ± 19.7
1998	13.0 ± 4.0	24.6 ± 2.8	11.3 ± 3.8	28.0 ± 6.4	97.3 ± 14.8	36.0 ± 6.7
1999	NS	52.8 ± 6.7	84.8 ± 18.7	45.6 ± 10.1	NS	5.0 ± 11.5
2000	62.7 ± 13.1	34.4 ± 8.4	90.7 ± 20.6	40.8 ± 3.4	NS	76.0 ± 17.4
2001	2.0 ± 2.0	12.0 ± 5.9	20.7 ± 8.0	8.0 ± 2.8	48.0 ± 4.0	14.0 ± 6.6
2002	67.6 ± 12.1	1.6 ± 1.0	96.8 ± 39.0	145.6 ± 51.6	NS	303.2 ± 33.7
2003	57.6 ± 9.3	7.2 ± 2.7	49.6 ± 8.9	84.8 ± 13.7	NS	312.0 ± 62.1
2004	4.8 ± 1.5	0.0 ± 0.0	2.4 ± 1.6	21.6 ± 2.7	NS	93.6 ± 13.1
2005	3.2 ± 0.8	0.0 ± 0.0	1.6 ± 1.6	5.6 ± 3.7	69.3 ± 8.7	10.0 ± 6.0
2006	525.6 ± 138.8	660.0 ± 131.2	864.8 ± 69.5	990.4 ± 152.0	NS	60.8 ± 20.4
2007	884.0 ± 49.0	740.0 ± 43.6	373.6 ± 41.2	927.2 ± 73.9	NS	249.6 ± 29.1
2008	133.6 ± 14.0	66.4 ± 10.3	71.2 ± 5.1	112.0 ± 23.9	175.2 ± 23.6	8.8 ± 5.3
2009	53.6 ± 8.8	45.6 ± 7.8	56.8 ± 11.3	NS	NS	NS
2010	49.6 ± 14.6	36.0 ± 9.5	27.2 ± 4.1	53.6 ± 8.0	73.6 ± 13.9	8.0 ± 3.4
2011	71.2 ± 18.4	34.4 ± 14.5	28.0 ± 5.2	11.2 ± 3.4	56.0 ± 6.7	1.6 ± 1.0
2012	21.6 ± 3.7	18.4 ± 7.4	11.2 ± 4.6	19.2 ± 9.1	30.4 ± 9.7	1.6 ± 1.0
2013	128.8 ± 14.1	7.2 ± 2.9	90.4 ± 23.1	93.6 ± 8.9	NS	149.6 ± 13.2
2014	45.6 ± 7.8	0.0 ± 0.0	25.6 ± 3.0	68.8 ± 7.7	NS	38.4 ± 9.9
2015	73.6 ± 11.3	0.0 ± 0.0	29.6 ± 5.6	65.6 ± 8.8	112.0 ± 22.9	16.8 ± 2.3

NS = No samples taken

Table 2. Mean density (# oysters/m^2) ± 1 SE for oysters (shell height >60 mm) on oyster reefs in the Great Bay Estuary (NH Fish & Game SCUBA quadrat data).

	Harvestable Reefs			**Non-Harvestable Reefs**		
Year	**Adams Point**	**Nannie Island**	**Woodman Point**	**Oyster River**	**Squamscott River**	**Piscataqua River**
1991	NS	146.0 ± 5.3	274.0 ± 45.3	NS	NS	NS
1992	NS	NS	NS	NS	NS	NS
1993	228.7 ± 44.4	223.3 ± 17.5	112.2 ± 11.1	145.1 ± 17.7	NS	67.4 ± 18.0
1994	NS	NS	NS	NS	NS	NS
1995	NS	64.4 ± 6.9	74.9 ± 11.7	68.0 ± 6.2	NS	NS
1996	72.7 ± 12.9	123.0 ± 9.0	120.0 ± 11.9	70.4 ± 13.8	NS	NS
1997	NS	NS	NS	NS	NS	5.3 ± 3.5
1998	39.0 ± 3.3	48.4 ± 4.6	60.0 ± 9.1	36.7 ± 6.0	16.0 ± 3.3	6.9 ± 3.0
1999	NS	21.6 ± 3.7	30.4 ± 4.8	15.2 ± 7.5	NS	0.8 ± 0.8
2000	14.7 ± 7.1	7.2 ± 2.3	17.3 ± 4.8	18.4 ± 6.9	NS	4.0 ± 4.0
2001	10.0 ± 2.6	53.0 ± 23.7	42.0 ± 10.1	39.2 ± 7.4	18.7 ± 10.9	10.0 ± 4.8
2002	20.8 ± 3.6	20.0 ± 8.7	21.6 ± 6.2	20.8 ± 6.6	NS	5.6 ± 2.0
2003	30.4 ± 3.3	24.8 ± 2.7	19.2 ± 3.2	27.2 ± 5.3	NS	6.4 ± 2.7
2004	61.6 ± 15.4	5.3 ± 1.3	49.6 ± 15.5	135.2 ± 21.9	NS	10.4 ± 2.0
2005	85.6 ± 24.4	4.0 ± 0.0	18.4 ± 3.3	98.4 ± 35.0	401.3 ± 41.6	30.0 ± 10.0
2006	44.8 ± 8.5	0.0 ± 0.0	51.2 ± 7.9	85.6 ± 12.2	NS	25.6 ± 5.3
2007	24.0 ± 2.8	26.4 ± 7.0	22.4 ± 6.2	81.6 ± 10.5	NS	40.0 ± 9.0
2008	65.6 ± 4.7	65.6 ± 17.7	88.0 ± 17.1	273.6 ± 22.3	186.4 ± 28.0	1.6 ± 1.0
2009	108.8 ± 14.6	102.4 ± 24.1	99.2 ± 10.6	NS	NS	NS
2010	36.8 ± 11.6	72.8 ± 13.6	58.4 ± 6.7	96.0 ± 23.0	90.4 ± 10.6	9.6 ± 3.3
2011	49.6 ± 9.5	37.6 ± 6.4	40.8 ± 6.3	51.2 ± 4.8	56.0 ± 6.3	11.2 ± 2.9
2012	25.6 ± 8.4	18.4 ± 9.4	28.0 ± 5.5	28.8 ± 5.0	34.4 ± 5.7	0.0 ± 0.0
2013	24.8 ± 4.5	8.8 ± 2.0	21.6 ± 6.0	31.2 ± 5.4	NS	11.2 ± 3.2
2014	17.6 ± 4.1	6.4 ± 2.4	17.6 ± 3.9	15.2 ± 2.0	NS	4.8 ± 1.5
2015	10.4 ± 2.0	4.8 ± 1.5	31.2 ± 8.4	24.8 ± 6.7	68.8 ± 14.4	4.0 ± 1.3

NS = No sample taken

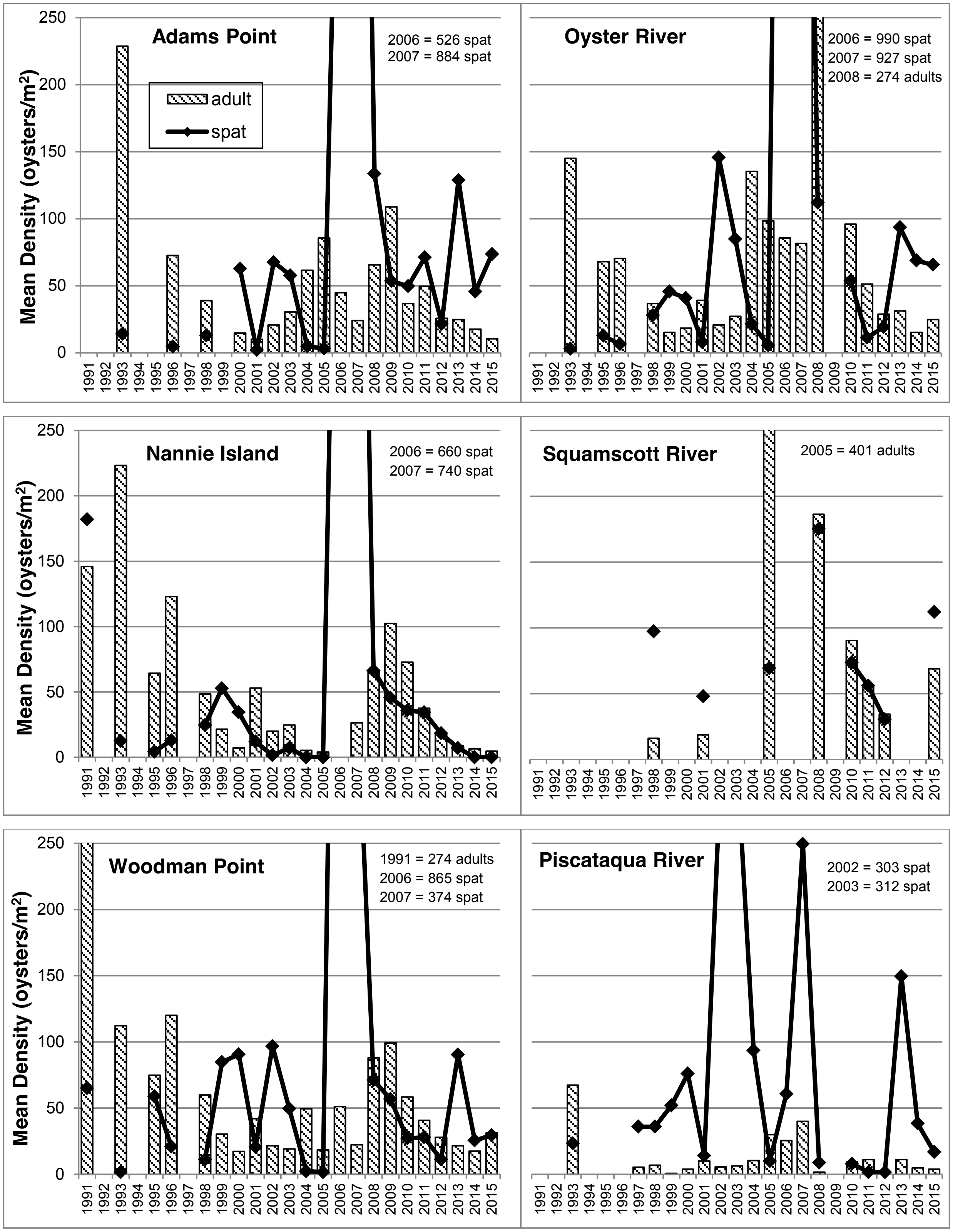

Figure 5. Mean density (# oysters/m^2) for adult oysters (shell height >60 mm) and spat (shell height <40 mm) on oyster reefs in the Great Bay Estuary from 1991 to 2015 (NH Fish & Game quadrat data).

Discussion

There are few published fisheries independent studies on the densities of oysters on natural reefs over historical time frames. The New Hampshire Fish and Game Department has independently monitored oyster reefs with replicate quadrat samples since 1991. This 25-year dataset of oyster density shows a high degree of variability in both spatfall and abundance of larger oysters. The Squamscott River oyster reef is the smallest reef in Great Bay proper, but had the highest recruitment in seven of the eight surveyed years and the highest adult oyster densities in six of the eight surveyed years.

The Great Bay Estuary is extremely small in comparison to other Atlantic coast estuaries such as Long Island Sound or Chesapeake Bay. The oyster reefs surveyed within Great Bay proper are all within 5 kilometers from each other. Although, reef proximity rarely resulted in similar recruitment rates, above average recruitment events occurred at most reefs during the same years. However, the Piscataqua River reef had different peaks in recruitment than other reefs in the Great Bay Estuary, which would suggest that the Piscataqua River reef receives recruits from a separate source reef or is not affected in the same manner as the other reefs with respect to reproductive events.

The quadrat sampling methodology used to determine spat set and population composition in the Great Bay Estuary gives an accurate assessment of living oyster densities, but is not designed to assess changes in reef area or other reef characteristics. Unlike some state agencies that measure total shell and brown shell volume in each quadrat (Mann et al. 2009), NH Fish and Game only enumerates and measures live oyster shell height. Therefore, NH Fish and Game cannot assess the available suitable substrate in each sample or if the reefs are experiencing shell loss or accretion. Taking these measurements in the future could enable the agency to determine the available shell substrate for oyster settlement and if the oyster reefs are experiencing shell loss or accretion.

Recreational harvest of oyster in Great Bay predominantly occurs at the Adams Point, Woodman Point, and Nannie Island oyster reefs. The number of licenses issued dramatically declined from over 1000 per year in the early 1990s, to around 200 in 2015. Although the number of licenses declined, the maximum shell height of oysters observed at those reefs also declined. Furthermore, the adult oyster densities at both harvest and non-harvest reefs were stable between 1991 and 1995, when the number of harvest licenses peaked.

The decline in oyster populations in the Great Bay Estuary in the mid-1990s coincides with the introduction of MSX and Dermo in the area (Figure 4). Studies have shown that these diseases can dramatically decrease the life span of oysters. Before these diseases were prevalent, oyster longevity was 10 to 20 years, but infected oysters today typically die less than five years (Mann et al. 2009; Southworth et al. 2010). This, coupled with the decrease in average shell height, suggests that the increased prevalence of MSX and Dermo has limited the life expectancy and growth of oysters in the estuary. This is evident in the Great Bay Estuary based on the drastic decline in maximum oyster size (Figure 3) since MSX and Dermo were introduced with oysters succumbing to diseases and dying after three to four years.

Relatively high recruitment events throughout the Great Bay Estuary occurred during the same years. A study conducted by Mann et al. (2009) in the James River system found that above average recruitment events are observed when winter temperature remains at or above 8^{o}C, which also corresponds to high salinity in the following summer. Although Great Bay freezes over in the winter, the Chesapeake Bay and Great Bay had similar years of high recruitment (Harding et al. 2012; Mann et al. 2009). The high recruitment events also occurred at both estuaries during summers with high salinities, except for 2006 in Great Bay.

Southern New Hampshire experienced historical flood events in May 2006 and April 2007 (Olson 2007; Flynn 2008). During both of these years, the highest recorded recruitment occurred throughout the Great Bay Estuary, with 2007 having slightly higher recruitment. A study conducted by Pollack et al. (2011) found that flood events can temporarily reduce salinity and cause reductions in oyster abundance, spat settlement, disease levels, and filtration rates. However, flood disturbances can also cause reductions in predation and disease, allowing for rapid reestablishment of oyster populations (Pollack et al. 2011). Furthermore, the prevalence of Dermo in Great Bay decreased in both 2006 and 2007.

A time-series high adult oyster density at the Squamscott River (401.2 adults/m^2) preceded the large recruitment in 2006. The other reefs located in Great Bay proper had low to average adult densities in 2005 and 2006, suggesting that the Squamscott River could be a source reef that supplies other reefs in Great Bay proper with spat. A study conducted by Harding et al. (2012) found that the presence of large broodstock oysters on a reef might contribute to high recruitment events. In addition, spat density in the Great Bay Estuary support Schulte et al. (2009) and Lipcus et al. (2015), who determined spat density was a function of the reproductively viable oyster abundance. Furthermore, McCormick-Ray (2005) suggest that oyster reefs throughout an estuary are connected by hydrologic corridors that facilitate dispersion, migration, and recruitment. Thus, recruitment levels are likely a result of factors affecting oyster condition as well as location, which affects larval distribution patterns.

The oyster populations in the Great Bay Estuary declined dramatically in numbers and shell size after the introduction of MSX and Dermo. Although, populations rebounded after large spatfall events (1999, 2002, 2006, and 2007), three to four years after these events population levels declined, probably mainly a result of disease. Research is needed on what the impact of a shorter life span of oysters has on the ability of oyster reefs to accrete shell material. Great Bay Estuary is recruitment limited, substrate limited, and has a major problem with oyster mortality. Unless expansive reef restoration and research on limiting the impacts of MSX and Dermo occur, the prospects for the oyster populations in Great Bay look bleak. The continued monitoring of oyster reefs is necessary for resource managers to assess the health of oyster reefs in the Great Bay Estuary and to gain an understanding of the mechanism that cause variability in oyster populations.

CHAPTER 2

RECRUITMENT STUDIES ON CONSTRUCTED AND NATIVE REEFS IN THE GREAT BAY ESTUARY

Introduction

Oysters provide vital ecosystem services that include water filtration, creation of habitat, shoreline stabilization, and nutrient sequestering (Coen et al. 2007; Grabowski et al. 2012). Historically, the eastern oyster supported a multi-million dollar industry in North America (Beck et al. 2011; MacKenzie Jr 1996); however, natural oyster populations have dramatically declined over the last century (Lotze et al. 2006). Explanations for the decline include the combined impacts of disease (Ford and Tripp 1996), habitat degradation (MacKenzie Jr 1983), pollution (Levinton et al. 2013), and past exploitation (Rothschild et al. 1994; Jordan and Coakley 2004). This decline has caused ecosystem degradation in estuaries (Jackson et al. 2001) and prompted a focus on oyster reef restoration.

Oyster populations in New Hampshire's Great Bay Estuary have experienced dramatic declines similar to populations along the east coast. Restoration efforts in NH began in 2000 with the intent of restoring the ecosystem services that oyster reefs provide. Restored oyster reefs can provide water-quality improvements soon after construction (Grizzle et al. 2008b). They can also significantly increase denitrification rates and enhance nutrient sequestration (Kellogg et al. 2013). More than 20 oyster restoration projects (Konisky et al. 2011, 2012, 2014) have been completed in NH since

2000. By 2011, a total of 12.3 acres of oyster reefs had been constructed in the Great Bay Estuary, with a total goal of 20 acres by 2020.

The success of restoration projects in Great Bay has been inconsistent, due to ongoing oyster mortality from parasitic diseases (MSX and Dermo). In response to the prevalence of diseases, there has been an increased interest in the introduction of non-native species. For example, managers in the Chesapeake Bay are considering stocking an Asian oyster species (*Crassostrea ariakensis*) that has shown to be more disease resistant. However, stocking of a non-native species can have unintended consequences that can alter the estuarine ecosystem (Fulford et al. 2011).

Site selection in the Great Bay Estuary involves restoring areas that historically supported oyster populations. However, these locations may currently be unsuitable for restoration due to changes in water circulation or sedimentation (Kennedy and Sanford 1999; Mann and Evans 2004). Powell et al. (1995) determined that reef location was the most important factor in determining accretion, or loss of oyster reefs.

A major focus in many areas has been on providing substrate material for natural recruitment and subsequent reef development (Coen and Luckenbach 2000; O'Beirn et al. 2000; Soniat and Burton 2005; Powers et al. 2009; La Peyre et al. 2014). However, oyster populations in the northeastern US, including New Hampshire, are typically substrate and recruitment limited and therefore require more complex restoration methods. Current methods in NH involve the construction of shell bases and the use of live oyster spat-on-shell produced by remote setting methods (Castagna et al. 1996).

The University of New Hampshire started a community-based restoration effort in 2006 that was designed to allow public participation in the overall restoration effort. This program is now conducted collaboratively with The Nature Conservancy (Patrick et al. 2016). The Oyster Conservationist (OC) Program is made up of volunteers who raise oysters on private docks or moorings. After reaching a size that minimizes predation by crab, the spat-on-shell is then planted on restored reefs throughout the Great Bay Estuary. Programs like the OC inform the public about the declining condition of the estuary and enables them to assist in the restoration efforts.

After decades of restoration efforts in the Chesapeake Bay, it was suggested that restoration of natural oyster populations is improbable (Mann and Powell 2007). However, there have been restoration successes there and elsewhere (Taylor and Bushek 2008; Powers et al. 2009; Schulte et al. 2009). Despite these successes, no detailed methods have been developed to consistently result in success (Kennedy et al. 2011). In New Hampshire, none of the restoration sites had been assessed past the immediate end date of the project. Thus, no data were available on long-term success. In the present study, I investigated natural recruitment on restored and natural oyster reefs focusing on how differences in recruitment might affect success of restored reefs and as related to restoration site selection.

Methods and Materials

Field Methods

Oysters were collected from a pontoon boat using patent tongs between August 7 and October 14, 2013 from eight natural reefs and twelve restored oyster reefs in the Great Bay Estuary (Figures 6 - 8). The patent tongs were calibrated to retrieve 0.16 m^2 of bottom substrate. Patent tong samples provide quantitative data on oysters by size class and therefore the characteristics of the oyster population (Mann and Evans 2004). Two to six replicate tong samples were taken randomly at each site by allowing the boat to drift between sample locations; GPS coordinates were taken for each sample location within a site. In the event the patent tongs did not close properly or the sample did not contain shell material the sample was discarded. The contents of the patent tong sample were put into buckets and rinsed with water after returning to shore. The recorded dimension on each oyster was from the hinge to the shell growth margin (shell height). All live oysters were counted and shell height was measured to the nearest millimeter (mm) with vernier calipers. For each sample taken on restored reef sites, the shell substrate was recorded; clam shell was used in reef base construction and oyster shell was used to produce spat-on-shell. While both clam shell and oyster shell would have natural recruitment, the oyster shell would also have spat-on-shell.

Spat Size Estimation

The range of shell heights for new recruits (spat) was estimated by sampling reefs before and soon after reproduction occurred. On 7/16/13 and 7/26/13, oysters were collected with patent tongs at Adams Point and Woodmans Point; no oyster spat were found. Oyster spat were first observed in samples taken at Fox Point on 8/27/13. Shell height frequency distributions were then constructed; oysters that were < 30 mm were considered spat (recruits in 2013) and oysters > 60 mm were considered adult oysters.

Data Analysis

Differences in oyster density were assessed by reef, reef type (natural and restored), and proximity of the restored reef from the nearest natural reef (< 1 km and > 1 km from natural reef) using a one-way analysis of variance followed by post hoc Tukey tests or Student's t-test. Data from reefs sampled before 2013 spatfall (approximately late July; see above) were not used in analysis. In addition, reefs constructed in 2013 that used spat-on-shell were excluded from analysis. All data were tested for normality using Shapiro-Wilk ($p>0.05$). If necessary, data were transformed ($\log(x)$) prior to analysis to meet the assumptions of equal variance and normal distribution. Data that did not meet these assumptions after transformation were analyzed using nonparametric Kruskal-Wallis test. Oyster density data were converted to number of individuals per square meter after being back-transformed. Data was analyzed using JMP 12 software.

Figure 6. Native oyster reefs and Restoration sites (year constructed on map) surveyed in Great Bay Proper, 2013.

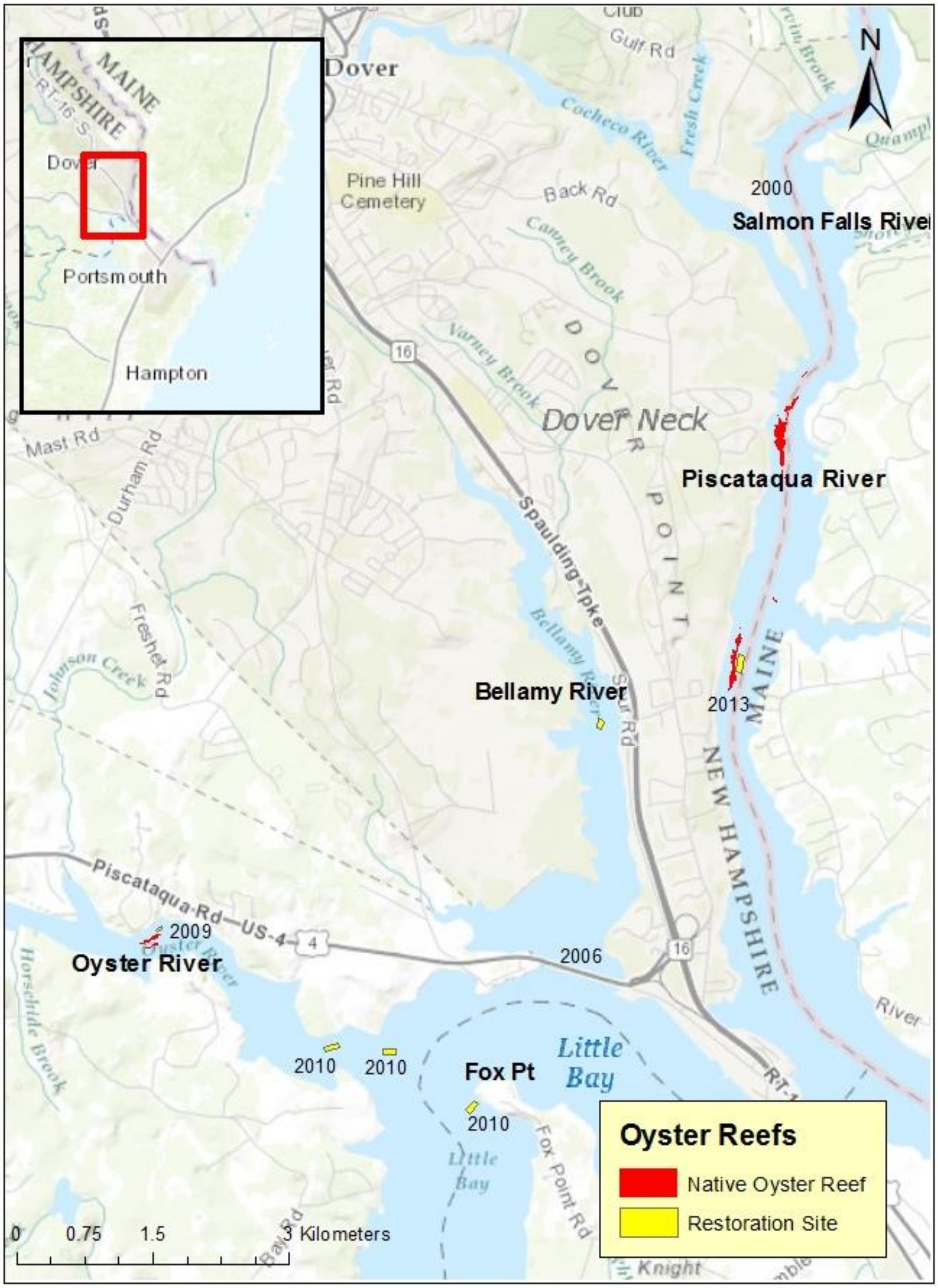

Figure 7. Native oyster reefs and Restoration sites (year constructed on map) surveyed in northern part of Great Bay Estuary, 2013.

Figure 8. Patent tongs used to collect samples at native oyster reefs and restoration sites in 2013.

Results

Natural and restored reefs varied in acreage (Table 3 and 4). The shell height of oysters collected between 8/27/2013 and 10/14/2013 ranged from 3 mm to 129 mm (Figure 9). The densities of spat (shell height <30 mm) differed throughout the estuary (Figure 10). Reefs located in the southwest corner of Great Bay proper had the highest densities of spat (Squamscott and Lamprey rivers). Natural reefs in Great Bay proper had similar densities of adult oysters (Figure 11).

There was a significant difference ($p < 0.01$) in spat density between native and restoration reefs (Figure 12). There was also a significant difference in spat density between native reefs, restoration reefs less than 1 km from native reef ($p < 0.01$) and restoration reefs greater than 1 km from native reef distance ($p < 0.01$) (Figure 13).

Table 3. Natural oyster reefs surveyed in the Great Bay Estuary in 2013.

Location	Acreage	Date Surveyed	Tong sample replicates
Adams Point (AP-N)	13.1	9/19/2013	6
Fox Point (FP-N)	1.0	9/10/2013	5
Lamprey River (LR-N)	2.0	9/28/2013	5
Nannie Island (NI-N)	24.7	9/19/2013	5
Oyster River (OR-N)	1.7	9/11/2013	5
Piscataqua River (PR-N)	19.9	9/12/2013	5
Squamscott River (SR-N)	3.9	10/4/2013	3

Table 4. Restored oyster reefs surveyed in the Great Bay Estuary in 2013.

Location	Date constructed	Acreage	Date Surveyed	Distance from Natural Reef	Tong sample replicates
Adams Point (AP-R1)	2003	0.1	8/28/2013	< 1 km	5
Bellamy River (BR-R1)	2006	1.6	9/17/2013	> 1 km	4
Fox Point (FP-R1)	2010	1.0	8/28/2013	< 1 km	5
Lamprey River (LR-R1)	2012	0.5	9/28/2013	< 1 km	3
Lamprey River (LR-R2)	2013	2.0	9/28/2013	< 1 km	2
Oyster River (OR-R1)	2009	0.2	9/11/2013	< 1 km	5
Oyster River (OR-R2)	2010	1.0	9/10/2013	> 1 km	5
Oyster River (OR-R3)	2010	1.0	9/11/2013	> 1 km	5
Piscataqua River (PR-R1)	2013	1.5	9/12/2013	> 1 km	4
Salmon Falls River (SF-R1)	2000	0.1	9/12/2013	> 1 km	5
Squamscott River (SR-R1)	2012	2.0	10/4/2013	< 1 km	3
Woodmans Point (WP-R1)	2004	2.5	10/15/2013	< 1 km	5

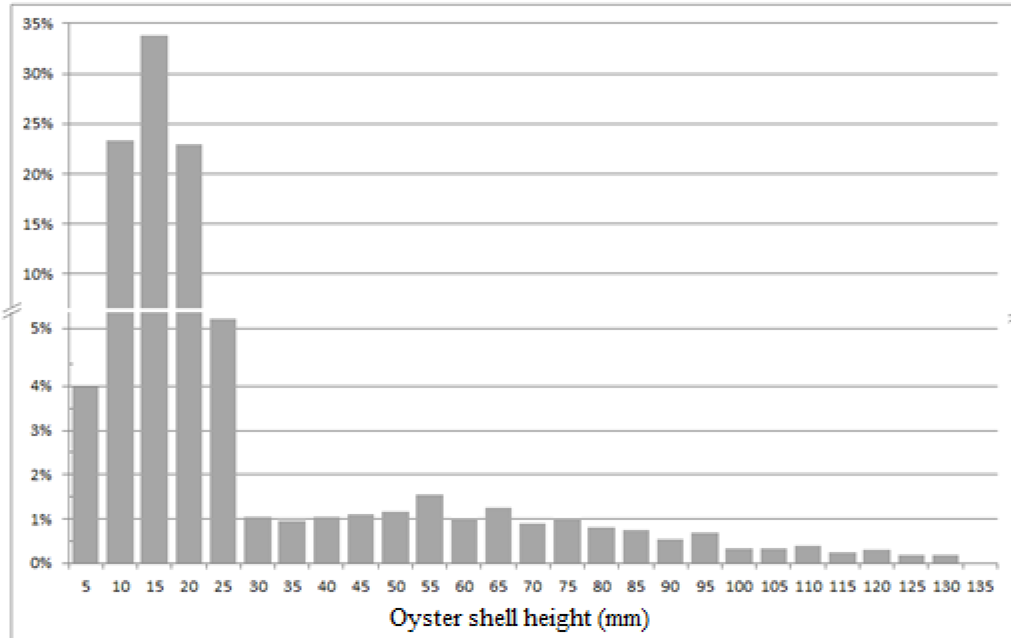

Figure 9. Length Frequency Distributions of shell height (mm) of all oysters sampled on natural and restoration oyster reefs within Great Bay.

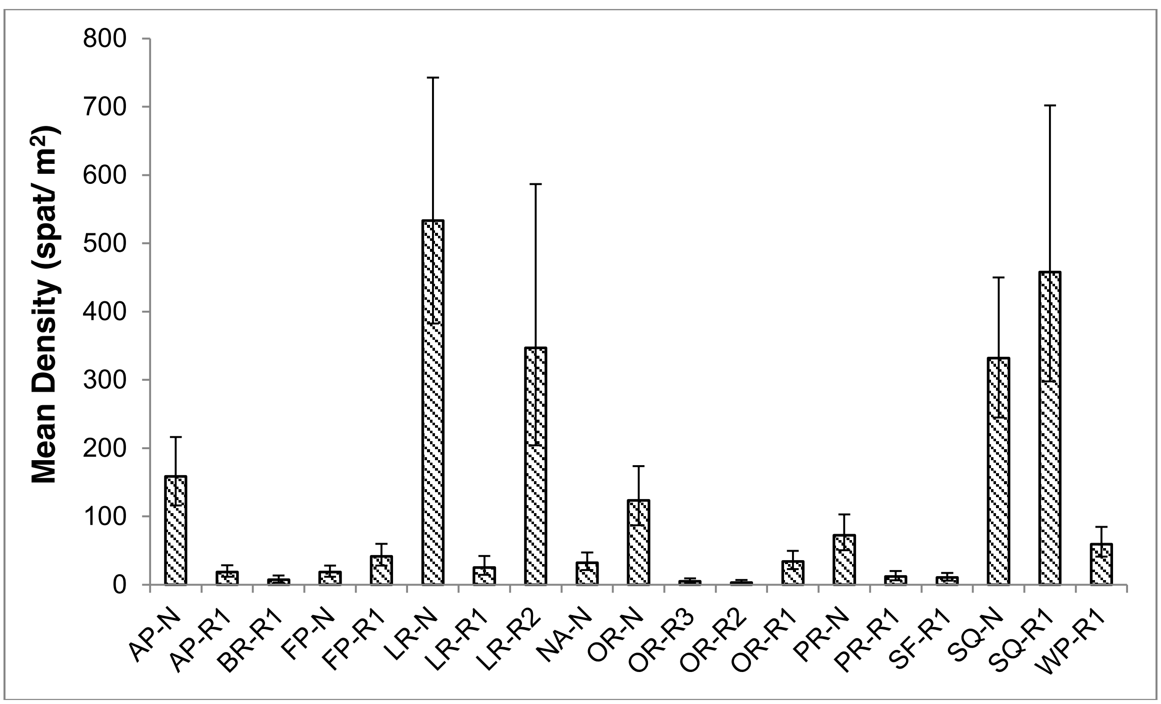

Figure 10. Mean native spat density (number of oysters < 30 mm shell height / m^2) by location. Error bars denote ±1 SE.

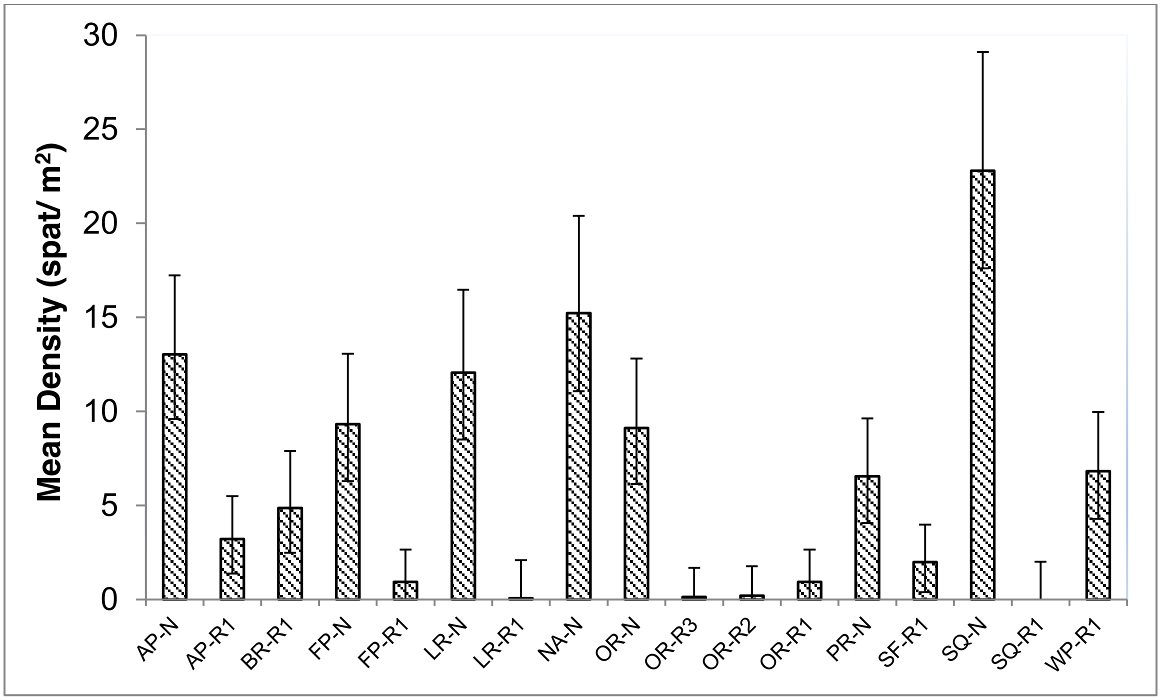

Figure 11. Mean native spat density (number of oysters > 60 mm shell height / m^2) by location. Error bars denote ±1 SE.

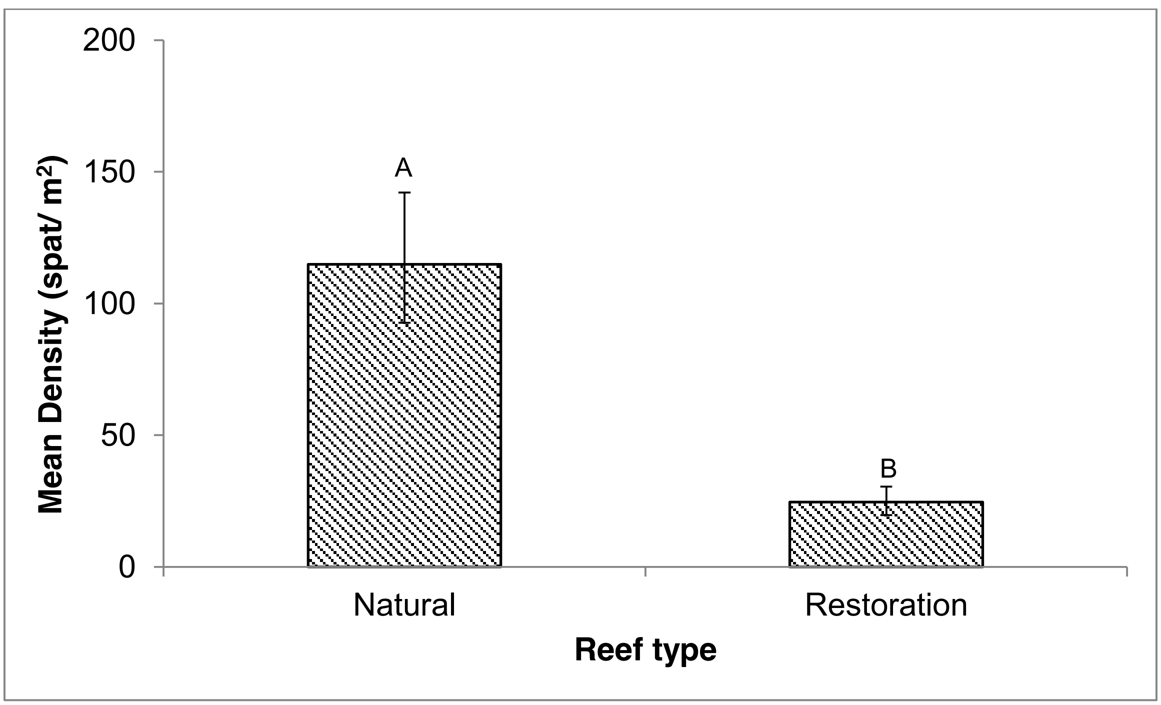

Figure 12. Mean native spat density (number of oysters ≤ 30 mm shell height / m^2) by reef type (Native and Constructed). Error bars denote ±1 SE. Levels not connected by same letter are significantly different ($p < 0.05$).

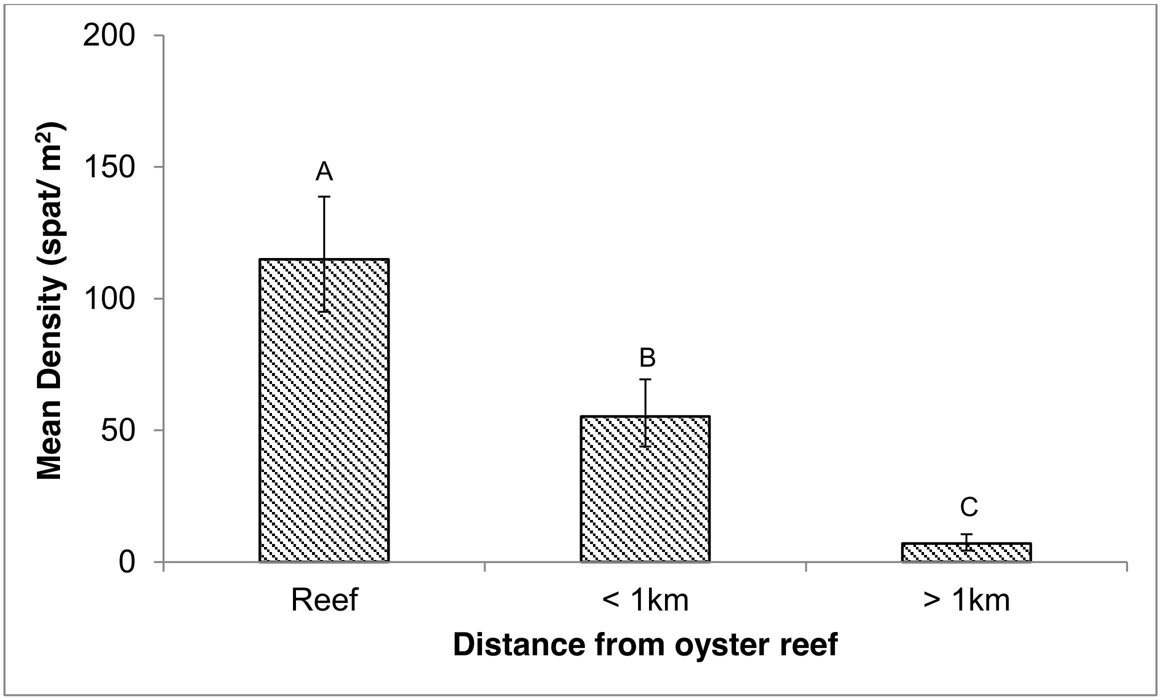

Figure 13. Mean native spat density (number of oysters ≤ 30 mm shell height / m^2) by distance (< 1 km and > 1 km) of restored reef from native reef within Great Bay Estuary, NH during Fall 2013. Error bars denote ±1 SE. Levels not connected by same letter are significantly different ($p < 0.05$).

Discussion

Before discussing the major findings, some discussion of methods is warranted. Patent tongs were used in this study to collect quantitative oyster samples and they have been shown to be comparable to the efficiency of SCUBA diving quadrat samples, which are assumed to collect 100% of the shell in an area (Chai et al. 1992). The patent tongs worked consistently throughout the estuary, except for some areas on the Squamscott River natural reef, which had harder substrate and oysters with greater vertical relief. Although, other studies have shown that the efficiency of the patent tongs can vary from sample to sample depending on the underlying substrate and variation in the amount of clumping of oysters, patent tongs have become a standard method for quantitative sampling of subtidal oyster reefs (Ayer et al. 1970; Mann et al. 2004).

After decades of declining oyster populations, restoration of oyster reefs in New Hampshire began in 2000. Initial restoration efforts began with selecting sites that historically had oyster reefs and using adult transfers and spat-on-shell. The restoration protocol continued to adapt, with the construction of reef bases using gravel and shell at historic reef locations. However, locations that historically had oyster reefs may currently be unsuitable for restoration due to changes in water circulation or sedimentation (Kennedy and Sanford 1999; Mann and Evans 2004). In addition, burial by sediment is commonly observed on restored reefs (Powers et al. 2009; Schulte et al. 2009). The major finding from my assessment was that natural recruitment was significantly and substantially higher on restoration reefs that were < 1 km from a natural reef.

Site location has been a major topic of research because the success of a restored reef depends on a variety of environmental factors, including natural recruitment (Mann and Evans 2004). Powell et al. (1995) determined that reef location was the most important factor in determining accretion, or conversely loss of oyster reefs. Moreover, constructed oyster reefs can fail to accrete reef material at sufficient rates to compensate for losses due to shell degradation and sedimentation (Powell et al. 2006; Mann and Powell 2007). Several field studies have also documented a positive relationship between adult densities and recruitment to restoration sites (Southworth and Mann 1998; Schulte et al. 2009; Lipcius et al. 2015). This indicates that long-term monitoring of restored reefs is necessary to determine what factors contribute to making reefs successful.

Recruitment within the Great Bay Estuary during 2013 showed the high degree of spatial variability characteristic of recruitment studies (Nelson 1903). In 2013, an average recruitment year for the Great Bay Estuary based on NH Fish and Game historical data (Smith 2014), natural oyster reefs located in the southwest corner of Great Bay (Squamscott and Lamprey rivers) had the highest recruitment. Furthermore, historical data indicates that the Squamscott River oyster reef consistently had greater recruitment when compared to other reefs in Great Bay (Smith 2014).

The most successful restored reefs, those showing highest recruitment, were LR-R2 and SQ-R1, and both were in close proximity to the natural reefs with the highest live oyster densities in Great Bay. The LR-R1 restoration site was also close to the most successful reefs, but had low spat recruitment. However, the LR-R1 site still had higher recruitment than six of the other restoration reefs. The construction material used could explain the relative low recruitment density at the LR-R1 (25 spat / m^2) site when compared to the LR-N site (347 spat / m^2). The restored reef was composed of small clam shell fragments, unlike the other restored reefs, which lack substantial roughness and has been shown to have lower recruitment densities when compared to natural oyster reefs (Whitman and Reidenbach 2012).

There are few published studies on spatial patterns in natural recruitment. However, trends in the natural recruitment on restored and natural oyster reefs were apparent throughout the estuary. Restored reefs with poor recruitment and low adult densities were generally greater than 1 km from a natural reef. However, restored reefs within 1 km of natural oyster reefs had greater oyster densities. Similarly, Harding et al. (2012) reported high recruitment on constructed reefs within 1 to 2 km of productive natural oyster reefs. Quayle (1988) also observed that oyster settlement decreased with increased distance away from spawning oysters. Thus, although my data and previous research, indicate a strong relationship between natural recruitment patterns and distance to a reproducing population of oysters (i.e. a healthy natural reef), additional research is needed to refine the spatial scales involved.

Another potentially important factor is reef age. Newly formed reefs had significantly greater recruitment than older restored reefs. Furthermore, older restored reefs had greater adult oyster densities than reefs constructed in 2009 and 2010. Quan et al. (2012) observed that oyster abundance on newly formed reefs increased rapidly after creation and then decreased sharply after three years of development. After the sharp decline in oyster abundance, the oyster population stabilized.

The difficultly researchers in New Hampshire, and the rest of the east coast, are having with oyster reef restoration is identifying the most effective strategy for determining location of an oyster reef that will provided enhanced ecological function. Although restoration efforts could be conducted in numerous locations within an estuary, an unharvested restored oyster reef will have significantly greater vertical relief than a restored oyster reefs that allowed harvest (Lenihan and Peterson 1999). Restoration site selection should also factor in the spatial distribution of oyster recruitment and select sites within 1 km of natural reefs. Further research needs to be conducted on the spatial distribution of recruitment and its implications in reef development. The continued monitoring of restored oyster reefs is also necessary in order to assess the long-term success of these restoration projects in the Great Bay Estuary.

CHAPTER 3

RECRUITMENT STUDIES IN GREAT BAY WITH IMPLICATIONS FOR RESTORATION SITE SELECTION

At present, observers are divided into two schools. One class believes that spawn 'strikes' very near where it is emitted. A second class believes that it may be carried miles away. Perhaps under certain conditions either result might be reached. Is it worthwhile to solve a problem of this sort?

Julius Nelson (1892)

Introduction

The long-term success of restored reefs depends on consistent and adequate larval settlement and recruitment. Therefore, since oyster recruitment has been shown to vary spatially and temporally (Nelson 1903; Mackenzie 1970), with some regions within an estuary consistently having higher recruitment than others (Kennedy 1980), site selection of restoration reefs is critical. The type of estuary can also affect recruitment, with high-flushing estuaries having consistent, low to moderate, annual recruitment and trap-type estuaries having higher but irregular recruitment, with some years experiencing complete failure (Andrews 1983). Pritchard (1953) attributed the pronounced patchiness of oyster larvae to larval behavior, although Jacobsen et al. (1990) attributed larvae patchiness to physical processes. However, Haase et al. (2012) used a hydrodynamic model for determining oyster larvae dispersal in Pamlico Sound and found that self-recruitment occurred at nine of the ten no-take oyster broodstock reserves. In addition, Quayle (1988) found evidence that oyster settlement decreases with increased distance away from spawning oysters. The success or failure of restoration work depends on proper site selection and an understanding of larvae behavior.

Swimming behavior of planktonic larvae can influence the direction and intensity of larvae transport and dispersal (Genin et al. 2005; Knights et al. 2006; North et al. 2008). Although, the relatively weak swimming speed of oyster larvae, horizontal swimming speeds of 0.2cm/s (Mileikovsky 1973), may suggest that they are primarily passive particles in the water column, Tamburri et al. (1992) observed oyster larvae sinking or swimming downward in response to physical and chemical cues. In addition, comparing passive coal particles with similar size and density to oyster larvae, Wood and Hargis (1971) showed that larvae are not passive and that they responded to salinity cues associated with a flood tide. Larvae will also swim more actively with increases in salinity (Nelson and Perkins 1931) and swimming speeds will increase with higher temperatures and greater larval length (Hidu and Haskin 1978). Larval stages also exhibit different vertical distribution patterns, with younger stages passively flowing with the tide and older stages sinking onto the bottom on the ebb and rising into water column on the flood (Carriker 1947; Kunkle 1957). In addition, older, larger larvae will accumulate near an oyster reef in order to respond to settlement cues so that they have an increased likelihood of contacting the bottom (Finelli and Wethey 2003).

Oyster larvae are gregarious settlers (Cole and Knight-Jones 1939) and exhibit active substrate choices (Turner et al. 1994; Zimme-Faust and Tamburri 1994), suggesting some degree of active transport during settlement. Oyster larvae respond similarly to waterborne substances released both from adult oysters and from biofilms (Tamburri et al. 1992). Chemical cues released by oysters and biofilms stimulate larvae to swim vertically downward in the water column towards and actively search for substrate for settlement (Tamburri et al. 1992). Once contacting the oyster reef, if unsuitable, larvae can release themselves and move to another location (Soniat et al. 2004; Fuchs et al. 2007). Finelli and Wethey (2003) determined that larvae make contact with the oyster bed or resist turbulent motions by dive-bombing vertically, accelerating to 12.7 cm/s, through the water column.

When selecting sites for oyster restoration it is important to consider source-sink dynamics (Lipcius et al. 2011). Source-sink dynamics can influence settlement between individual reefs (Lipcius et al. 2008) and between populations in different tributaries (North et al. 2008). Adding shell material and/or oyster spat to a metapopulation that is a source may increase the chance that the restoration project will be successful. A metapopulation sink area may benefit more from adding shell material than by adding spat-on-shell since larvae from source reefs are likely to recruit to these reefs (Lipcius et al. 2008). Brumbaugh et al. (2006) suggested that restoration reefs should be constructed in sink habitats in order to provide greater ecosystem services throughout an estuary. However, larvae produced from sink habitat may not contribute to the metapopulation (Lipcius et al. 2015). Source oyster reefs also have functional genetic differences that provide the oyster larval pool of an estuary with abundant genetic variation for survival across different salinities (Eierman and Hare 2013). A combination of restoration reefs in sink and source habitats could enhance both broodstock and ecosystem services throughout an estuary (Lipcius et al. 2015).

The question regarding where larvae settle that Julius Nelson stated in 1892 may not have mattered a century ago, but now with major declines in oyster populations and considering that the success of a restoration reef depends on natural spat settlement, it may be a worthwhile problem to solve. In this study, I investigated Julius Nelson's question by testing the effect distance from a natural oyster reef had on recruitment within the Great Bay estuary. The study took place over the course of two years and determined both spatial and temporal patterns of oyster recruitment. Understanding how proximity to a native oyster reef affects recruitment patterns could assist in restoration site selection.

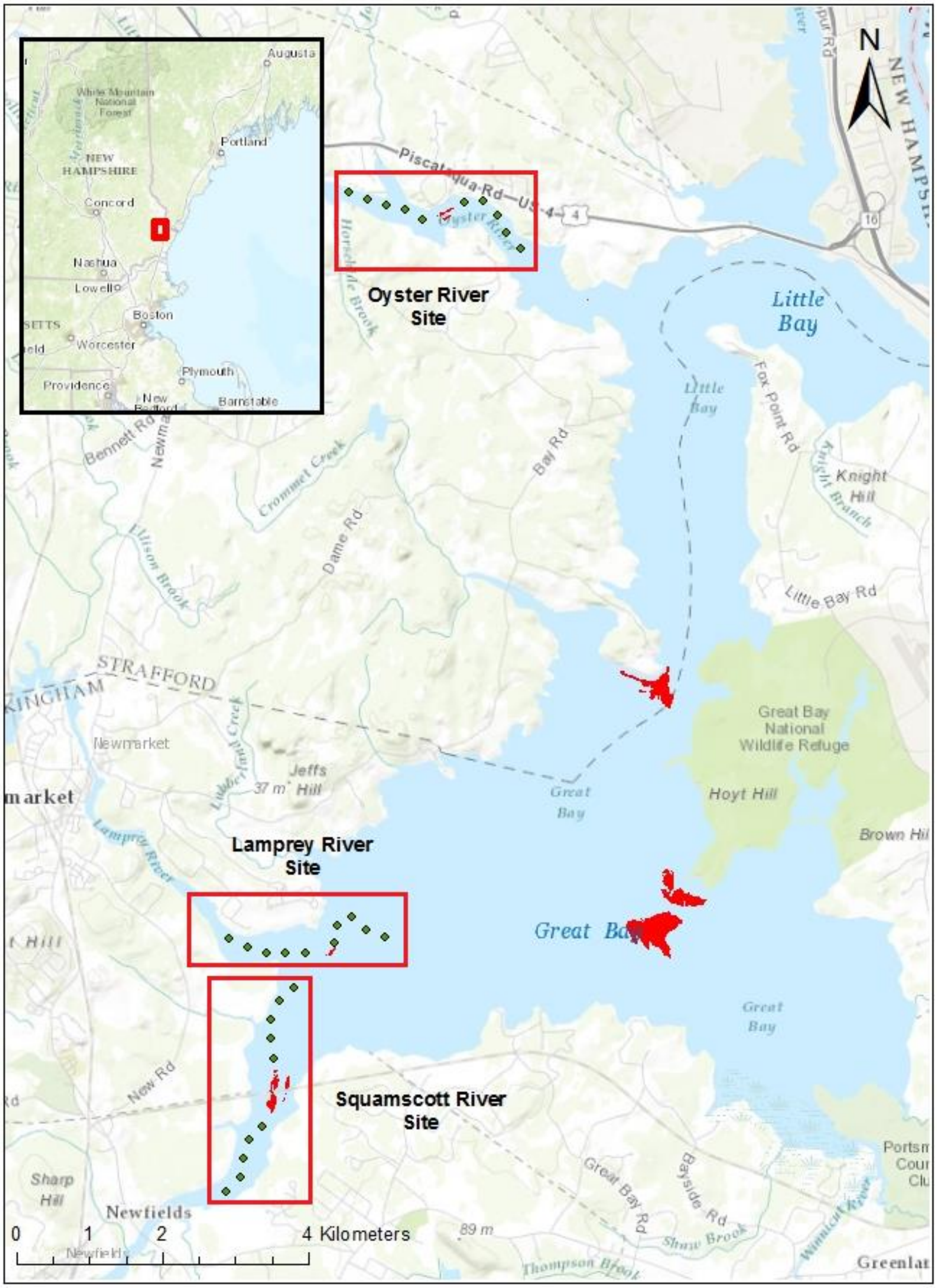

Figure 14. Study sites within Great Bay Estuary, NH during 2014 and 2015.

Methods and Materials

Oyster recruitment was studied at three sites (Lamprey, Oyster, and Squamscott rivers) on natural oyster reefs in the Great Bay Estuary, NH during 2014 and 2015. At each study site, four replicate shell bags were deployed 200, 400, 600, 800, and 1000 meters upstream and downstream of the native oyster reef and eight shell bags were deployed near the mid-point on each of the oyster reefs (Figure 15). At each of the six different distances, one shell bag was deployed along the left and right edge of the channel and two shell bags were deployed in the center of the river channel at low tide; bags at each distance were attached together with string. A pvc pole was used to mark the samplers along the edges of the channel.

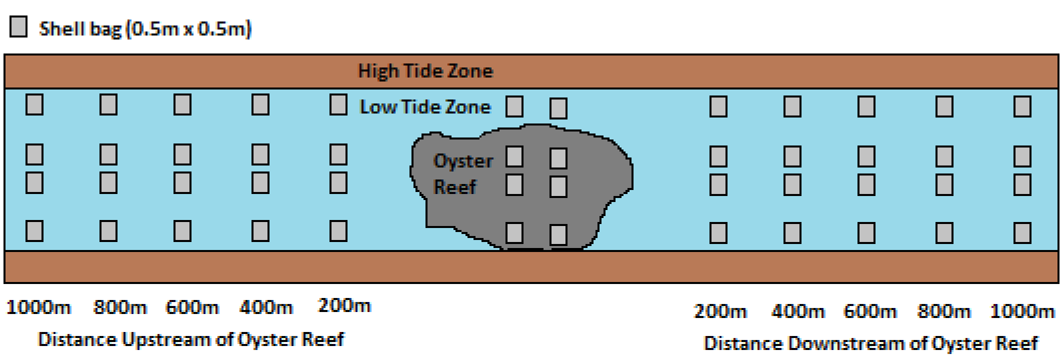

Figure 15. Experimental design for this study. Forty-eight shell bags were deployed at each of the three study sites (Oyster, Lamprey, and Squamscott Rivers).

Sampler Design

Samplers were constructed with mesh bagging (mesh size 2.5 cm) and edges were secured with zip-ties. Each mesh bag was filled with approximately 250 oyster shells (filled bags were approximately 50 x 50 x 10 cm) and held in place with pvc poles cut to lengths of approximately 1 m. Forty-eight samplers were deployed at each study site (Figure 16).

Figure 16. Shell bags before deployment.

Field Methods

Deployment and Retrieval

The timing of shell bag deployment was determined by weekly gonad analysis of Great Bay oysters obtained from multiple native reefs in order to estimate when spawning had occurred. At least ten oysters, greater than 60 mm, were collected with oyster tongs or by hand from Oyster River, Adams Point, Nannie Island, or Squamscott River. All oysters were dissected and gonad appearance, i.e., size and color, was assessed visually to estimate the timing of spawning. Adult oysters are ripe when the gonad region is large and has a cream-colored appearance. During the spawning period, the thickness of the gonadal region gradually decreases, and in spent oysters the layer becomes extremely thin and watery (Loosanoff 1942). Typically, in Great Bay Estuary spawning occurs in the months of July and August (Ayer et al. 1970). Shell bags were deployed approximately three weeks prior to larval settlement (2-3 week larval duration).

In 2014, 144 shell bags were deployed during low tide the first week of July and retrieved during the third week of September. In 2015, 144 shell bags were deployed during low tide during the second week of July and retrieved during the third week of September. After retrieval (Figure 17), shell bags were kept in tanks with circulating seawater until spat were counted and measured.

Figure 17. Shell bag after 12 weeks in Great Bay estuary.

Data Analysis

Trends in oyster density were evaluated by year, distance from native oyster reef, upstream and downstream of reef, and location in river channel using analysis of variance followed by post hoc Tukey tests or Student's t-test. All data were tested for normality using Shapiro-Wilk ($p>0.05$). If necessary, data were transformed (log(x)) prior to analysis to meet the assumptions of equal variance and normal distribution. Data that did not meet these assumptions after transformation were analyzed using nonparametric Kruskal-Wallis test. Estimates of oyster density were converted to oyster per square meter after being back-transformed. Data was analyzed using JMP 12 software.

Results

Settlement of oysters occurred between the first and third week of August at all three study sites in both 2014 and 2015. Spat ranged in shell length from 2 mm to 36 mm, had a mean shell height of 11.4 mm and 90% of spat were less than 21 mm in 2014 (Figure 18). In 2015, spat ranged in shell height from 2 mm to 46 mm, had a mean shell height of 17.1 mm and 90% of spat were less than 29 mm (Figure 19).

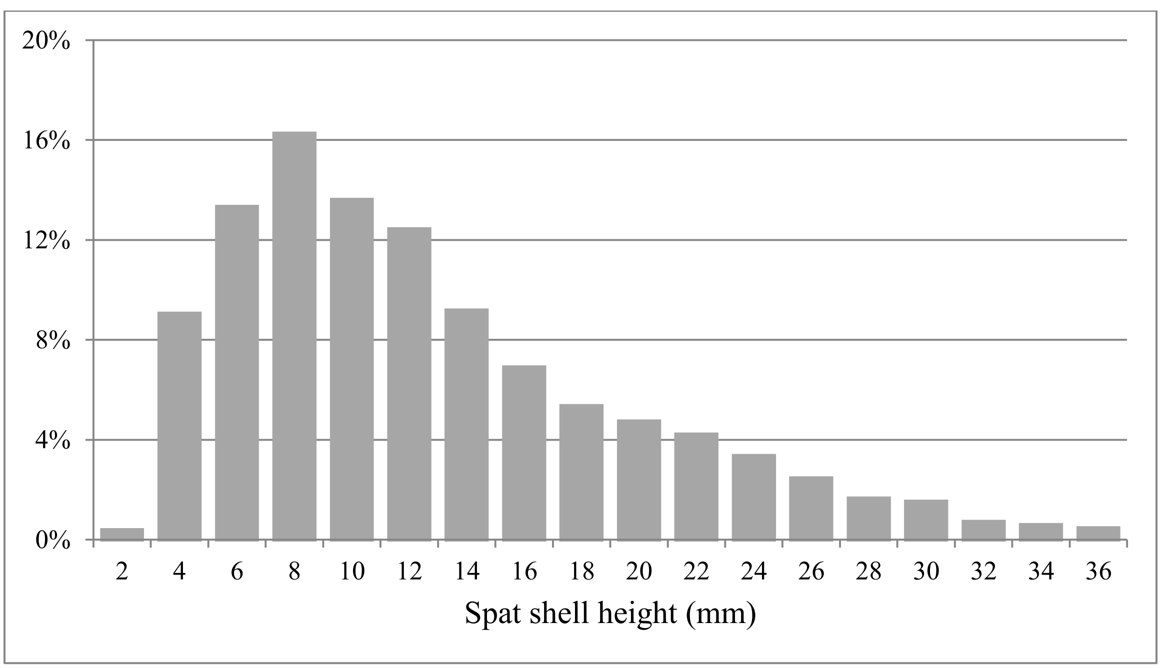

Figure 18. Oyster length frequency distribution for all study sites combined within Great Bay Estuary, NH during 2014.

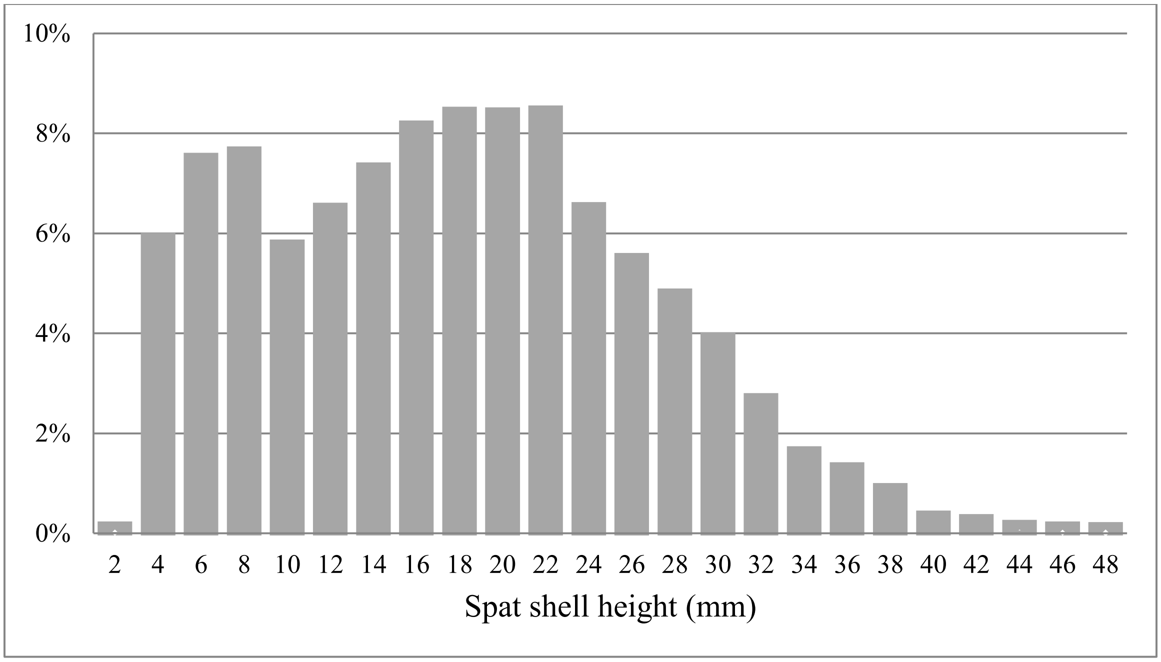

Figure 19. Oyster length frequency distribution for all study sites combined within Great Bay Estuary, NH during 2015.

Recruitment (mean spat density, all sites combined) was significantly greater in 2015 ($p < 0.01$) (Figure 20). In both 2014 and 2015, recruitment also differed significantly when comparing the mid-point of the oyster reefs (distance “0”) and all five distances away from the reef (200, 400, 600, 800 and 1000 meters) ($p < 0.01$) (Figure 21 and Figure 22). Recruitment was not significantly different upstream or downstream of the oyster reefs in 2014 or 2015 (Figure 23). Recruitment also did not differ along the channel edge and in the center of the river channel in 2014 or 2015 (Figure 24).

Water temperatures in Great Bay during 2014 and 2015 showed typical seasonal oscillations (Figure 25). However, in 2015, water temperatures during August and September were approximately 2^{o}C higher than in 2014.

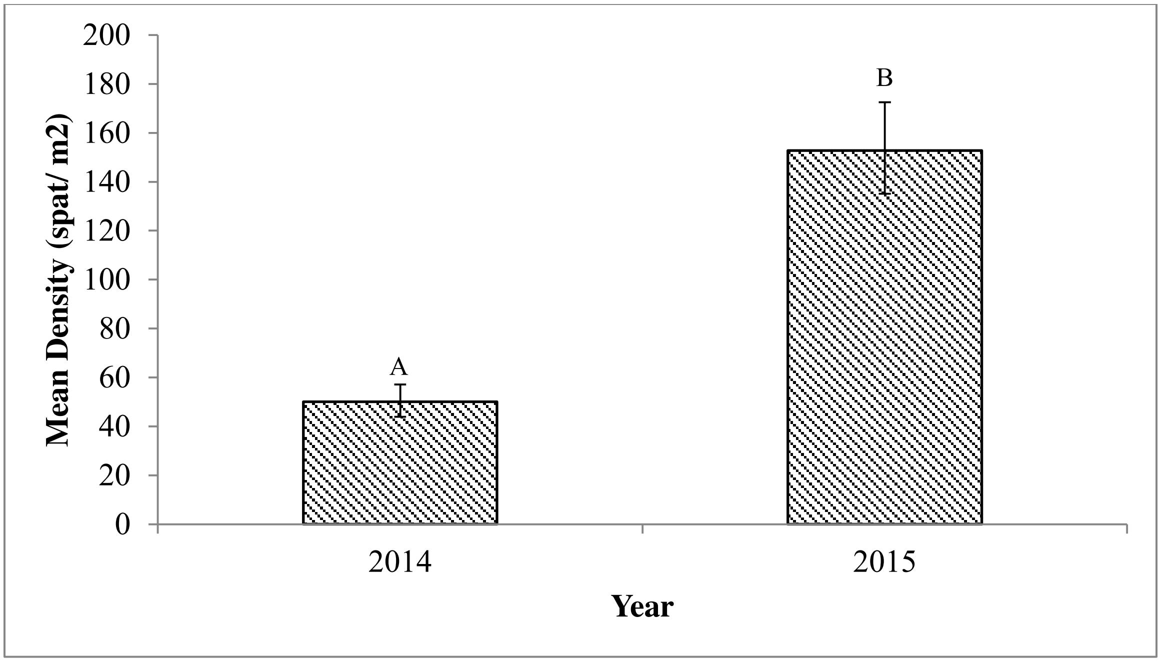

Figure 20. Mean spat density in Great Bay in 2014 and 2015. Error bars denote ±1 SE. Levels not connected by same letter are significantly different ($p < 0.05$).

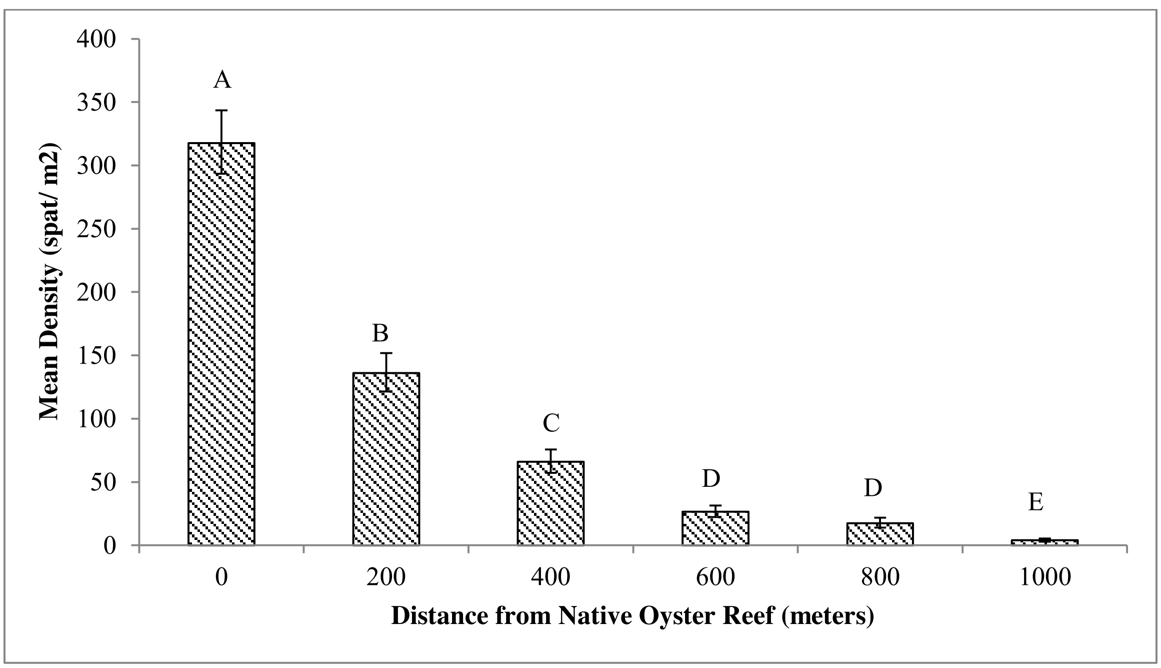

Figure 21. Mean spat density on native oyster reefs (0) and at five distances away from a native oyster reef (200, 400, 600, 800 and 1000 meters) within Great Bay Estuary, NH during Fall 2014. Error bars denote ±1 SE. Levels not connected by same letter are significantly different ($p < 0.05$).

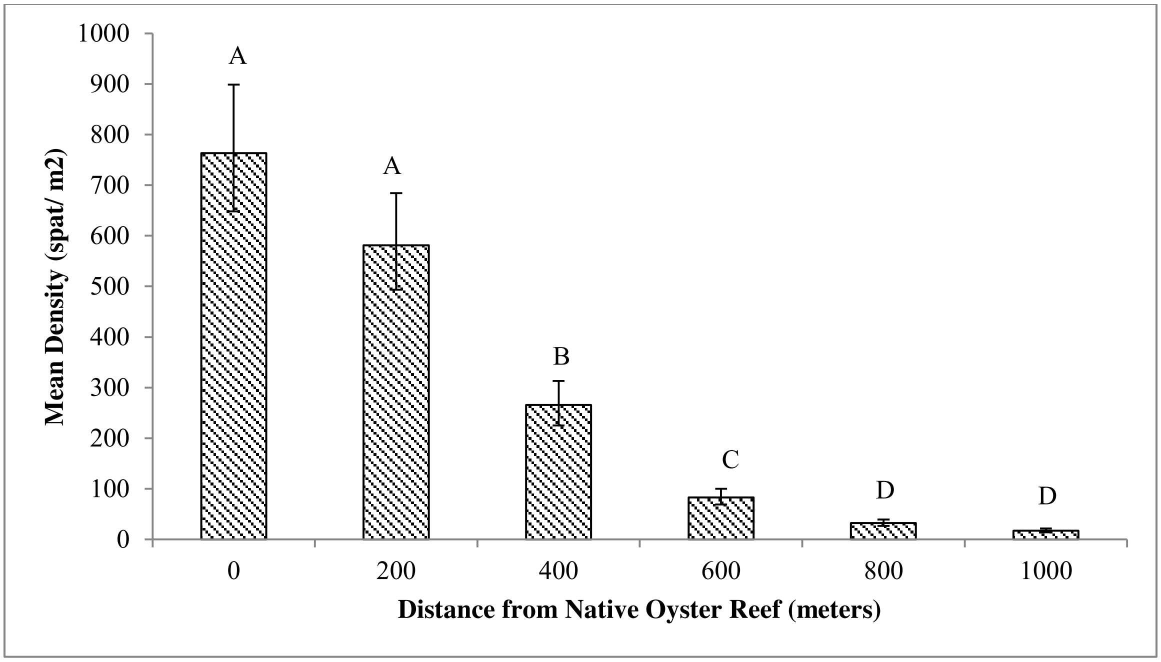

Figure 22. Mean spat density on native oyster reefs (0) and at five distances away from a native oyster reef (200, 400, 600, 800 and 1000 meters) within Great Bay Estuary, NH during Fall 2015. Error bars denote ±1 SE. Levels not connected by same letter are significantly different ($p < 0.05$).

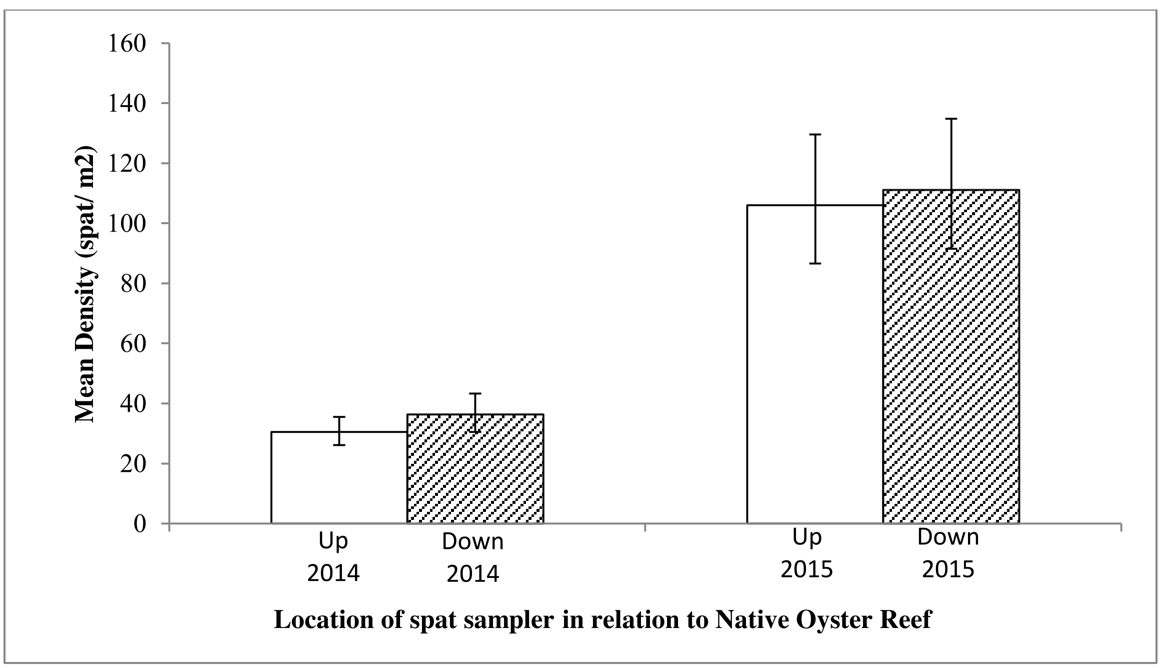

Figure 23. Mean spat density upstream and downstream in relation to native oyster reefs within Great Bay Estuary, NH during Fall 2014 and 2015. Error bars denote ±1 SE.

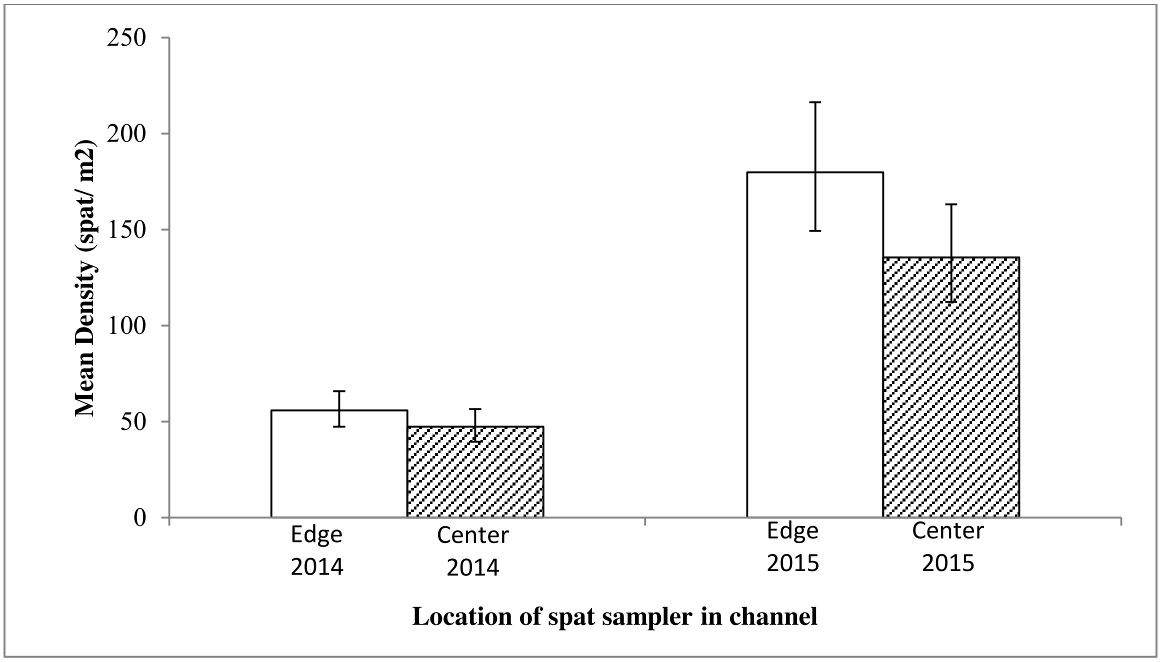

Figure 24. Mean spat density along the edge and in the center on the river channel within Great Bay Estuary, NH during Fall 2014 and 2015. Error bars denote ±1 SE.

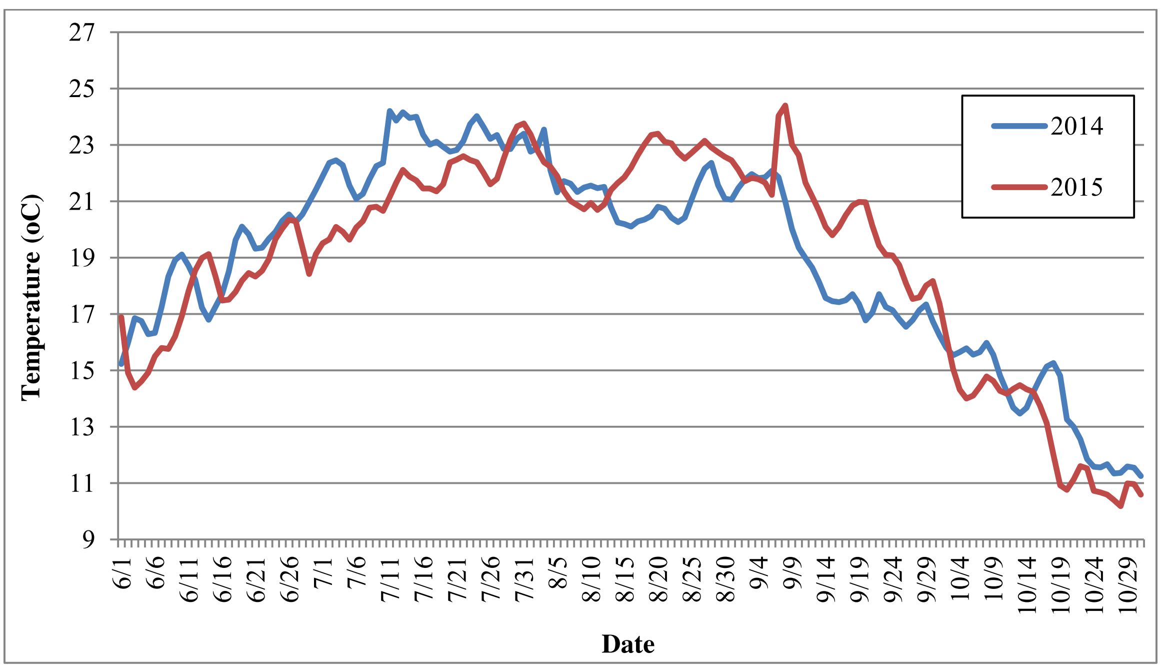

Figure 25. Water temperature data in Great Bay between June 1st and October 31st in 2014 and 2015.

Discussion

There are few published studies on the spatial distribution of recruitment, particularly at the spatial scales of my research. Such studies may not be pertinent to estuaries along the mid and south Atlantic that are not recruitment and substrate limited. However, understanding recruitment distribution could provide valuable information to restoration efforts in recruitment-limited estuaries like New Hampshire's Great Bay Estuary.

In previous years, replicate quadrat samples (Smith 2014) and patent tongs have been used to determine spat set in Great Bay. The recruitment sampling methodology used in this study allowed for comparative spat density measurements. The spat sampling bags provided similar surface area for settlement. The surface area of the bags also allowed for the bags to remain in place throughout the study and not sink into soft sediment. Spat samplers were deployed shortly after spawning to prevent the accumulation of sediment and allow samplers to accumulate a biofilm. Differences in sediment cover were not noticed during sample bag retrieval during 2014 or 2015 (pers. obs.). However, the sample bags may have accumulated sediment if they were deployed for a longer period and experienced storm events.

Great Bay Estuary, like many northern estuaries typically has a single spawning and recruitment peak period that occurs between late July and mid-August (Medcof 1939; Medcof 1955). A sudden rise in water temperature in early July (NERRS 2016) likely trigged spawning (Medcof 1939; Butler 1956) in both 2014 and 2015. However, 2015 apparently had a second spawning event occurring in late July after another sudden rise in water temperature. Multiple spawning events typically occur in estuaries south of Connecticut (Hidu 1978; Kenny et al. 1990; Kennedy 1980). The two spawning events in 2015 could explain the three-fold increase in recruitment over 2014. In addition, increased phytoplankton abundance observed during July and August 2015 (pers. obs.) could have played a role in the increased growth rate of the oysters. Moreover, phytoplankton blooms may also initiate spawning and could be a more reliable spawning cue than the variability of water temperatures (Nelson 1955; Starr et al. 1990).

The first spawning events occurred around the same time of the year in both 2014 and 2015. However, the range of spat growth was greater in 2015. Furthermore, the water temperature in 2015 was about 2^{o}C higher in August and September. Prytherch (1928) found that years with higher than average temperatures could experience greater abundances of spat and increased feeding activity. The increased pumping rates of oysters in 2015 could explain the larger growth of spat as compared to spat in 2014 (Galtsoff 1928).

Recruitment within the Great Bay Estuary during 2014 and 2015 showed the high degree of variability, both spatially and temporally, characteristic of recruitment studies (Nelson 1903). Although the spatial scale I studied was relatively small, within 1 kilometer of oyster reef, the same trends were apparent during both study years strongly indicating that recruitment decreases as proximity from a native reef increases.

There have been few studies on the spatial dimensions of natural recruitment, but my results are consistent with some previous research. For example, Harding et al.

(2012) reported high recruitment on constructed reefs within 1 to 2 km of productive natural oyster reefs. In addition, evidence for decreased oyster settlement with increased distance away from spawning oysters was observed from a single source population of Pacific oysters, which are broadcast spawners, in 1932 and 1936 (Quayle 1988).

The increased recruitment of oysters near natural reefs may be due to numerous environmental and biological factors. Oyster larvae exhibit selective swimming; moving into the water column during flood tide and resting on bottom during ebb (Carriker 1951; Wood and Hargis 1971). *Crassostrea virginica* larvae are relatively weak swimmers, which would suggest that larvae may primarily be dispersed as passive particles. However, Tamburri et al. (1992), observed oyster larvae sinking or swimming downward in response to physical and chemical cues. In addition, oyster larvae are gregarious settlers and exhibit active substrate choices suggesting some degree of active transport during settlement (Zimmer-Faust and Tamburri 1994).

There was no significant difference in oyster densities upstream and downstream of native oyster reefs in 2014 or 2105. These results are in contrast to Andrews 1983, who observed recruitment increasing upstream in an estuary. There was also no significant difference in recruitment in the center or along the edge of the river channels. Lenihan (1999) found similar results, concluding that recruitment was comparable in deep and shallow waters.

In sum, my research has demonstrated a strong relationship between oyster recruitment and proximity to a population of adult oysters, as reported previously

(Southworth and Mann 1998; Schulte et al. 2009; Lipcius et al. 2015). However, the magnitude of the differences in recruitment levels at the spatial scales involved was surprising. With respect to the design of oyster restoration projects, my findings suggest that restoration efforts should consider where practical extending the existing boundaries of natural oyster reefs in order to provide the greatest potential for natural recruitment onto the restoration site, and thus long-term reef development. This might be accomplished simply by adding shell to the margins of natural oyster reefs, as compared to reef construction in areas where no oysters exist, which would likely be a cost effective strategy to restoring oyster populations (Harding et al. 2012).

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APPENDIX

Table A1. Oyster density data for natural oyster reefs in the Great Bay Estuary for 2013 (number of oysters per patent tong sample, 0.16 m^2).

Location	Date	Sample #	# oysters < 30mm	# oysters >60mm	Total # of oysters	Comments
Adams Pt	9/19/2013	1	22	1	24	muddy bottom, lots of barnacles
Adams Pt	9/19/2013	2	10	2	12	muddy bottom, lots of barnacles
Adams Pt	9/19/2013	3	16	3	20	sandy-mud bottom, lots of barnacles
Adams Pt	9/19/2013	4	45	2	49	sandy-mud bottom, lots of barnacles
Adams Pt	9/19/2013	5	34	1	38	sandy-mud bottom, lots of barnacles
Adams Pt	9/19/2013	6	48	5	55	sandy-mud bottom, lots of barnacles
Fox Pt	9/10/2013	1	1	1	3	lots of algae, sandy-muddy
Fox Pt	9/10/2013	2	4	3	7	lots of algae, sandy-muddy
Fox Pt	9/10/2013	3	7	2	9	lots of algae, sandy-muddy
Fox Pt	9/10/2013	4	11	3	19	lots of algae, sandy-muddy
Fox Pt	9/10/2013	5	0	0	0	muddy, only two oyster shell in sample
Lamprey R.	9/28/2013	1	70	0	71	muddy, lots of barnacles, long oyster shells
Lamprey R.	9/28/2013	2	61	3	64	muddy, lots of barnacles, long oyster shells
Lamprey R.	9/28/2013	3	99	2	103	muddy, lots of barnacles, long oyster shells
Lamprey R.	9/28/2013	4	107	5	116	muddy, lots of barnacles, long oyster shells
Lamprey R.	9/28/2013	5	100	2	105	muddy, lots of barnacles, long oyster shells
Nannies Is.	9/19/2013	1	9	4	15	muddy
Nannies Is.	9/19/2013	2	13	2	16	muddy
Nannies Is.	9/19/2013	3	7	7	16	oyster drill, muddy
Nannies Is.	9/19/2013	4	3	0	4	oyster drill, muddy
Nannies Is.	9/19/2013	5	1	3	4	oyster drill, muddy
Oyster R.	9/11/2013	1	12	0	12	muddy, buried shell
Oyster R.	9/11/2013	2	17	2	19	muddy, buried shell
Oyster R.	9/11/2013	3	11	2	13	muddy, buried shell
Oyster R.	9/11/2013	4	27	1	29	muddy, buried shell
Oyster R.	9/11/2013	5	48	4	54	muddy, buried shell

Table A1 cont. Oyster density data for natural oyster reefs in the Great Bay Estuary for 2013 (number of oysters per patent tong sample, 0.16 m^2).

Location	Date	Sample #	# oysters < 30mm	# oysters >60mm	Total # of oysters	Comments
Piscataqua R.	9/12/2013	1	19	1	23	10-12 feet, sandy-mud
Piscataqua R.	9/12/2013	2	17	0	21	10-12 feet, sandy-mud
Piscataqua R.	9/12/2013	3	7	2	11	20 feet, sandy-mud
Piscataqua R.	9/12/2013	4	10	1	12	20 feet, sandy-mud
Piscataqua R.	9/12/2013	5	9	2	12	20 feet, sandy-mud
Squamscott R.	10/4/2013	1	57	6	70	5 feet deep, muddy
Squamscott R.	10/4/2013	2	75	3	84	5 feet deep, muddy
Squamscott R.	10/4/2013	3	45	2	55	5 feet deep, muddy
Squamscott R.	10/4/2013	4	33	4	40	6-8 ft deep, muddy
Squamscott R.	10/4/2013	5	52	3	56	6-8 ft deep, muddy
Squamscott R.	10/4/2013	6	68	5	82	6-8 ft deep, muddy

Table A2. Oyster density data for restored oyster reefs in the Great Bay Estuary for 2013 (number of oysters per patent tong sample, 0.16 m^2).

Location	Date	Sample #	# oysters < 30mm	# oysters >60mm	Total # of oysters	Comments
Adams Pt.	8/28/2013	1	4	0	4	low-density oyster shell mucky, algae
Adams Pt.	8/28/2013	2	1	1	2	high-density oyster shell, mucky, algae
Adams Pt.	8/28/2013	3	12	1	13	low-density concrete, mucky, algae
Adams Pt.	8/28/2013	4	7	0	7	low-density oyster shell, mucky, algae
Adams Pt.	8/28/2013	5	0	1	1	high-density concrete, mucky, algae
Bellamy R.	9/17/2013	1	0	0	0	2 feet deep, large oyster shell, small patches, sandy/muddy
Bellamy R.	9/17/2013	2	0	4	4	2 feet deep, large oyster shell, small patches, sandy/muddy
Bellamy R.	9/17/2013	3	2	0	2	2 feet deep, large oyster shell, small patches, sandy/muddy
Bellamy R.	9/17/2013	4	7	1	8	2 feet deep, large oyster shell, small patches, sandy/muddy
Fox Pt.	8/28/2013	1	1	1	3	loaded with algae, sandy
Fox Pt.	8/28/2013	2	2	0	5	loaded with algae, sandy
Fox Pt.	8/28/2013	3	30	0	30	loaded with algae, sandy
Fox Pt.	8/28/2013	4	27	0	29	loaded with algae, sandy
Fox Pt.	8/28/2013	5	4	0	5	loaded with algae, sandy
Lamprey R.	9/28/2013	1	31	0	37	spat on shell, muddy-buried shell, approx 108 dead spat on shell
Lamprey R.	9/28/2013	2	105	0	134	spat on shell, muddy-buried shell, approx 280 dead spat on shell
Lamprey R.	9/28/2013	7	93	0	93	1/4 bucket full of all clam shell
Lamprey R.	9/28/2013	6	352	0	374	**mounded shell, sample to represent spat on shell ONLY - 33 natural recruited spat (0-30mm)**

Table A2 cont. Oyster density data for restored oyster reefs in the Great Bay Estuary for 2013 (number of oysters per patent tong sample, 0.16 m^2).

Location	Date	Sample #	# oysters < 30mm	# oysters >60mm	Total # of oysters	Comments
Lamprey R.	9/28/2013	3	12	0	12	mounded shell, All on clam shell, lots of barnicles
Lamprey R.	9/28/2013	4	1	0	1	mounded shell, All on clam shell, lots of barnicles
Lamprey R.	9/28/2013	5	4	0	4	mounded shell, split medium and small pieces.
Oyster R.	9/10/2013	1	2	0	2	GSS, clam shell and rocks
Oyster R.	9/10/2013	2	0	0	0	GSS, clam shell and rocks
Oyster R.	9/10/2013	3	2	0	2	GSS, clam shell and rocks
Oyster R.	9/10/2013	4	0	0	0	GSS, clam shell and rocks
Oyster R.	9/10/2013	5	1	0	1	GSS, clam shell and rocks
Oyster R.	9/11/2013	1	6	0	7	inter-tidal, TNC 2009, small clam shell, muddy bottom
Oyster R.	9/11/2013	2	12	0	13	inter-tidal, TNC 2009, small clam shell, muddy bottom
Oyster R.	9/11/2013	3	5	0	5	inter-tidal, TNC 2009, small clam shell, muddy bottom
Oyster R.	9/11/2013	4	1	0	1	inter-tidal, TNC 2009, small clam shell, muddy bottom
Oyster R.	9/11/2013	5	9	1	10	inter-tidal, TNC 2009, small clam shell, muddy bottom
Oyster R.	9/11/2013	1	1	0	1	wagon hill, TNC 2010, very muddy, lots dead buried shell, some algae grow, clam shell
Oyster R.	9/11/2013	2	0	0	0	wagon hill, TNC 2010, very muddy, lots dead buried shell, some algae grow, clam shell
Oyster R.	9/11/2013	3	1	0	1	wagon hill, TNC 2010, very muddy, lots dead buried shell, some algae grow, clam shell
Oyster R.	9/11/2013	4	0	0	0	wagon hill, TNC 2010, very muddy, lots dead buried shell, some algae grow, clam shell
Oyster R.	9/11/2013	5	1	0	1	wagon hill, TNC 2010, very muddy, lots dead buried shell, some algae grow, clam shell

Table A2 cont. Oyster density data for restored oyster reefs in the Great Bay Estuary for 2013 (number of oysters per patent tong sample, 0.16 m^2).

Location	Date	Sample #	# oysters < 30mm	# oysters >60mm	Total # of oysters	Comments
Piscataqua R.	9/12/2013	1	0	0	0	10-15 feet, sandy
Piscataqua R.	9/12/2013	2	1	0	1	10-15 feet, sandy
Piscataqua R.	9/12/2013	3	8	0	8	10-15 feet, sandy
Piscataqua R.	9/12/2013	4	3	0	3	10-15 feet, sandy
Salmon Falls R.	9/12/2013	1	1	1	5	10-12 feet deep, sandy-mud
Salmon Falls R.	9/12/2013	2	0	0	1	10-12 feet deep, sandy-mud
Salmon Falls R.	9/12/2013	3	2	0	2	10-12 feet deep, sandy-mud
Salmon Falls R.	9/12/2013	4	3	0	4	10-12 feet deep, sandy-mud
Salmon Falls R.	9/12/2013	5	5	1	9	10-12 feet deep, sandy-mud
Squamscott R.	10/8/2013	1	97	0	102	6-8 ft deep, muddy
Squamscott R.	10/8/2013	2	71	0	71	6-8 ft deep, muddy
Squamscott R.	10/8/2013	3	57	0	64	6-8 ft deep, muddy
Woodmans Pt.	10/15/2013	1	6	3	9	some gravel
Woodmans Pt.	10/15/2013	2	25	4	30	some gravel
Woodmans Pt.	10/15/2013	3	8	1	14	some gravel
Woodmans Pt.	10/15/2013	4	5	0	5	some gravel
Woodmans Pt.	10/15/2013	5	12	0	15	some gravel

Table A3. Mean monthly water temperature (Celsius) in Great Bay for May through October from 1991 to 2015. (Yellow = large recruitment events, Red = water temperatures greater than the time series average, Blue = water temperatures less than the time series average)

Year	May	June	July	August	September	October
2015	14.6	17.7	21.5	22.2	20.2	14.8
2014	13.0	18.6	22.4	21.3	18.7	13.8
2013	15.0	19.3	23.9	20.9	18.6	14.1
2012	15.3	19.6	22.6	23.3	18.8	13.3
2011	13.6	18.5	22.7	22.2	19.1	12.2
2010	14.6	19.6	22.8	21.3	19.1	12.9
2009	14.5	17.6	20.2	22.7	18.6	12.2
2008	13.0	18.9	22.3	21.5	18.7	12.9
2007	14.0	18.2	20.4	21.7	18.4	14.7
2006	12.9	19.0	22.6	21.3	18.6	12.6
2005	11.6	17.2	22.3	22.5	19.6	11.1
2004	14.1	16.0	20.8	21.1	*	12.6
2003	13.2	17.5	21.8	21.6	19.0	14.4
2002	13.0	17.9	21.6	23.3	19.1	10.0
2001	14.7	19.4	20.6	22.1	18.6	13.0
2000	13.5	18.4	20.4	21.1	18.1	12.5
1999	14.4	20.6	22.0	21.0	19.6	12.1
1998	14.4	17.4	21.0	21.1	18.5	12.4
1997	11.3	18.0	21.0	20.8	17.6	12.0
1996	13.1	18.4	19.9	21.2	18.0	12.0
1995	*	*	23.4	22.3	17.4	13.4
Average	13.7	18.4	21.7	21.7	18.7	12.8

*No measurements taken

Table A4. Mean monthly salinity (ppt) in Great Bay for May through October from 1991 to 2015. (Yellow = large recruitment events, Red = salinity greater than the time series average, Blue = salinity less than the time series average)

Year	May	June	July	August	September	October
2015	23.6	26.6	27.1	30.3	30.3	28.7
2014	21.7	25.5	25.6	25.1	29.4	30.2
2013	23.8	18.7	19.2	28.1	18.6	27.1
2012	20.2	17.9	27.4	25.5	29.7	28.3
2011	17.0	17.5	21.1	27.8	20.2	19.2
2010	21.9	23.3	25.5	24.9	26.6	26.5
2009	19.6	20.3	16.0	19.3	25.5	26.4
2008	18.1	26.1	24.3	15.6	19.5	18.8
2007	16.1	19.4	28.0	**29.1**	**28.1**	29.8
2006	12.9	13.3	22.3	**23.7**	**27.9**	23.3
2005	15.1	18.1	23.5	29.0	29.4	17.1
2004	17.5	21.7	28.2	28.2	*	26.0
2003	20.4	21.8	28.2	28.2	28.0	25.0
2002	18.3	21.2	29.2	34.1	34.5	31.2
2001	23.0	22.8	27.0	30.2	30.7	30.0
2000	16.3	20.8	26.5	24.5	26.7	25.2
1999	22.8	28.6	29.3	29.9	24.1	21.7
1998	16.3	14.4	18.6	28.1	29.9	26.0
1997	17.7	23.2	24.8	27.4	26.5	27.3
1996	15.2	21.9	22.4	25.9	27.8	21.5
1995	*	*	25.6	29.7	32.1	30.3
Average	18.9	21.2	24.7	26.9	27.3	25.7

*No measurements taken

Table A5. Recruitment data for Squamscott, Lamprey, and Oyster river study sites in 2014 (number of spat per sampler bag, 0.25 m^2).

Squamscott

Upstream	Left	Center	Center	Right	Downstream	Left	Center	Center	Right
Reef	95	142	82	136	**Reef**	51	111	109	126
200	52	32	49	80	**200**	46	29	47	68
400	17	18	18	21	**400**	14	25	23	25
600	4	3	3	26	**600**	6	22	10	11
800	24	15	7	6	**800**	13	*	*	2
1000	1	0	3	2	**1000**	11	3	1	5

Lamprey

Upstream	Left	Center	Center	Right	Downstream	Left	Center	Center	Right
Reef	116	96	152	77	**Reef**	129	142	145	104
200	27	*	*	40	**200**	55	72	43	34
400	38	18	28	39	**400**	39	*	*	12
600	12	11	6	2	**600**	*	14	7	11
800	10	1	5	20	**800**	*	*	*	*
1000	1	0	2	14	**1000**	*	*	*	*

Oyster

Upstream	Left	Center	Center	Right	Downstream	Left	Center	Center	Right
Reef	48	40	51	24	**Reef**	34	23	46	32
200	7	21	12	15	**200**	15	*	*	19
400	4	6	9	4	**400**	7	*	*	12
600	4	2	7	11	**600**	6	2	2	3
800	8	2	2	3	**800**	2	2	1	0
1000	1	3	3	0	**1000**	1	0	1	0

*no sample, sampler bag was lost.

Table A6. Recruitment data for Squamscott, Lamprey, and Oyster river study sites in 2015 (number of spat per sampler bag, 0.25 m^2).

Squamscott

Upstream

	Left	Center	Center	Right
Reef	221	264	304	120
200	358	168	164	245
400	122	84	84	110
600	29	89	27	78
800	32	15	23	22
1000	45	6	0	1

Downstream

	Left	Center	Center	Right
Reef	341	198	217	259
200	82	116	152	420
400	79	72	127	160
600	28	40	24	44
800	*	*	*	*
1000	27	2	13	42

Lamprey

Upstream

	Left	Center	Center	Right
Reef	273	274	184	126
200	229	172	115	156
400	80	61	32	87
600	*	*	*	*
800	20	3	2	6
1000	*	*	*	*

Downstream

	Left	Center	Center	Right
Reef	312	397	418	168
200	164	148	150	129
400	165	76	64	100
600	25	24	23	28
800	4	7	8	6
1000	5	0	2	8

Oyster

Upstream

	Left	Center	Center	Right
Reef	126	117	77	119
200	48	104	72	128
400	25	28	52	48
600	11	9	10	5
800	4	6	4	5
1000	7	2	0	4

Downstream

	Left	Center	Center	Right
Reef	141	154	95	157
200	154	124	196	92
400	23	50	70	30
600	10	15	10	9
800	14	4	4	4
1000	4	1	4	9

*no sample, sampler bag was lost.