

Draft

History and Current Status of the Eastern Oyster (*Crassostrea virginica*) in Maine¹

(with notes on related activities)

By

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Abstract

The American or Eastern oyster, *Crassostrea virginica*, is an important foundation species in estuaries throughout the eastern United States. In addition to being an important resource species, oysters provide valuable ecological services unmatched by any other ecosystem component. Oyster reefs, however, are one of the most threatened habitats in the world. Oysters were once abundant in the Gulf of Maine but have declined over the centuries largely due to natural changes in the environment. Currently, oysters are limited to warm water pockets, called Virginian refugia, in the northwest Atlantic region. Several of these areas have been identified but none are really well documented. Recent history has shown that periods of warm water or environmental modifications can lead to a resurgence of oyster populations. There is evidence of oyster population expansion in recent years. Climate change is expected to make more areas in Maine suitable for oysters. It is important to identify and document existing and potential oyster habitat in preparation for effective restoration efforts.

Introduction

The oyster, *Crassostrea virginica*, commonly referred to as the eastern or American oyster, is native to eastern North America. The eastern oyster naturally occurs from the Gulf of St. Lawrence to the Gulf of Mexico with a notable gap along the shores of Maine, southern New Brunswick and western Nova Scotia (Ganong 1890). The development, maintenance and alternative futures of this gap are overarching themes of this report. Any mention of ‘oyster’ in this document refers to the eastern oyster unless otherwise indicated.

The eastern oyster is a relatively large, epifaunal, bivalve mollusc. The oyster is usually considered an estuarine species. It does have wide tolerances to salinity, temperature and turbidity and to changes in these and other environment factors (Shumway 1996). Within these wide tolerances there are optimal levels, which may vary geographically, for different life stages and functions. These are well summarized in Shumway (1996). Some values to keep in mind are that feeding is greatly reduced when water temperatures dip to about 8°C or below (Galtsoff 1964) and effectively stops at 5°C (Loosanoff 1965). They need a period of time at water temperatures of 20°C or more for successful spawning and spat settlement (Galtsoff 1964). Within the wide range of tolerable salinities the optimal is considered to be between 14 and 28 PSU (Galtsoff 1964). In the mid-Atlantic and northern region of their range oysters are found in the central and inner parts of estuaries. These locations exhibit the preferred temperature and salinity ranges and protect the oysters from the deprivations of predation, fouling and disease. Predators, biofoulers and disease organisms are more specialized and have narrow ranges of tolerances. In southern regions oysters often live in the intertidal zone that provides a refuge from predation. The normal maximum depth of subtidal oysters is probably on the order of six meters (Merrill *et al.*, 1965).

Ecological Services

There are several characteristics of the species and its biology that make the oyster one of the most ecologically and economically important inhabitants of the coastal ecosystem (Coen *et al.* 2007). As an adult it is completely sessile. It rests on its left side on the bottom often cemented to hard substrates such as rocks or other oyster shells. The effect can be the buildup of shells from small masses to extensive reef structures many acres in size. Hence, the oyster is a major ecosystem engineer. The complex habitat provided by the accumulated living and dead shells offers food and refuge for many other species including invertebrates, fishes, birds and mammals. In fact, hundreds of species, both obligate and opportune, are associated with oysters (Wells 1961, Larsen 1975, 1985). The ecological value of this concentration of biotic resources has been demonstrated in recent comparative research on the secondary production of various estuarine habitats. Wong *et al.* (2011) have determined that secondary production in oyster beds is at least four times that of salt marshes, the next most productive habitat. In addition, the simple presence of living and dead oysters on creek sides and bottoms stabilizes sediments and reduces erosion.

Oysters are prolific filterers of seawater and as such provide another valuable ecosystem function. The oyster’s method of feeding is to pass water over its gills and sort out the particulate material suspended in water. Food particles are retained and moved to the stomach while inorganic and low nutrition particles are bound together with mucus

and discharged as pseudofeces. The effect is a clearing of particles from the water column and their ingestion or deposition on the bottom. A single oyster may filter over 400 liters of water daily (Galtsoff 1964); hence, the total impact of the filtering of all living oysters on a reef can have a very significant effect on the ecosystem. In fact, historically oyster populations were capable of filtering all the water in an estuary in just days. The result was a transport of materials from the water column to the benthic environment resulting in greater light penetration to support sea grasses and benthic diatoms (Newell and Koch 2004; zu Ermgassen *et al.* 2013) and the removal of nutrients that could support harmful algal blooms.

In spite of the oysters' importance as a commercial resource and a driving ecosystem engineer, oyster reefs are being threatened on a global basis (Beck *et al.* 2009). Overharvesting, destructive fishing techniques, toxic pollutants, diseases, hydrographic modifications and other insults have reduced oyster populations in most estuaries. Indeed, Beck *et al.* (2009) estimate that 85% of the world's oyster reefs have been lost. There is an imperative, then, to maintain and restore oyster habitat in areas that have been less severely impacted and where restoration has a higher chance of success. As we will see below, oyster populations have been declining in the Gulf of Maine for centuries. The decline has been largely natural and conditions may now be swinging in the oyster's favor.

There is a critical need to protect and restore native Maine oyster populations. Restoration efforts in our region, however, are severely limited by the lack of basic knowledge of their history and present distribution in the northern Gulf of Maine. This very basic information is required before any meaningful plans for protection and restoration can be initiated. With the advent of climate change, it may be expected that Maine estuaries will become increasingly hospitable to the resurgence of natural oysters and enhanced biodiversity and ecosystem services.

Methods

The basic information presented in this report was derived from a variety of sources. We perused the published scientific and historical literature. Special attention was given to gray literature reports from Maine's fisheries and environment agencies, university and public libraries, land trusts, environmental organizations, town offices, historical societies and State archives. Interviews were conducted with researchers, fishermen, outdoor activists, historians, journalists, archeologists and resource managers. A partial list of people and organizations contacted is presented in Appendices 1 and 2, respectively. These are partial lists because only 50% or less of the contacts led to useful information.

Findings

Background

The distributions of warm temperate (Virginian) estuarine and shallow water species in New England and the Canadian Maritimes are disjunct, i.e. they generally occur south of Cape Cod or in the southwestern Gulf of Saint Lawrence. Bousfield and Thomas (1975) presented a hypothetical explanation for the development of this

circumstance based on climatological and physiographic changes occurring since the last glaciation and continuing to the present. Briefly, 14,000 yr bp (before present) the land was depressed by the weight of the glacial ice burden. As the ice retreated, seawater flooded far inland relative to the present coastline (Fig. 1). Then the land mass rebounded from the removal of the ice overburden, relative sea level fell to tens of meters below the present. Much of the outer continental shelf including Georges Bank, Browns Bank and the Sable Island region became emergent and effectively formed a nearly continuous environment that was hospitable for colonization by estuarine and shallow water southern species (Fig. 2) (Ganong 1890, Bousfield and Thomas 1975, others). Because sea level was lower in the Gulf of Maine, tides were minimal or non-existent resulting in a Gulf that was lagoonal in nature (Campbell, 1986) and the warm temperate species occupied all the suitable habitats within the Gulf. During the warmest time, the hypsothermal period, approximately 7,000 yr bp, the distribution of warm temperate species was continuous from the mid-Atlantic to the Gulf of St. Lawrence (Bousfield and Thomas 1975). As sea level rose in succeeding millennia and larger and larger tides developed (Grant 1970; Greenberg, *et al.* 2012), the surface waters of the Gulf cooled due to tidal mixing and warm temperate species were increasingly restricted in their range within the Gulf of Maine. The populations of several species became disjunct from the main population centers in the mid-Atlantic region, and with one another, with the result that groupings of warm temperate species are now limited to isolated pockets, called Virginian refugia, where summer water temperatures, in most years, still reach levels sufficient (mid-20's °C) for the reproduction of these species with southern affinities. The Virginian refugia are usually located near the heads of estuaries and are largely confined to mid-coast Maine, particularly to the complex Sheepscot estuary and its tributaries. Resident species include xanthid and horseshoe crabs, certain amphipods and isopods and, most characteristically, the Eastern oyster *Crassostrea virginica* (Stickney 1959). These are ancient, natural populations of oysters. In the 1970's oyster aquaculture was introduced into Maine. These operations used oysters imported from southern New England and were located lower in a few estuaries.

Geological, Archeological and Historical Evidence of the Distribution of Oysters

Bousfield and Thomas' (1975) arguments, although hypothetical, were sound and have been supported by subsequent geological and oceanographic research (Shaw *et al.* 2002; Greenberg *et al.* 2012). It is possible, however, to add support to their thesis using far-flung geological, ecological, archeological and historical observations. Placement of observations into the aforementioned, somewhat arbitrary, categories is an attempt to make the findings more comprehensible. This compilation of the observed distributions of oysters in time and space is intended to provide a comprehensive overview of the history of the oyster in the Gulf of Maine region, to offer a framework within which additional details can be included as they are found and to spur further investigation.

Geological and Ecological Observations

The oldest marine fossils in Maine since the last glaciation were found 112 km inland from the present shoreline (Dow 1965, 1977). The site was probably at the edge of the retreating ice and the land was still depressed by tens of meters. All of the faunal

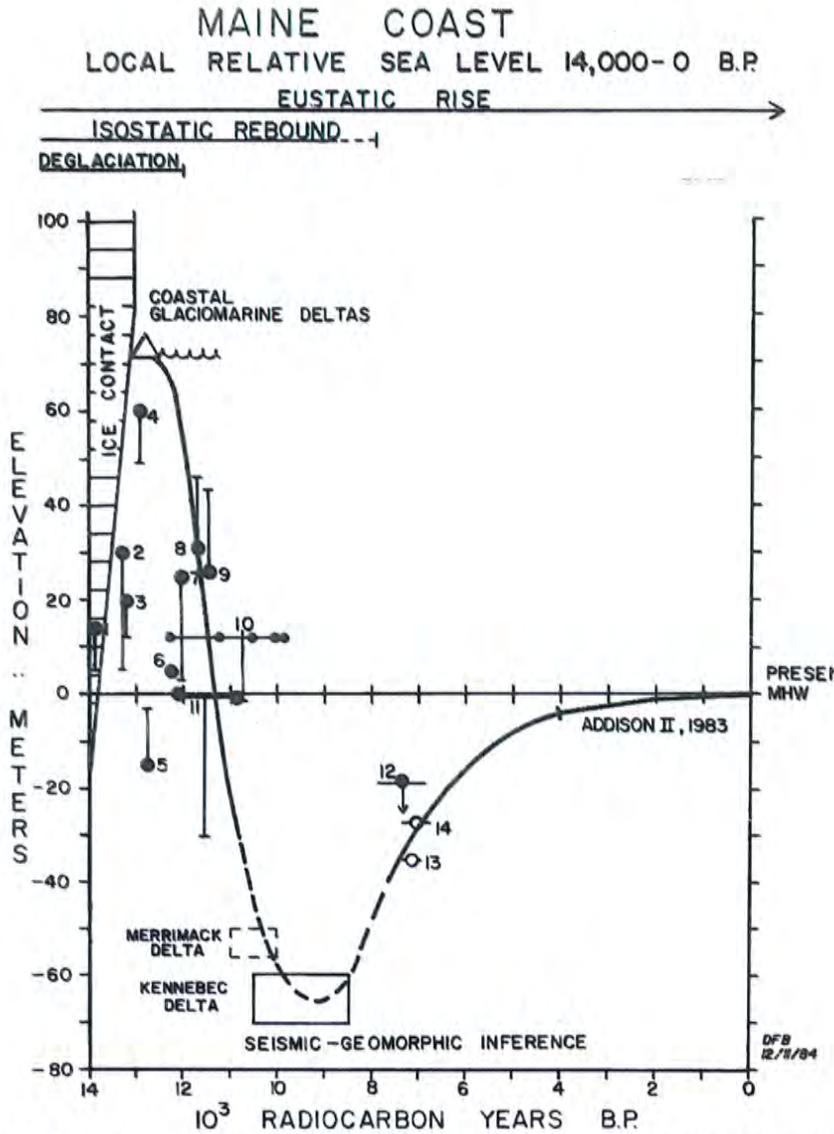


Fig. 1. Relative sea level on the Maine coast from 14k yr bp to the present (Belknap *et al.*, 1987).

remains represented in the nearly 12,000 year old deposits are of cold water animals. We can deduce that the Gulf of Maine was still cold and that Virginian species like the oyster had not yet made an appearance near the ice edge.

That oysters occurred at a lower stand of sea level on what is now the continental shelf is evidenced by observations of Merrill *et al.* (1965). They found pre-fossil oyster shells at 71 stations between Cape Cod and Cape Hatteras with most at depths of 38 to 59 m. Undoubtedly, the oysters inhabited estuaries and lagoons along the ancient coastline warmed by southern ocean currents. One 1960 cruise found oyster shells at 33 of 113 stations. Several shells were radiocarbon dated to 8,130 to 10,850 yr bp, +/- 400 or 500 years. The authors believe the shells may actually be older and the dates are skewed because of fouling and boring organisms. These observations are extended northward by



Fig. 2. The palaeogeography of the Gulf of Maine/Maritime Canada region 11k yr bp showing the emergent banks and islands (from Shaw *et al.* 2002).

Medcof *et al.* (1965) who found oyster shells on Georges Bank and in the Northumberland Strait in the Gulf of St. Lawrence dated at 10,600 and 6,850 years old, respectively. Further documentation of the occurrence of oysters on what is now continental shelf is provided by Whitmore *et al.* (1967) who describe the distribution of mammoth and mastodon teeth on the formerly emergent shelf. The geological evolution of the continental margin from ice to estuaries, lagoons and boreal forest and finally to submerged offshore banks is concisely related in Emery *et al.* (1965).

One of the consequences of the rising sea-level in the Gulf of Maine is that previous coastal landforms and any associated archeological sites are generally submerged and, hence, there is a gap in the geological and archeological record covering the period of 10,000 to 5,000 yr bp. Kelley *et al.* (2010) set out to describe submerged former terrestrial and shoreline environments that had been protected from erosion by underwater topography near Bass Harbor, ME. Coring revealed articulated oyster shells in life positions beginning at a depth of 2.5 m. These shells were radiocarbon dated to 9,500 to 8,000 yr bp.

In an effort to find and geologically characterize potential submerged archeological sites formed in the pre-5,000 yr bp period when most of the sites were flooded or destroyed by rising sea-level, Leach (2007) used modern geological techniques to survey the Dodge Basin in the central Damariscotta estuary. Whereas no

cultural features, i.e. middens, were found, Leach described in detail the evolution of the basin relative to sea-level rise. Natural oyster shells and beds were perceived in most analyses. Briefly, as sea-level rose, a sill at the entrance to Dodge Basin was over-topped and the formerly freshwater environment became brackish and then marine in nature. The habitat became suitable for oysters about 4,800 yr bp. No natural oysters occur in the basin presently. The inference, which supports the conjecture of Sanger and Sanger (1986), is that as sea-level rose, one after another of the several sills characterizing the Damariscotta River were over-topped and became colonized by oysters. With continued sea-level rise oysters moved landwards as the proper conditions for their feeding and reproduction migrated upriver. Oysters in the lower basins were extirpated due to insufficient temperatures and/or increased predation.

The Bras d'Or Lakes in eastern Nova Scotia were marine in the period immediately after deglaciation (Shaw *et al.* 2002). Once the land rebounded, however, they became fresh until about 5,000 yr bp when the sill was overtopped by the rising relative sea-level. Oyster have occurred in the lakes ever since.

In 1977 Bleakney and Davis (1983) discovered a prefossil oyster bed in the Bay of Fundy's Minas Basin that had been exposed by modern erosion. This extensive bed indicated that the climate and oceanographic conditions were more moderate than today's and the shells were radiocarbon dated to 3,800 yr bp.

Medcof *et al.* (1965) also remark on more recent oyster shells (1,290 and 500 yr bp) found in the vicinity of Halifax, NS where living oysters are not found today. Additionally, they mention a living population of native oysters in Ostrea Lake, near Halifax, precariously surviving separated from the cold North Atlantic by an unstable barrier beach.

Denys (1971) writing in 1672 notes the abundance of "immense oysters larger than a shoe and very plump" in what is now New Brunswick.

Castner (1950) relates an interesting story from his childhood concerning the history of the oyster in the Damariscotta River. In about 1900 dredging was undertaken just down river of the present Newcastle-Damariscotta bridge. The kids were allowed to ride the barge removing the sediment and discovered "great oyster shells in remarkable preservation". Apparently word of this got to Washington and there was enough interest that the Custom's Officer was instructed to buy some of them. One sold by Castner measured 16". Whereas we have no date or context for these specimens, it is further evidence that large oysters in the Damariscotta were not limited to the upriver middens.

Archeological Evidence

Archeological evidence is derived or inferred from the cultural artifacts left by early native peoples. Principal among these are the shell heaps or middens that accumulate from years of the consumption of shellfish at the same site and the tools, pottery and fire sites found within or behind the middens. They are most useful during the last 5,000 years because, as noted above, earlier sites have been submerged by rising sea-level.

Oysters have not been found in Minas Basin shell middens even though they were abundant there around 3,800 yr bp and are common in middens on the Atlantic and Gulf of Saint Lawrence shores of Nova Scotia (Bleakney and Davis 1983). Apparently native cultures utilizing shellfish did not appear in the region until 2,400 to 1,900 yr bp and their middens contain soft shell clam shells. It appears, therefore, that oysters were eliminated

from the region approximately 2,500 yr bp. Bleakney and Davis (1983) attribute this to the continuing trends of rising sea levels and increasing tidal range that made the environment unsuitable for oyster survival.

One coastal site that has been preserved is on Great Mosher Island in Casco Bay (Doyle *et al.* 1985). This site contains four identified strata with differing mollusk shells and human artifacts. The stratum second above the base was radiocarbon dated to about 3,400 yr bp at the bottom and it contained oyster shells. Shells from strata above this (dates not given) were sparser and contained soft shell clam shells. Oysters are not indicated. This could mean that the local site was no longer suitable for oysters or, perhaps, the marine conditions on a larger scale caused the extirpation of oysters from most of Casco Bay. We have seen a copy of a 1979 Archaeological Site Survey Report, probably attributable to D.R. Yesner, formerly of the University of Southern Maine, that records an oyster shell midden on White Island in the town of Harpswell that is dated to 2,770 yr bp. Other archeological survey reports indicate oysters in middens in several areas of Casco Bay including Flying Point, Pig Island and Bowman Island in Freeport, and Great Chebeague and Bustins Islands out in the bay. There are no dates associated with these reports. Art Spiess (Pers. Comm. 2011) believes oysters existed in the Portland region from 3500 to 2400 yr bp based on “sketchy evidence”. There are probably many further such records and interpretations that need to be uncovered.

Along the Maine coast, middens are quite common and most of the middens are composed of soft shell clam shells. Over two hundred middens have been identified in the Sheepscot and Damariscotta River areas alone. Several of these contain, or are almost entirely made up of, oyster shells. Most notable of these are the monstrous middens located on each side of the Damariscotta River just north of the villages of Newcastle and Damariscotta. In fact, these middens are among the largest in the world. The largest middens are the Glidden midden on the west bank and the Whaleback midden on the east. There are various descriptions of the sizes and content of the middens that are difficult to reconcile. In 1838, the Maine Geological Survey described an unnamed midden as “one hundred and eight rods long by eighty to a hundred wide, and twenty-five or six feet deep; making not less than forty-four million, nine hundred and six thousand cubic feet”. Elsewhere it was estimated that the heaps comprised 768,000 cubic feet and contained 170,000,000 oysters (Galtsoff and Chipman 1940). Someone else described the Whaleback midden as 347 ft long, 123 wide and 16 ft thick at the center. These numbers are close to those of Sanger and Sanger (1997) who describe it as 100 m long, 40 m wide and 5 m deep. Dow (1970) estimates that the middens originally contained 1.5 billion commercial size oysters. By any estimate, the middens were huge. Much of the Whaleback midden was mined for chicken feed, lime and road material in the 1880’s. Castner (1950) gives a good review of this activity with original photographs. Castner also remarks on oyster shells from the Whaleback midden that measure nearly 20 inches in length.

The sheer size of the Damariscotta middens brought early and wide attention. There was much speculation on their origin from a geological upheaval to the site being the location of the lost city of Norumbega. Tens of papers and stories were published in the 19th and early 20th centuries. Most of these are quite fanciful or involve out-dated concepts and, therefore, they are not considered here.

The most authoritative consideration of the formation and timing of the Damariscotta River middens is that of Sanger and Sanger (1997). These archeologists

used radiocarbon dated shells from deep within the Glidden midden and human artifacts collected from the Whaleback midden in the 1880's by antiquarians systematically searching for artifacts during the mining operations. Some of the artifacts are upwards of 4,000 years old and probably predate the establishment of the middens. The authors believe it is more likely that oysters colonized the area once a sill above the towns of Newcastle and Damariscotta was overtopped by the rising sea-level (see Leach above). Dated artifacts indicate that this may have happened 2,000 to 3,000 years ago whereas the oldest radiocarbon dates from shells specify about 2,400 yr bp. Humans then utilized the resource, probably on a seasonal basis, and the middens built up over hundreds of years. The evidence also suggests that the middens ceased to grow about 1,000 yr bp, well before the appearance of Europeans. The authors suggest that the continuing sea-level rise increased the salinity and ultimately allowed the immigration of oyster predators. They state that no oysters survive in the area today although, as we will see below, two other nearby locations still have surviving oysters.

Another potential source of information on this period could be the related anthropological literature. Anthropologists try to describe the culture and habits of the native peoples. We have read some of this literature but find that it needs further examination before it can be used. For example both Speck (1940) and Prins and McBride (2007) describe natives having a diet that included oysters in Penobscot Bay and the Mount Desert region, respectively. They are not specific about places or times but the archeological examination of shell heaps in those areas do not find oyster shells and the Abbe Museum on Mount Desert has no evidence of oyster utilization. Finally, Faulkner and Faulkner (1987) state that oysters were not found at Pentagoet (present day Castine) in the 17th century. This is a subject for further research.

Historical Evidence

Historical evidence is based on the written or spoken word. It is available from the time of the arrival of Europeans in New England until the present. The period is of little interest to geologists or archeologists, especially after 1800 or so, and hence has not been comprehensively studied. We describe below what we have learned to date in roughly chronological order. It should be noted that during this period the emphasis of most professional investigators was on the oyster as a commercial resource.

The earliest written record we have found to date involves Weymouth's 1605 cruise to our shores (Rosier 1906). It describes many natural features of the region including their penetration up the St. George River and the finding of oysters. Files in the Davistown Museum contains information on the Popham colony. One quotes a man named Gilbert who, in 1607, wrote that "their men found oysters there, nine inches long and heard of others twice as big". These oysters were from the Damariscotta River. The bigger ones were from the Sheepscot and the files, perhaps written in 1895, say the "big fat fellows still grow" there. Materials from this period need to be examined further.

Oysters must have been abundant in the St. George and Oyster Rivers in the towns of Warren and Thomaston in mid-coast Maine in historic times. Eaton (1877) reports that "in early times" vessels from Portsmouth and elsewhere carried away complete cargoes of oysters. The selectmen of the town of Warren, in 1796, imposed conditions on the taking of oysters by people from away. The town books show income from the oyster fishery from 1804 to 1813. Eaton notes the oyster population was in

decline during this period perhaps because of sawdust from the mills or “other causes not ascertained”.

Goode (1879) presents a catalog of specimens exhibited by the Smithsonian Institution and the US Fish commission in Philadelphia in 1876. These items are now in the US National Museum (E.E. Strong, Pers. Comm. 2014). Oysters shells from the Damariscotta and Sheepscot are included with the descriptor “Indigenous oyster, now extinct”. Just two years later, Ingersoll (1881) presents an account of “the natural beds of Sheepscot Bridge, Maine”. He says the surviving populations in the Sheepscot and Dyer Rivers are now small but had once been abundant from below the falls in the main stem of the Sheepscot to a point three miles upriver and “chief of all, a point about one and a half miles above the bridge”. Local tradition had it that 100 years before his writing smacks came from Boston to get oysters. Ingersoll doubted that tradition but does state that ca. 1870 a diver could harvest a bushel or two of oysters a day. By the time of his writing, however, he thought a peck a day would “be a good day’s work”. He describes the oysters growing to a foot or fifteen inches and being similar to the oysters of the Damariscotta. Ingersoll relates a tale of young oysters being common on the branches of a tree that had fallen into the Damariscotta River in about 1830 indicating that there must have still been a spawning population in that river.

Writing in 1890 Ganong uses his own observations, personal communications and literature (not easily available to us to review) of past and contemporary occurrences of oysters in the Gulf of Maine and eastern Canada (Ganong 1890). He notes oysters from an unknown source occur in Oak Bay in the Passamaquoddy Bay region. He speculates that they may be native. Oysters no longer occur there naturally and recent reports of their presence, ca. 2000, may have been caused by temporary storage (Arthur MacKay, Pers. Comm. 2011). Likewise a population reported near St. Andrews in Passamaquoddy Bay was actually imported in the 1950’s or 60’s (Shawn Robinson, Pers. Comm. 2011). Ganong also notes the presence of oyster shells on Sable Island and in Cole Harbour, ten miles east of Halifax. No living oysters are presently found at those sites although a 1787 report notes living oysters on Sable Island.

There was obviously ongoing interest in oyster propagation in Maine. Williamson (n.d.) records that oysters were repeatedly planted in the Belfast area but none grew due to the cold water. In 1887, Charles Burd petitioned the state legislature for exclusive rights to raise oysters in Belfast Bay. He was denied but a Captain Grindle did plant 50 bushels there to no success (Williamson 1913). Beginning in about 1903 Commissioner Nickerson and several succeeding commissioners of the Maine Department of Sea and Shore Fisheries sought to refresh the oyster industry with experimental planting along the western coast (Galtsoff and Chipman 1940, Taxiarchis *et al.* 1954). In 1906, ten barrels of oyster seed were planted in each of the York, Saco, New Meadows and Damariscotta Rivers by the Maine Department of Sea and Shore Fisheries. Experiments occurred with planting from 1908-10 at unknown locations. In 1914, 50,000 seed oysters were placed in the Damariscotta River and they survived the winter. Further experiments in the Damariscotta were done using Sheepscot River and out-of-state oysters. Nathan Thompson conducted experimental oyster plantings in Casco Bay in 1940 as did A.H. Raye in Boothbay Harbor (Galtsoff and Chipman 1940). Undoubtedly several other government and private efforts continued through these decades.

In its report for fiscal year 1904 the Bureau of Fisheries indicated that, while oysters were at one time very abundant in Maine, they were practically extinct at the time

of European settlement (Anonymous 1906). They acknowledge a scattering of large oysters and few small ones survived at Sheepscot when spat and young oysters were noticed on a dam built at Alna (Sheepscot) in 1898. The dam apparently improved the environmental conditions and by 1904 every suitable substrate was covered with oysters for several miles upstream. Galtsoff and Chipman (1940) state that the oysters flourished for several years but then declined after the mill burned and the dam was not rebuilt. Somewhat confoundingly, bills were introduced during this period to protect the Sheepscot oysters. The Committee on Shore Fisheries of the state legislature in 1905 reported on a bill entitled “An act prohibiting the taking of oysters from Dyer’s and Sheepscot rivers in the County of Lincoln”. Later, in 1909, a bill entitled “Protection of oysters in the Sheepscot and Dyer’s Rivers, Lincoln County, Maine” was passed (Galtsoff and Chipman 1940). This bill gave the selectmen of surrounding towns the authority to give permits for the taking of only one bushel of oysters per week per person.

During the year 1904 the US Bureau of Fisheries also surveyed the Maine coast from Portsmouth, NH to Rockland, ME at 59 locations (Anonymous, 1906). They concluded that only three sites would support oysters, Great Bay NH, behind the dam at York Harbor and behind the dam at Sheepscot, but thought none of these areas had sufficient feed to grow market quality oysters.

In contradiction to the above paragraphs, Commissioner Donahue of the Maine Department of Sea and Shore Fisheries reported that 3,000 bushels of oysters were taken from the Sheepscot River in 1910. Furthermore he added that the oysters were showing “splendid growth” and were spreading up and down the river for three to five miles (Taxiarchis *et al.* 1954).

Oysters in Maine are most successful during periods of warm water temperatures that seem to occur in cycles (Dow n.d.). There was such a warm period in the years 1908 to 1913 (Welch 1977) and Dow attributes the year-classes of 1908-1910 to the successful oyster harvest in the Sheepscot River in subsequent years (Dow, n.d., Taxiarchis *et al.* 1954). These strong year-classes seem to have echoed through the decades as Dow (n.d.), working in 1954, found survivors from the 1931-1933 and 1937 year classes that were most likely derived from the 1908-1910 year-class. Another warm period from 1947-1960 allowed the fishery to revive. Taxiarchis *et al.* (1954) report that several hundred bushels of oysters were landed from the Sheepscot River in 1954. In 1964, Harriman noted that the oyster population in the Sheepscot was dominated by the 1955 year-class with limited recruitment from the 1962-64 year-classes (Harriman, 1964). He also opines that this clean river has been “virtually denuded by a recent and intense fishery”. Note that these authors are concerned about commercial harvest and not the survival of the populations and their ecological services. Obviously, developments in the early 20th century need to be investigated further to get an accurate portrayal of the health and survival of these oyster populations. The continued survival of the oysters at Sheepscot Village has been confirmed in the 1950’s and 1970’s by Stickney (1959) and Larsen and Doggett (1978), respectively.

Cowger (1975) lists two native populations in Maine. One is located in the Piscataqua River on the New Hampshire border and is not considered in this report. The other is in the Marsh River and Deer Meadow Brook, a tributary of the upper Sheepscot River estuary. Cowger considered this to be the northernmost U.S. native oyster population and its existence resulted in the site being registered by the Maine Critical Areas Program (Cowger 1975). The oyster, together with a concentration of other natural

attributes in this undeveloped and pristine site, led to its nomination as a NOAA estuarine sanctuary (MSPO, 1981). The oyster population is undoubtedly the largest in mid-coast Maine. Taxiarchis *et al.* (1954) surveyed the area and found oysters near the railroad bridges pictured in Fig. 3 and in Deer Meadow Brook upstream of the second bridge. Notably, they did not find oysters in the stretch between the bridges. Ricker (Pers. Comm. 2011) also found large oysters near the bridges ca. 1968-70. In 2008, Larsen and Barker (unpublished) did a video survey at 12 stations in the Marsh River and Deer Meadow Brook and viewed oysters at stations 11, 8, 2, 3, 4, and sparsely at 7 (Fig.3). Good video footage was collected by John Lindsay and the NOAA Media Center in 2010. Currently there is still a limited harvest in the Deer Meadow Brook (Jon Lewis, Pers. Comm) and when market conditions are right poaching has been noted in the Marsh River (Dan White, Pers. Comm. 2011).

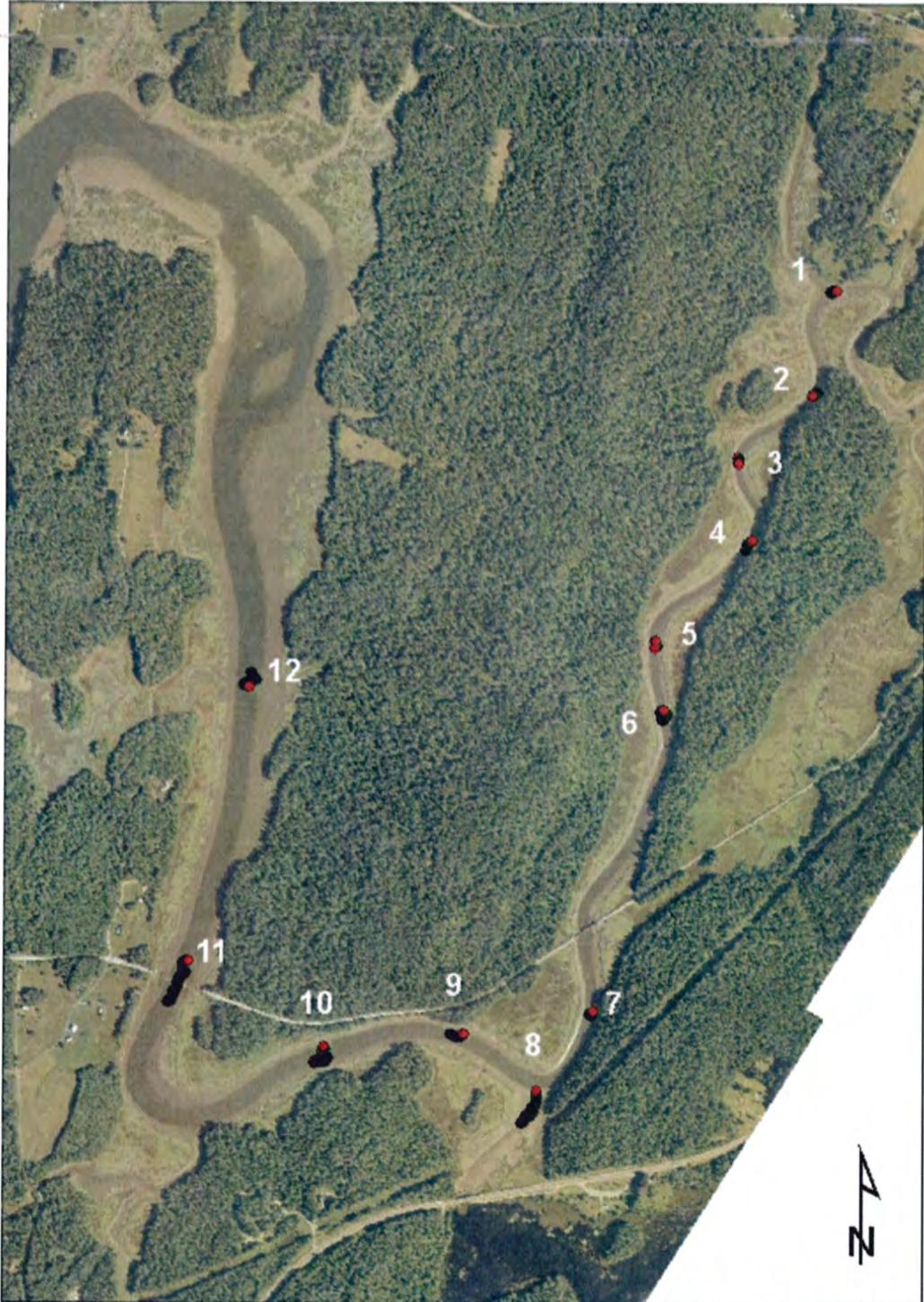
Another Sheepscot estuarine site that has recently yielded an oyster is Montsweag Brook in Westport. Kulik (1975) found a 22.1 cm oyster there in 1974. Dow believed that the oyster was from the strong year-classes of the mid-1950's and local residents stated that oysters had been present but not abundant in past years in Montsweag Bay.

There is little written about the survival of oysters in the Damariscotta system in the last 100 years. Castner (1950) notes a couple of times that the oysters disappeared from the Damariscotta River at about the time of the arrival of Europeans in the early 1600's. Sanger and Sanger (1997) state that the Damariscotta middens stopped growing about 1,000 yr bp. And they imply the demise of the oyster in the Damariscotta River. In contradiction to these conclusions we have Ingersoll's reference to oyster spat being found on a fallen tree in the 1830's (Ingersoll 1881). Cushman (1882), writing in 1852, recounts a conversation with Captain Glidden that "within the period of his remembrance a bushel of oysters have been taken out of this creek in a single tide". The creek was Oyster Creek on the east side of Great Salt Bay, part of the upper Damariscotta River, less than two kilometers from the giant middens. Castner (1950) also cites two places in Great Salt Bay where oysters occurred in the late 19th and early 20th centuries. These are at Oyster Creek on the eastern side of the bay and at Little Oyster Creek nearby Oyster Creek. He notes that in 1895 sufficient oysters were collected from Oyster Creek to supply a men's supper at the Damariscotta Baptist Church.

From a series of interviews it is possible to establish further the survival of oysters in the upper Damariscotta system and their continuity with earlier documented populations. That is, these are native populations and not simply byproducts of the oyster aquaculture industry of the 1970's. We need to note, of course, with the widespread distribution of introduced oyster stock, that genetic studies are needed to document the "nativeness" of any population. Furthermore, oyster larvae spend two to three weeks moving with the tidal water, therefore, these populations in close proximity are undoubtedly panmictic and also related to the oysters making up the large middens. We have established the survival of the two populations mentioned by Castner (1950). Oyster Creek was so named by 1659 so we can assume there were oysters present at that time. Arthur Jones, a 95 year old native, remembers oysters on and around the bridge over Oyster Creek in the early and mid 1920's (Arthur Jones, Pers. Comm. 2013). They were still present in the 1950's (Keith Plummer, Pers. Comm. 2013) and in the 1970's before the advent of aquaculture (Gretchen Hull, Pers. Comm. 2012). The other site in Great Salt Bay with a surviving native oyster population is at Damariscotta Mills where the outflow

of Damariscotta Lake enters the bay. Here the population was undoubtedly impacted by the

Station Sequence - Deer Meadow and Marsh River Survey - 11-21-2008



11-24-2008 SB

0 125 250 500 Meters

Fig. 3. Marsh River and Deer Meadow Brook and stations occupied by Larsen and Barker (unpublished).

several mills located there in the 19th century. The building of a railroad causeway in 1870, however, improved the habitat and the oysters persevered. The late Keith Plummer, Sr. remembered seeing oysters in the area in the 1920's (Keith Plummer, Pers. Comm.) and they still persist (Dan White, Pers. Comm.).

A couple of other observations can be made. There is a chance that some oysters might survive in the St. George River (Sam Chapman, Pers. Comm. 2013) although none have been seen for ten years (Mike Young, Pers. Comm. 2011). In an unspecified report that we haven't seen, it is stated that some oysters were present in the Union River in 1900 (Mark Honey, Pers. Comm. 2009).

Synopsis of the history of the oyster in Maine

At the end of the last glaciation ocean waters covered the present coastal zone and the fauna was characterized by cold-water species. As the land rebounded from the depression by the glacier, the land rose and the relative sea-level was tens of meters lower than at present. Much of the continental shelf was emergent and bathed by warm ocean water from the south. Oysters and other warm water fauna moved northward until distributed continuously from the mid-Atlantic to the Gulf of St. Lawrence. As the Gulf of Maine warmed, oysters moved in and became quite abundant along the coast from Cape Cod to the Minas Basin and around the coast of Nova Scotia. As sea-level rose and the tidal range increased many areas became unsuitable for oyster reproduction and survival. Over two to three thousand years the oyster's range became more restricted and disjunct from other population centers to the north and south. Most of this retraction occurred before the arrival of Europeans so we can be confident that, except in a small number of situations, the decrease was natural. Declines in oyster populations, and diminution of their range, has continued in historic times. The potential for an oyster resurgence, however, is evidenced by spikes in abundance and revived harvests that occur during warm periods or when the environment is modified as by an impoundment.

Current Status of Native Oyster Populations in Maine

A handful of relict Eastern oyster populations survive in mid-coast Maine. They have been isolated from the main populations for perhaps 4,000 years and from one another for shorter periods. They occur, with other species of Virginian origins, in isolated warm water pockets known as Virginian refugia. Unfortunately, there has been very limited documentation of their locations and characteristics, knowledge needed to support protection and restoration efforts.

There are approximately seven named sites where oysters are known, or are believed, to survive. We have visited all of them but we were not able to accomplish any analytical documentation. Galtsoff and Chipman (1940) believed, as we do, that there are more undiscovered sites that harbor oysters presently or did in the not too distant past.

The best known sites are in the complex Sheepscot estuary and include the area around Sheepscot Falls, the Dyer River, the Marsh River, Squam Creek and the Montsweag Bay area. The sill that forms Sheepscot Falls and the basin upstream of it supported a large oyster population in the past followed by a period of decline. Presently, oysters are supposedly fairly abundant on the sill, in the basin and on the shore of the

west bank of the Sheepscot River across from the falls (Doug, no last name available, Pers. Comm.). Because of strong currents and poor visibility this is a difficult place to survey but it is important to do so. Just above the falls is the mouth of the Dyer River. We have qualitatively surveyed this area (2014) and found abundant oysters on rocks in the shallow water. The proximity to Sheepscot Falls means that this is one population. We reconnoitered further upriver, where oysters were reported to be abundant in the early 20th century, and found no oysters. Furthermore, the salinity did not seem adequate to support oysters in spite of the early reports.

The Marsh River, a tributary of the Sheepscot, has a large, healthy oyster population. At Station 4 in Deer Meadow Brook (Fig. 3) the oysters are dense and growing vertically. Recent growth can be observed at the edges of shells. Through this stretch of the river most hard surfaces harbor oysters and some actually grow on sandy bottoms. Taxiarchis *et al.* (1954) found no oysters between the railroad bridges (Fig. 3) in 1954. In 2013, a preliminary survey by the Maine Department of Marine Resources found oysters so thick in that reach that it was difficult to clear the quadrats (Marcy Nelson, Pers. Comm. 2013). Certainly the population is expanding. Further evidence for expansion is reported by Larsen *et al.* (2013) who documented the movement of oysters into Sherman Marsh after the causeway across the Marsh River was removed in 2005. Oysters are now found on most suitable substrates throughout the marsh.

Lower in the Sheepscot estuary there have been scattered reports of the presence of oysters. They have been reported on the causeway at Squam Creek (Chris Hilton, Pers. Comm. 2011) and Sam Chapman (Pers. Comm. 2013) took out a lease for an oyster grow-out area because of the presence of native oysters. Indeed, Chapman and Richard Clime (Pers. Comm. 2013) note that early oyster aquaculturalists looked for the presence of Virginian refugia as a criterion for selecting lease sites. Across the Sheepscot from Squam Creek is Montsweag Bay where Kulik (1975) previously found a native oyster. Sam Chapman (Pers. Comm. 2013) has heard recent reports of the presence of oysters in Montsweag Brook and/or Chewonki Creek. These areas need investigation.

In the Damariscotta system, Seth Barker (Pers. Comm. 2014) reports observing healthy oysters of various sizes, including spat, at the mouth of Oyster Creek in 2013. Oysters are also still present in Damariscotta Mills (Chris Hilton, Pers. Comm. 2011).

Finally, there is a chance that some native oysters survive in the upper St. George River (Sam Chapman, Pers. Comm. 2013).

Notes on Related Activities

The search for information on the history and current status of the Eastern oyster in Maine produced several synergistic opportunities that we felt would be beneficial to the overall project. Of note was the discovery that the return of tidal flow into Sherman Marsh after 70 years created 2.5 linear km of new potential habitat area to the relict oyster population of the Marsh River. Oysters recruited to the new habitat quickly, demonstrating the restoration potential of isolated, relict populations. The resultant larger population size and areal extent should provide increased stability and survivability of the oyster and its associated community. These observations have implications for both the restoration potential of relict oyster populations and the consequences of climate change. With collaborators from the University of Southern Maine and the Sea Grant Program at the University of Maine, we documented this recruitment and prepared a manuscript that was recently published in the *Northeastern Naturalist* (Larsen *et al.* 2013).

Working with staff of the Maine Department of Transportation and Maine Sea Grant, we continue to document the occurrence of intertidal oysters in the Marsh River system. Due to extreme low temperatures and ice scour, oysters were believed not to survive in the intertidal in our region. Capone *et al.* (2008) noted limited occurrences of oysters in Maine under thick rockweed low in the intertidal zone and asked if this was a new phenomenon. Our observations show adult oysters rather high on exposed intertidal ledges. Interviews with several retired shellfish biologists failed to find any previous records of this sort. We have searched the unpublished manuscripts of former Maine Department of Marine Resources investigators and found no references to intertidal oysters. We continue to research and analyze tidal and temperature data to better describe and understand the factors at work.

A basic question concerning the survivability of relict oyster populations is the frequency and intensity of spawning and spat settlement. For three years we put out a limited number of spat collectors in the Marsh River or Sherman Marsh. During this time not one settled oyster spat was collected. Several factors influence the success of spat collectors including materials used, location, fouling, predation, etc. This exercise has shown that a more comprehensive and sustained effort than has been feasible to date is needed to document oyster recruitment.

During our investigations we discovered that the Eastern oyster had not been barcoded. The Barcode of Life Data Systems (BOLD) of the Biodiversity Institute of Ontario at the University of Guelph agreed to process three populations for us. With the cooperation of Dr. Roger Mann of the Virginia Institute of Marine Science and Dr. Gretchen Hull, director of the Gulf Aquarium and Marine Station, Cheticamp, Nova Scotia, we procured samples of native oysters from Bras d'Or Lakes, Nova Scotia, the Marsh River, Maine and the Chesapeake Bay, Virginia. Whereas the conservative gene used in barcoding showed little difference between the populations, we now have frozen specimens and extracts that can be analyzed to determine the degree of genetic isolation, if any, between these far-ranging populations. We will archive the samples until funding becomes available.

As noted above, there are three theories in circulation as to why oyster populations declined along the Maine coast. Briefly, they are 1) rising sea level caused cool seawater to intrude into oyster habitat resulting in water temperatures insufficient for gonad maturation and spawning; 2) rising sea level caused saline seawater to intrude into oyster habitat allowing the invasion of oyster predators that exterminated populations; and 3) siltation, sawdust and toxics from industrialization after the arrival of Europeans smothered the oyster beds. Since so many sites became devoid of oysters long before the colonial period, it seems likely that theory three was only a factor in localized areas. A series of dated oyster shells (actually digital images) provided by Arthur Spiess of the Maine Historic Preservation Commission gave us the opportunity to collaborate with Dr. Roger Mann of the Virginia Institute of Marine Science. After some discussion and a brief examination of the images it was concluded that the shells, without corresponding salinity information, could not tell us much. Most predation occurs on juvenile oysters that are not well represented in the middens. Furthermore, predation occurs by boring through the shells (oyster drills) or more commonly at the edge of the valves (flat worms and small snails). Since the shells have been manipulated in harvest and in the subsequent accumulation, i.e. thrown about, walked upon, etc., there will be no reliable evidence of edge effects. Furthermore, drills cannot penetrate thick adult shells. Dr. Mann was

fascinated with the history of native Maine oysters and has expressed an interest in further collaboration.

Recommendations

Native Maine oysters provide valuable ecological services and may provide a divergent genetic resource that will be significant in the face of climate change. The oyster communities were characteristic of upper estuaries in centuries past. This is the same habitat area where the first signals of climate change are likely to be observed along the coastal zone because the freshwaters entering the estuaries will warm faster than seawater. Understanding the structure and function of these oyster populations will provide a sensitive sentinel of climate change. In order to realize this potential, the location and characteristics of the relict communities must be documented. Information developed will serve as the basis for the protection, restoration and expansion of these unique oyster populations, their associated community and the valuable ecological services they provide.

Whereas we have come a long way, there is more to be done. The search of older documents and archeological and anthropological materials could help locate other past oyster sites that could again become productive with restoration. Galtsoff and Chipman (1940) believed there were still undiscovered former sites and Harriman (1964) recommended an effort “to discover the locations which are suitable but have not been populated.” Two major sources that we were unable to search thoroughly are the Maine State Library and the Maine Legislative Archives. Another developing source are dictionaries of local Native American languages that are being assembled. In addition, the finding of Native American place names related to oysters, or the lack thereof, would be insightful. We also have identified several more people we wish to interview.

Once actual and potential oyster habitats have been identified, proper surveys of the populations and environmental characteristics of the sites will provide necessary information needed for evaluating the prospects for recovery or restoration. Such surveys should include population age structure, health of the individuals, salinity and temperature records for the sites together with substrate conditions. Divers and/or ROV’s will be necessary for the population and habitat studies. Recording instruments could be placed at promising sites to describe the physical milieu. We also recommend a more concerted program to document reproductive potential. Individual oysters should be sampled for reproductive ripeness. A systematic effort involving the deployment of spat collectors should be instituted to evaluate the actual reproductive and recruitment potential. The latter could be enhanced by a series of plankton tows in search of easily identifiable oyster larvae in the water column (Herb Hidu, Pers. Comm. 2012). Many of these tasks can be accomplished using volunteers and/or students and the results could be combined into a habitat suitability index to rank the sites.

Finally, there are compelling questions that can be addressed by the rapidly evolving (no pun intended) genomic science. How distinct are the various oyster populations? When did the gene flow between populations cease? Does the relict oysters’ genetic makeup provide a unique environmental fitness to survive in Maine estuaries? To what degree has there been cross-fertilization with the introduced aquacultural oysters? There are now people and procedures available in Maine to address these and other issues related to genetic fitness.

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Literature Cited

- Anonymous. 1906. Report of the Commissioner of Fisheries to the Secretary of Commerce and Labor for the Fiscal Year Ended June 30, 1905. Government Printing Office, Washington, D.C.
- Beck, M.B., R.D. Brumbaugh, L. Airoidi, A. Carranza, L.D. Coen, C. Crawford, O. Defeo, G.J. Edgar, B. Hancock, M. Kay, H. Lenihan, M.W. Luckenbach, C.L. Toropova and G. Zang. 2009. Shellfish Reefs at Risk: A Global Analysis of Problems and Solutions. The Nature Conservancy, Arlington, VA. 52 pp.
- Belknap, D.F., B.G. Andersen, R.S. Anderson, W.A. Anderson, H.W. Borns, Jr., G.L. Jacobson, J.T. Kelley, R.C. Shipp, D.C. Smith, R. Stuckenrath, Jr., W.B. Thompson and D.A. Tyler. 1987. Late quaternary sea-level changes in Maine. In: Nummedal, D., Pilkey, O.H. and Howard, J.D., (eds.) Sea-level Fluctuation and Coastal Evolution, SEPM Society of Economic Paleontologists and Mineralogists Special Publication 41, p. 71-85.
- Bleakney, J.S., and D. Davis. 1983. Discovery of an undisturbed bed of 3800 year old oysters (*Crassostrea virginica*) in Minas Basin, Nova Scotia. Proc. N.S. Inst. Sci. 33:1-6.
- Bousfield, E.L., and M.L.H. Thomas. 1975. Postglacial changes in distribution of littoral marine invertebrates in the Canadian Atlantic region. Proc. Nova Scotia Inst. Sci. 27, Supplement 3, 47-60.
- Campbell, D.E. 1986. Process variability in the Gulf of Maine – A macroestuarine environment. Pp. 261-275. In D.A. Wolfe (Ed.) Estuarine Variability. Academic Press, Orlando, FL. 509 pp.
- Castner, H. W. 1950. A story of the mystifying, prehistoric shell heaps of the Damariscotta River. Castner files, Skidompha Library, Damariscotta, ME.

- Coen, L.D., R.D. Brumbaugh, D. Bushek, R. Grizzle, M.W. Luckenbach, M.H. Posey, S.P. Powers and S.G. Tolley. 2007. Ecosystem services related to oyster restoration. *Mar. Ecol. Prog. Ser.* 341:303-307.
- Capone, M., R. Grizzle, A.C. Mathieson and J. Odell. 2008. Intertidal oysters in Northern New England. *North. Natur.* 15:209-214.
- Cowger, J. 1975. Natural Occurrence of the American Oyster, *Crassostrea virginica*, in Maine and its Relevance to the Critical Areas Program. Planning Report Number 4, Maine State Planning Office, Augusta, ME 04333. 21pp.
- Cushman, D.Q. 1882. *The History of Ancient Sheepscot and Newcastle.* E. Upton and Son, Printers, Bath, ME. 458pp.
- Denys, N. 1971. *Coasts of North America (Acadia) 1672.* Champlain Society, Ontario, ON. 625pp.
- Dow, R.L. n.d. Effects of climatic cycles on the relative abundance and availability of commercial marine and estuarine species. Unpublished manuscript, Department of Marine Resources Library, West Boothbay Harbor, ME. 11pp.
- Dow, R.L. 1965. Fossils, middens and sea water temperatures. Unpublished manuscript MA 166, No. 150. Department of Marine Resources Library, West Boothbay Harbor, ME. 3pp.
- Dow, R.L. 1977. Problems of comparative ecology of post-glacial and modern marine organisms. Unpublished manuscript MA 166, No. 222. Department of Marine Resources Library, West Boothbay Harbor, ME. 2pp.
- Doyle, R.A., Jr., J.R. Petersen and N.D. Hamilton. 1985. A late archaic shell midden on Great Mosher Island, Casco Bay, Maine. *Bull. Maine Archaeo. Soc.* 25:41-50.
- Eaton, C. 1877. *Annals of the Town of Warren in Knox County, Maine.* Masters and Livermore. Hallowell, ME. 47pp.
- Emery, K.O., R.L. Wigley and M. Rubin. 1965. A submerged peat deposit off the Atlantic coast of the United States. *Limnol. Oceanogr. Spec.* 10:R97-R102.
- Faulkner, A., and G.F. Faulkner. 1987. *An Archeological Portrait of the Acadian Frontier.* Occasional Publications in Marine Archeology, No. 5, Spec. Pub., New Brunswick Museum. 330 pp.
- Galtsoff, P.S. 1964. The American Oyster *Crassostrea virginica* Gmelin. *Fish. Bull.* 64. 480 pp.

- Galtsoff, P.S., and W.A. Chipman, Jr. 1940. Oyster Investigations in Maine. Unpublished Report, U.S. Fish and Wildlife Service, Washington, D.C. 25pp. plus appendices.
- Ganong, W.F. 1890. Southern invertebrates on the shores of Acadia. Trans. Roy. Soc. Can. VII:167-185.
- Goode, G.B. 1879. Catalogue of the Collection to Illustrate the Animal Resources and the Fisheries of the United States. Government Printing Office, Washington, D.C.
- Grant, D.R. 1970. Recent coastal submergence of the Maritimes Provinces, Canada. Can. J. Earth Sci. 7:676-689.
- Greenberg, D.A., W. Blanchard, B. Smith and E. Barrow. 2012. Climate change, mean sea level, and high tides in the Bay of Fundy. Atmosphere-Ocean 50:261-276.
- Harriman, D.M. 1964. American oysters (*Crassostrea virginica*) in Maine. Unpublished report MA 166 no. 325. Department of Marine Resources Library, West Boothbay Harbor, ME. 4 pp.
- Ingersoll, E. 1881. The History and Present Condition of the Fishery Industries: The Oyster-Industry. Government Printing Office, Washington, D.C.
- Kelley, J.T., D.F. Belknap and S. Claesson. 2010. Drowned coastal deposits with associated archaeological remains from a sea-level "slowstand": Northwestern Gulf of Maine. Geology 38:695-698.
- Kulik, B. 1974. Oyster discovery in Montsweag Bay, Maine. The Maine Biologist 7:1.
- Larsen, P.F. 1975. A preliminary checklist, with annotations, of potential associates of the American oyster, *Crassostrea virginica*, in New England. Publ. No. 9, The Res. Inst. Gulf of Maine, S. Portland, ME. 42 pp.
- Larsen, P.F. 1985. The macrobenthos associated with the oyster reefs of the James River estuary, Virginia, USA. Intern. Rev. ges. Hydrobiol. 70: 797-814.
- Larsen, P.F., and L.F. Doggett.. 1978. Benthos Study of the Sheepscot River Estuary. Technical Report Number 10-78. Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, ME. 555pp.
- Larsen, P.F., K.A. Wilson and D. Morse. 2013. Observations on the expansion of a relict population on Eastern oysters (*Crassostrea virginica*) in a Maine estuary: Implications for climate change and restoration. North. Natur. 20:N28-N32.
- Leach, P.A. 2007. Marine Geoarchaeological Investigation of Damariscotta River, Maine, USA. MS Thesis, University of Maine, Orono. 164 pp.

- Loosanoff, V.L. 1965. The American of Eastern Oyster. Circular 205. Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service, Washington, D.C. 37 pp.
- Maine State Planning Office. 1981. Application for Federal Funds to Establish the Maine Coast Estuarine Sanctuary. Maine State Planning Office, Augusta, ME 04333. 32pp.
- Medcof, J.C., A.H. Clarke, Jr. and J.S. Erskine. 1965. Ancient Canadian east-coast oyster and quahaug shells. *J. Res. Bd. Can.* 22:631-634.
- Merrill, A.S., K.O. Emery and M. Rubin. 1965. Ancient oyster shells on the Atlantic continental shelf. *Science* 147:398-400.
- Newell, R.I.E., and E.W. Koch. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries* 27:793-806.
- Prins, H.E.L., and B. McBride. 2007. Anticou's Island Domain: Wabanaki People at Mount Desert Island, 1500-2000. National Park Service, Boston. 618 pp.
- Rosier, J. 1906. A True Relation of the Voyage of Captaine George Weymouth, 1605. Pp. 353-394 in H.S. Burrage (ed.), *Early English and French Voyagers, 1534-1608*. Scribners, New York.
- Sanger, D., and M. Sanger. 1986. Boom and bust on the river: The story of the Damariscotta oyster shell heaps. *Arch. East. North Amer.* 14:65-78.
- Sanger, D., and M. Sanger. 1997. The Damariscotta oyster shell heaps. *North. Natur.* 4:92-102.
- Shaw, J., P. Gareau and R.C. Courtney. Palaeogeography of Atlantic Canada 13-0 kyr. 2002. *Quarter. Sci. Rev.* 21:1861-1878.
- Shumway, S. E. 1996. Natural Environmental Factors. Chap. 13 in *The Eastern Oyster Crassostrea virginica*. V.S. Kennedy, R.I.E. Newell and A.F. Eble (eds.). Maryland Sea Grant. College Park.
- Speck, F.G. 1940. Penobscot Man: The Life History of a Forest Tribe in Maine. University of Pennsylvania Press, Philadelphia. 325 pp.
- Stickney, A.P. 1959. Ecology of the Sheepscot River Estuary. U.S. Fish and Wildlife Service, Special Scientific Report – Fisheries No. 309. 21 pp.
- Taxiarchis, L.N., R.L. Dow and F.T. Baird. 1954. Survey of the Oyster Beds (*Crassostrea virginica*) in the Sheepscot River and its Tributaries. Sheepscot Area Report No. 1. General Bulletin #7, Department of Sea and Shore Fisheries, Augusta, ME. 8pp.

- Welch, W.R. 1977. Monthly and annual means of surface sea water temperature Boothbay Harbor, Maine 1905 through 1977. Unpublished manuscript MA 166, No. 582. Department of Marine Resources Library, West Boothbay Harbor, ME. 6pp.
- Wells, H.W. 1961. The fauna of oyster beds, with special reference to the salinity factor. *Ecol. Monogr.* 31:239-266.
- Whitmore, F.C., Jr., K.O. Emery and D.J.P. Swift. 1967. Elephant teeth from the Atlantic continental shelf. *Science* 156:1477-1481.
- Williamson, J. n.d. The History of the City of Belfast, Maine from it First Settlement in 1770 to 1875. Vol. I. Picton Press, Rockport, ME.
- Williamson, J. 1913. The History of the City of Belfast in the State of Maine, Vol. II 1875-1900. Houghton Mifflin Company.
- Wong, M.C., C.H. Peterson and M.F. Piehler. 2011. Evaluating estuarine habitats using secondary production as a proxy for food web support. *Mar. Ecol. Prog. Ser.* 11:11-25.
- Zu Ermgassen, P.S.E., M.D. Spaulding, R.E. Grizzle and R.D. Brumbaugh. 2013. Quantifying the loss of marine ecosystem service: Filtration by the Eastern oyster in US estuaries. *Est. and Coasts* 36:36-43.

Appendix 1

Interviews Conducted – The following is a partial list of people were interviewed one or more times. It does not include people with no information or interest

Ronald Aho - Maine Department of Marine Resources
Augusta, ME

John Banks - Penobscot Nation Director of Natural Resources
Indian Island, ME

Seth Barker - Retired Maine Department of Marine Resources
Boothbay, ME

Bruce Bourque - Archeologist, Maine State Museum
Augusta, ME

Heidi Bray - Maine Department of Marine Resources
West Boothbay Harbor, ME

Sam Chapman - Shellfish Biologist and Oyster Aquaculturist
Waldoboro, ME

Julia Clark - Abby Museum
Bar Harbor, ME

Richard Clime - Oyster Aquaculturist, Coastal Enterprises
Brunswick, ME

Arlene Cole - Local Historian
Newcastle, ME

Steven Crawford - Passamaquoddy Tribal Environmental Office
Pleasant Point, ME

Chris Davis - Oyster Aquaculturist, University of Maine
Orono, ME

Daniel Devereaux - Town of Brunswick Marine Warden
Brunswick, ME

Richard Ferren - Local Historian
Warren, ME

Walter Foster - Retired Shellfish Biologist
Friendship, ME

James Francis - Penobscot Nation Historian
Indian Island, ME

Herbert Hidu - Retired Shellfish Biologist
Wiscasset, ME

Chris Hilton - Marine Patrol Warden
West Boothbay Harbor, ME

John Hilton - Local Historian
Newcastle, ME

Mark Honey - Journalist
Ellsworth, ME

Gretchen Hull - Environmental Scientist
Newcastle, ME

Arthur Jones - Local Historian
Newcastle, ME

Brandon Kulik - Environmental Scientist, Kleinschmidt Group
Pittsfield, ME

Peter Lawton - Fisheries and Oceans, Canada
St. Andrews, NB

Jesse Leach - Aquaculturist
Penobscot, ME

Jon Lewis - Maine Department of Marine Resources
West Boothbay Harbor, ME

David Libby - Maine Department of Marine Resources
West Boothbay Harbor, ME

Sandy Macfarlane - Retired Shellfish Manager
Duxbury, MA

Arthur MacKay - Environmental Scientist
Bocabec, NB

Roger Mann - Virginia Institute of Marine Science
Gloucester Point, VA

Dana Morse - UMaine Cooperative Extension
Walpole, ME

Jean McGowen - Local Historian
Georgetown, ME

Marci Nelson - Maine Department of Marine Resources
West Boothbay Harbor, ME

Bonnie Newsome – Penobscot Tribal Historic Preservation Office
Indian Island, ME

Micah Pawling - Canadian-American Center, University of Maine
Orono, ME

Steven Perrin - Town of Bar Harbor
Bar Harbor, ME

Keith Plummer – Oyster Creek landowner
Damariscotta, ME

Frank Ricker - Retired Shellfish Biologist
Winthrop, ME

Shawn Robinson - Fisheries and Oceans, Canada
St. Andrews, NB

Mary Sheldon - Local Historian
Nobleboro, ME

Stuart Sherburne - Retired Shellfish Biologist
East Boothbay, ME

Sandy Shumway - University of Connecticut
Groton, CT

Donald Soctomah - Passamaquoddy Nation
Princeton, ME

Arthur Spiess - Archeologist, Maine Historic Preservation Commission
Augusta, ME

Peter Thayer - Maine Department of Marine Resources
West Boothbay Harbor, ME

Stanley Waltz - Town of Newcastle Code Enforcement Officer

Newcastle, ME

George Weston - Local Historian
Newcastle, ME

Daniel White - Marine Patrol Warden
West Boothbay Harbor, ME

Michael Young - Marine Patrol Warden
West Boothbay Harbor, ME

Appendix 2

Partial list of organizations contacted:

Bath Historical Society

Boothbay Land Trust

Boothbay Region Historical Society

Damariscotta Historical Society

Damariscotta River Association

Georgetown Historical Society

Kennebec Estuary Land Trust

Maine Historical Society

Newcastle Historical Society

Nobleboro Historical Society

Pejepscot Historical Society

Pemaquid Historical Association

Phippsburg Land Trust

Saint Croix International Waterway Commission

Sheepscot Valley Conservation Association

Thomaston Historical Society

Warren Historical Society

Westport Historical Society