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Stable Isotopic Shifts in Late Holocene Fish Bones from Multiple Archaeological Coastal Middens in Penobscot Bay, Maine

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Stable Isotopic Shifts in Late Holocene Fish Bones from Multiple Archaeological Coastal Middens in Penobscot Bay, Maine

An Honors Thesis

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By

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To Mom for making school fun and to Dad for making science cool

Table of Contents

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Abstract

Changes to nearshore systems and food web dynamics over the past 2,400 years were assessed using stable carbon and nitrogen isotope analysis of fish bone collagen recovered from archaeological middens in Penobscot Bay, Maine. The stable isotope composition of Atlantic cod (*Gadus morhua*), winter flounder (*Pseudopleuronectes americanus*), and longhorn sculpin (*Myoxocephalus octodecemspinosus*) from seven coastal middens was compared to two modern samples: one nearshore in Penobscot Bay and one 20-30 km offshore on Georges Bank, Gulf of Maine. The ^{13}C of flounder decreased by 4‰ from 2,400 BP to the present and may reflect a prehistoric loss of eelgrass (*Zostera marina*) along Maine's coast. The ^{15}N of cod, an apex predator, decreased by 2‰ from 2,400 BP until the present, suggesting that the trophic level of cod declined. This may indicate that the population was under constant fishing pressure by indigenous people. The ^{15}N of sculpin and flounder, both mesopredators, increased between 2,400 BP and 1,000 BP, suggesting an increase in trophic level. These populations may have been released from cod predation and permitted to increase in size and abundance, allowing them to feed at higher trophic levels. The ^{15}N of all species decreased between 500 BP and the present likely indicating increased fishing pressures instigated by the arrival of western Europeans to Maine's coast. The magnitude of offsets among the ^{13}C and ^{15}N study species at each time period also decreased over time, possibly indicating that the ecological niches of omnivorous fish are smaller and may overlap in the modern Penobscot Bay system.

Table of Figures

Table of Tables

1. Introduction

1.1 Review of Stable Isotope Analysis in Ecosystem Studies

Stable isotope analysis is a powerful tool that is popular in ecosystem ecology because it can be used to track elemental cycling and energy flow at natural abundance levels (eg. Hobson and Welsh, 1992; Robinson et al., 2001). Chemical reactions can alter the stable isotope composition of substrates and products. The main causes of isotopic fractionation are isotope exchange reactions and kinetic processes (Faure, 1986**)**. No net reaction occurs in isotope exchange reactions, but isotope distribution changes occur between different chemical substances, phases, or molecules. Kinetic reactions are unidirectional processes such as those that occur with changes of state (evaporation, condensation, etc.), biologically mediated reactions (enzymatic processes), and dissociation reactions (Faure, 1986). Fractionation leads to small, but measurable, differences in environmental and biological materials (Peterson and Fry, 1987).

Many elements including carbon, nitrogen, sulfur, oxygen, and hydrogen have multiple isotopes that occur naturally in living organisms. For example, carbon has two commonly occurring stable isotopes: ^{12}C and ^{13}C. The ratio of the lighter, more abundant isotope to the heavier, less abundant isotope can be accurately measured using a stable isotope ratio mass spectrometer (Peterson and Fry, 1987).

Stable isotope analysis can be used to trace the flow of organic matter (nutrients and energy) in ecological studies because different primary producers have unique, naturally occurring isotopic signatures that are transferred to higher trophic levels in predictable patterns (Fry and Sherr, 1984; Peterson and Fry, 1987; Lajtha and Marshall, 1994; Hobson and Wassenaar, 1999; Vander Zanden and Rasmussen, 2001). The

isotopic signature of a consumer is directly dependent on the signatures of the consumer's food sources (Fry and Sherr, 1984).

Carbon isotopic analysis of organisms can be an indicator of the basal energy source of an ecosystem (Fry and Sherr, 1984; Peterson and Fry, 1987; Vander Zanden and Rassmussen, 1999). Plant species have a wide range in ^{13}C values depending on the type of photosynthesis they perform (i.e. C_3, C_4, Crassulacean Acid Metabolism (CAM), or algal plants) (Fry and Sherr, 1984). C_3 plants are less ^{13}C-enriched than C_4 plants. CAM plants are extremely isotopically variable (O'Leary, 1988). The most important factor causing these differences are the fractionations that occur during the enzymatic assimilation of carbon dioxide (CO_2). Aquatic ecosystems contain several additional primary producers including aquatic macrophytes such as kelps and seagrasses, which are generally more ^{13}C-enriched than C_3 or C_4 plants and have wide ^{13}C ranges (O'Leary, 1988).

In some cases, the isotopic signature of consumers does not directly equal that of their food source because of isotopic enrichment that occurs between trophic levels. Trophic level enrichment varies depending on the animal tissue (ie. bone collagen vs. muscle vs. blood) and isotope being analyzed (Deniro and Epstein, 1978; Tieszen et al., 1983). Typically, for each increasing trophic level, ^{15}N values increase ~3‰, ^{13}C values increase ~1‰, and ^{34}S values increase ~0-1‰ (Fry and Sherr, 1984; Fry, 1988; Hobson and Welsh, 1992; McCutchan et al., 2003). For ^{13}C, the trophic increase is most pronounced between primary producers and primary consumers because fractionation occurs during synthesis of proteins from carbohydrates; this involves many metabolic processes regulated by enzymes and can be as high as 5‰ (Fry and Sherr, 1984). Because of this variability in ^{13}C value enrichments, ^{15}N values are better indicators of trophic level (Fry, 1988).

One way of establishing baseline conditions for an ecosystem and for tracking long term ecological change is via stable isotope analysis (Fry and Sherr, 1984; Peterson, 1999). Changes to ecosystem structure and function would likely be reflected in the trophic level (N isotopic composition) and basal carbon source (C isotopic composition) of organisms inhabiting that environment (Wainright et al., 1993), such as certain predatory fishes in marine environments.

It is possible to reconstruct the diets of ancient marine organisms (which allows the vegetation of paleo-environments to be inferred) from stable isotope analysis of archaeological animal remains (**Figure 1**). This technique has been used successfully in terrestrial (eg. Fogel et al., 1997; Johnson et al., 1999; Miller et al., 2005) and marine systems (eg. Lawson and Hobson, 2000; Burton et al., 2001; Barrett et al., 2008; Misarti et al., 2009).

1.2 Characteristics of the Gulf of Maine

1.2.1 Geology, Bathymetry, Hydrology

Gulf of Maine

The Gulf of Maine (GoM), a continental shelf sea, is approximately 360 km by 230 km (90,700 km^2) and is located off the northeast coast of the United States (Uchupi, 1968). It is delineated to the east and south by underwater banks (Georges and Brown) that separate the GoM from the open ocean and is bounded by Cape Cod,

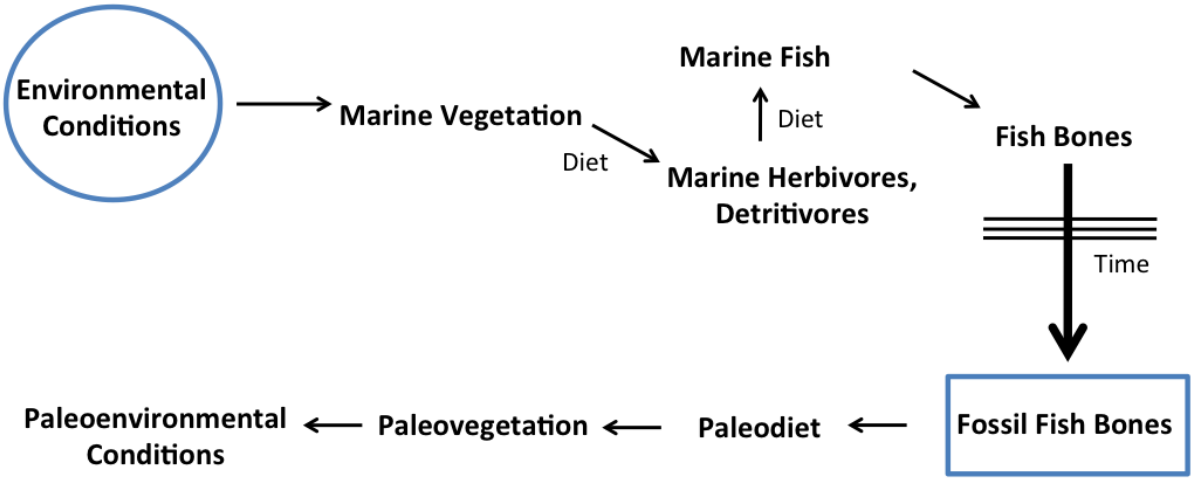

Figure 1. Schematic of Theoretical Approach
Model describing how fossilized fish bones are used as a proxy to reconstruct paleo-environmetal conditions. Modified after Fogel et al., 1997.

Massachusetts to the south and Cape Sable, Nova Scotia to the north. The GoM ranges from 9-337m deep, and it is 150m deep on average (Uchupi, 1968). The seafloor topography is made up of three main basins, Georges, Jordan, and Wilkinson Basins (~30% area of the GoM), that are surrounded by swells and flat-topped banks (~70% area) (Uchupi, 1965). The GoM fills and empties primarily from the Northeast Channel and over Georges Bank.

The Northeast Channel is a 40 km wide, 70 km long channel with a sill depth of 232m that separates the GoM from the Scotian Shelf to the east (Uchupi and Bolmer, 2008). This channel allows deep water to pass between the open ocean and Georges Bank and merges with Georges Basin to the northwest of Georges Bank. Deep slope water that has high nutrient (nitrate, silica, etc.) concentrations enters the bay through the Northeast Channel (Townsend, 1998). This deep slope water originates from two sources—the Labrador Sea slope, which brings cold, fresh water with little nutrients, and the Gulf Stream and North Atlantic Central water, which brings warmer, saline water with high nutrient concentrations. The Great South Channel is approximately 45km wide and 65km long with a sill depth of less than 80m and connects the other side of Georges Bank with the open ocean (Uchupi and Bolmer, 2008).

Georges Bank is a highly productive system located East of Cape Cod. It is approximately 150 km wide and 280 km long with a 40 m deep crest (Uchupi and Austin, 1987). Thus, it prevents warm waters from the Gulf Stream from entering the GoM. Georges Bank is important to both Canadian and American fisheries because many species spawn there (Lazzari and Tupper, 2002). Colder water and nutrients arrive to the GoM via the Labrador Current from the northeast. The turbulence of waves, more so than upwelling, causes mixing and brings nutrients to the surface (Uchupi and Bolmer, 2008).

The GoM encompasses the entire Maine coastline and is characterized by many rocky islands, some sandy beaches, and salt marshes (**Figure 2**). The current morphology is a result of deposition and erosion during the Pleistocene glacial and interglacial periods and marine processes that occurred during the Holocene (Uchupi and Bolmer, 2008). Its coast is mostly rocky because the last glaciation stripped the coast of sedimentary deposits and thus, there are few sandy beaches on Maine's coast (Uchupi and Bolmer, 2008).

The water column in different areas of the GoM has various degrees of vertical stability. Most areas of the GoM experience maximum stratification in the summer and minimum stratification in the winter. The deeper basins experience stronger stratification and therefore increased vertical stability. The western GoM has the most stable vertical water column, and Georges Bank and the southwest Scotian Shelf are the least stable regions (Jossi and Smith, 1989).

Bathymetry and tidal mixing are the dominant factors that determine the hydrology of the GoM. Flows are cyclonic around the GoM and anticyclonic around Georges Bank. There are two pronounced cyclonic gyres over Jordan Basin and Georges Basin (Xeu et al., 2000). The coastal current that forms in the GoM is divided into the Eastern Maine Coast Current (EMCC) and the Western Maine Coast Current (WMCC) (**Figure 3**). The EMCC flows offshore, away from the coast near the entrance to Penobscot Bay (Brooks and Townsend, 1989). This pattern is complicated by vertical mixing, particularly in shallow areas, and by freshwater inputs in coastal areas that increase vertical stratification.

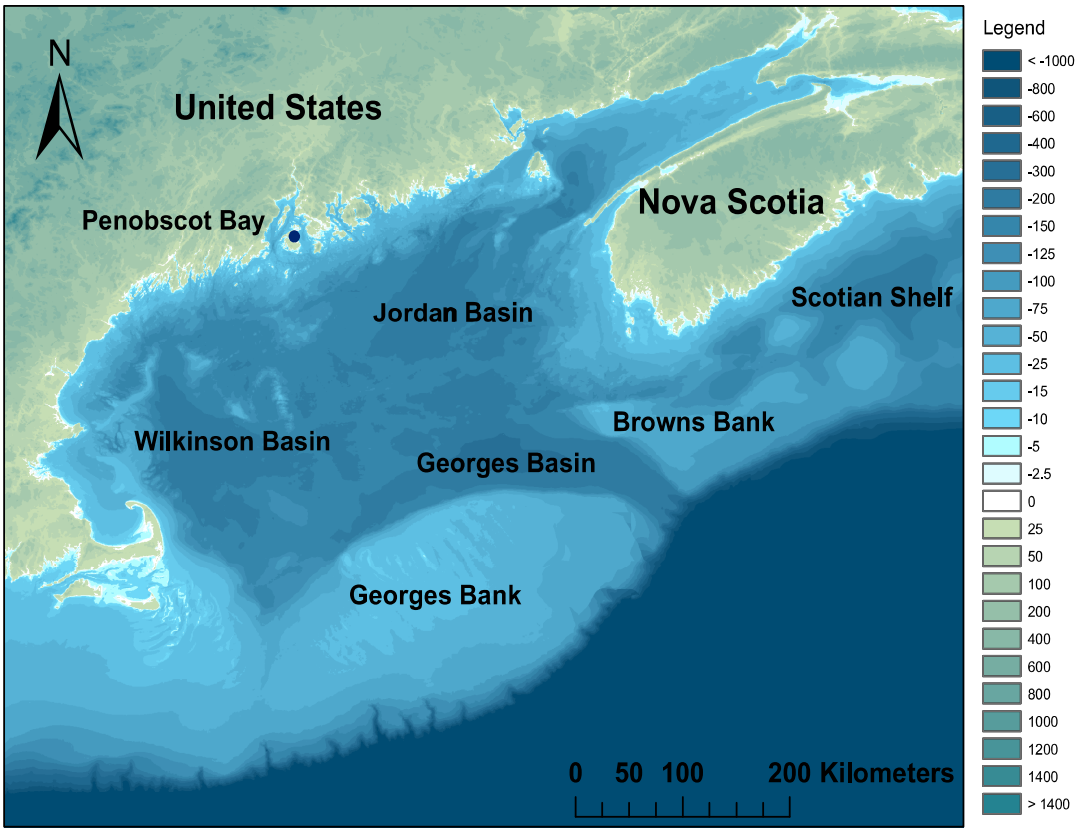

Figure 2. Map of the Gulf of Maine
The Gulf of Maine showing the main banks and basins.

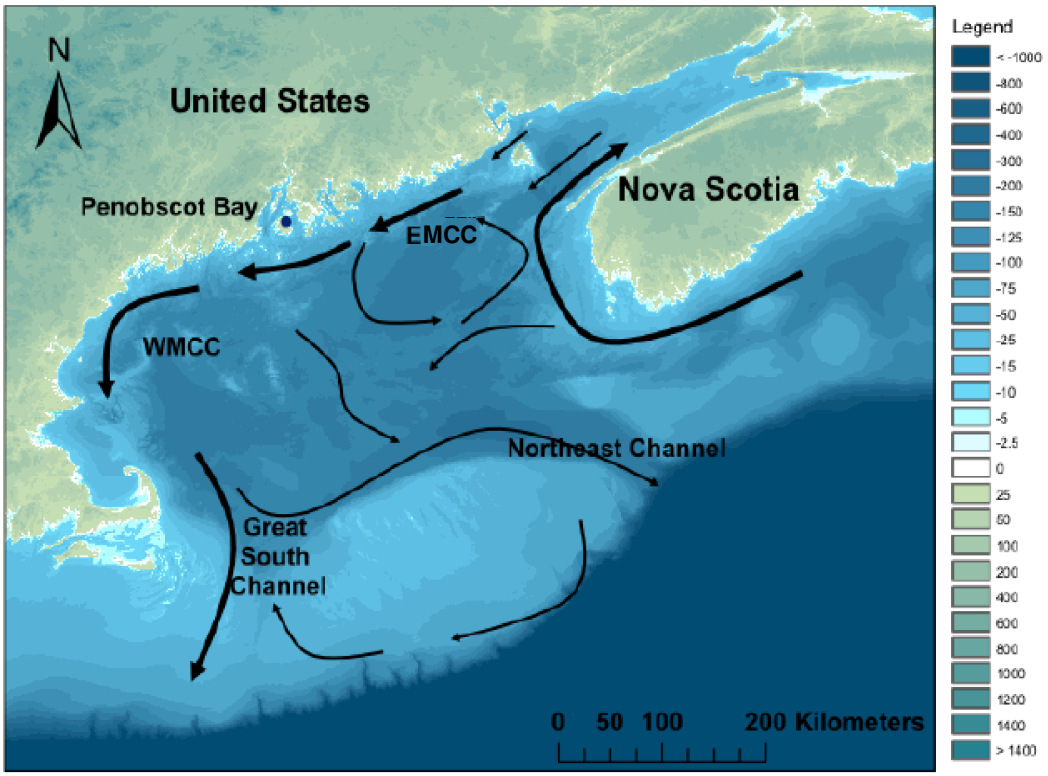

Figure 3. Ocean Current Map of the Gulf of Maine
The GoM with major current patters. Arrow thickness indicates the general magnitude of water movements.

Physical mechanisms (such as winter convection and tidal mixing) within the GoM distribute these nutrients to surface layers, where primary production is stimulated (Gatien, 1976). The GoM is known as a highly productive system whose primary production rate is, on average, 270 $gCm^{-2}y^{-1}$, although coastal waters are more productive than waters over deep basins (O'Reilly et al., 1987). The high rate of nutrient input to the GoM fuels this productivity.

The GoM is a unique location for marine life because it represents the southern-most boundary for many Arctic species and the northern-most boundary for many temperate species (Sinclair et al., 1992). It has relatively low species diversity due to the extreme temperature range it experiences, which few species can tolerate, and the extent of the last glacial maximum (~18,000 years ago), which caused local extinction events (Adey and Steneck, 2001). This lack of redundancy in ecological niches makes the GoM extremely susceptible to phase shifts because few species perform the same ecosystem function.

Penobscot Bay

Penobscot Bay and Frenchman's Bay are the two deepest embayments on Maine's coast (Kelley and Belknap, 1989). Penobscot Bay originates from the mouth of the Penobscot River, Maine's second largest river. It is connected to the GoM by two main north-south trending channels, the East Passage and the deeper West Passage, which divide the bay into three segments (**Figure 4**). West Passage is a low-relief region that separates the mainland from Islesboro Island and a cluster of smaller islands (Kelley and Belknap, 1989). The deep canyon on the seafloor through the West Passage reaches depths of 150m. Middle Passage is a shallow basin that trends east-west and separates North Haven and Vinalhaven Islands in the middle of the bay (Kelley and

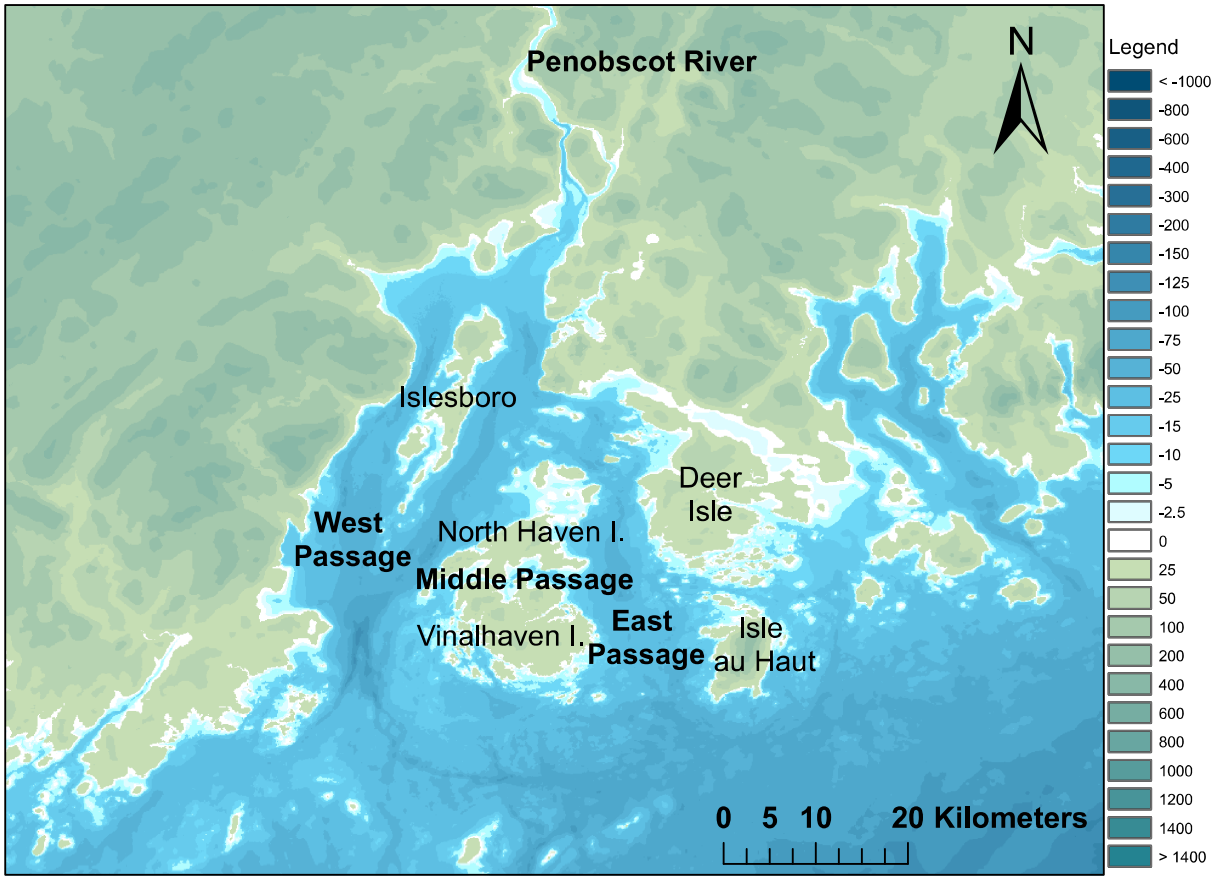

Figure 4. Map of Penobscot Bay
Penobscot Bay with major islands and water passageways.

Belknap, 1989). East Passage begins closer to the entrance of the bay than either West or Middle Passage. It is also shallower, reaching depths of only 60 m (Kelley and Belknap, 1989). The seaward section of the bay contains few islands and is characterized by a flat and muddy seafloor.

Penobscot Bay is underlain primarily by metamorphic rock and glacial sediments and contains many granite islands (Kelley and Belknap, 1989). These islands are surrounded by sand bars, which are sometimes strewn with boulders (Kelley and Belknap, 1989). The main seafloor is muddy or rocky rather than sandy. Relative sea level in Penobscot Bay has changed dramatically over the last 14,000 years due to isostatic rebound and the melting of the Laurentide Ice Sheet, although the sea level shifts over the last 4,000 years have been relatively slow and more consistent (Belknap et al., 1987).

The salinity in Penobscot Bay is generally high (~27‰) even though the Penobscot River introduces large amounts of fresh water to the bay (Burkholder, 2007). This freshwater also delivers many nutrients to the bay. Tide range is between 2.8 to 3.5m (Xue et al., 2000).

1.2.2 Primary Production

There are currently three main primary producers in GoM: phytoplankton, sea grass beds, and kelp forests. Phytoplankton and kelp are currently the most common primary producers in the Penobscot Bay, while other forms of submerged vegetation, such as seagrasses, are less common (Lazzari, 2008). These autotrophs can be distinguished by their ^{13}C signatures (Fry and Sherr, 1984; O'Leary, 1988; Lepoint et al., 2004 among others) (**Table 1)**. Phytoplankton is the most depleted in ^{13}C, with ^{13}C

values ranging from -27 to -20‰ (Fry, 1988). This variability is largely caused by interspecific differences and differences in environmental conditions (such as sea surface temperature, light availability, and CO_2 concentration) and growth rates (Burkhardt et al., 1999). Kelp have intermediate ^{13}C values that range from -20 to -15‰ (Duggins et al., 1989; Leduc et al., 2006). Seagrasses, such as eelgrass (*Zostera marina*), are the most enriched in ^{13}C, with ^{13}C values averaging -11 to -10‰ (Hemminga and Mateo, 1996). The most important factor causing this variation and enrichment is likely the fractionation that occurs during the enzymatic assimilation of carbon dioxide (CO_2). Seagrasses can assimilate bicarbonate (HCO_3^-) (0‰) or CO_2 (-8‰) during photosynthesis, but HCO_3^- is more enriched in ^{13}C than CO_2 (Hemminga and Mateo, 1996; Beer et al., 2002).

Phytoplankton in the GoM are responsible for the greatest amount of primary production in this system. The highest primary production rates in the GoM are 2-3 g $Cm^{-2}yr^{-1}$ on Georges Bank and in coastal areas near rivers that input high amounts of nutrients. The lowest levels of primary production are about 0.7 g $Cm^{-2}yr^{-1}$ over the deep basins in the GoM (O'Reilly and Zetlin, 1988). Dinoflagellates and diatoms are the dominant phytoplankton species in Penobscot Bay (Burkholder, 2007). The GoM typically experiences a short spring bloom, followed by a decrease in phytoplankton concentrations in the midsummer and a longer bloom in the fall (Thomas et al., 2003). Phytoplankton concentrations are low during the winter months, except near coasts. Spatial patterns of phytoplankton distribution during the seasons are mostly caused by tidal mixing and bathymetry differences (O'Reilly, 1987; Thomas et al., 2003).

Table 1. Reported $\delta^{13}C$ of Selected Autotrophs

Summary of C isotopic composition of the three main primary producers that are found in the Gulf of Maine: seagrasses, kelps, and phytoplankton. Averages were calculated using the midpoints when ranges were reported.

Species	**Location**	**^{13}C range**	**Reference**
Seagrass spp.	Coastal Ecosystems	-3 to -15	McMillan (1980)
Seagrass spp.	Coastal Ecosystems	-10 to -11	Hemminga and Mateo (1996)
Seagrass spp.	Mediterranean Sea	-9	Dauby (1989)
Zostera sp.	New Zealand	-7 to -11	Leduc et al. (2006)
Zostera sp.	Puget Sound, North Pacific	-8.5 to -12	Simenstad and Wissmar (1985)
Zostera marina	St. Margaret's Bay, Nova Scotia	-6 to -12	Stephenson et al. (1984)
Zostera noltii	Inland Sea, North Wales, UK	-7 to -11	Papadimitriou et al. (2006)
Zostera marina	Beaufort, North Carolina	-12.2	Thayer et al. (1978)
		-10	**Average**
Macroalgae	Mediterranean Sea	-19	Dauby (1989)
Laminaria sp.	Puget Sound, North Pacific	-15.3	Simenstad and Wissmar (1985)
Laminaria hyperborea	Norwegian Sea, W. Coast Norway	-15 to -17	Fredriksen (2003)
Laminaria longicruris	St. Margaret's Bay, Nova Scotia	-13 to -20	Stephenson et al. (1984)
Laminaria longicruris	Gulf of St. Lawrence, Canada	-13.8	Lesage et al. (2001)
Laminaria sp.	Gulf of Alaksa	-15 to -20	Duggins et al. (1989)
Laminaria sp.	Gulf of Alaska	-18.5	Misarti et al. (2009)
Laminaria spp.	Bering Island, North Pacific	-18	Simenstad et al. (1993)
		-17	**Average**
Phytoplankton	Puget Sound, North Pacific	-20 to -23	Simenstad and Wissmar (1985)
Phytoplankton	Norwegian Sea, W. Coast Norway	-18 to -26	Fredriksen (2003)
Phytoplankton	Mediterranean Sea	-23	Dauby (1989)
Phytoplankton	Temperate, coastal marine systems	-18 to -24	Deuser (1970), Haines and Montague (1979)
Phytoplankton	Gulf of Alaksa	-23 to -27	Duggins et al. (1989)
Phytoplankton	Georges Bank, Gulf of Maine	-20 to -23	Fry (1988)
Phytoplankton	Pacific and Atlantic Surface Waters	-20 to -22	Rau et al (1982)
Phytoplankton	Narragansett Bay, Rhode Island	-20 to -22	Gearing et al. (1984)
		-22	**Average**

Seagrasses colonize estuaries and shallow marine environments (Heck et al., 1989). The dominant species of seagrass in the GoM is *Zostera marina* (eelgrass). Eelgrass is an angiosperm that is found in the soft sediments to depths of 35m. Eelgrass beds are extremely productive; a *Zostera marina* bed in Cobscook Bay, Maine is estimated to produce 3.3-5.3 x 10^8 $gCyear^{-1}$ (Beal et al., 2004). Another study estimates daily production to be 4.8 gCm^{-2} per day during the growing season and total production for one growing season to be 812 gCm^{-2} (McRoy, 1974). Eelgrass beds in Penobscot Bay support a wide range of biodiversity, including decapods and fish as well as herbivorous and detritivorous invertebrates (Lazzari and Tupper, 2002). The leaves of this plant slow water flow, which increases the residence time of suspended particles, including larvae, and increases sedimentation rates (Abdelrhman, 2003; Abdelrhman, 2007). The enhanced sedimentation that occurs within *Zostera* beds causes the benthic environment to be more nutrient rich compared to benthic environments above bare substrate, resulting in increased productivity (Fonseca et al., 1982). Seagrasses stabilize otherwise mobile sediments, which alters the faunal abundance and diversity of the benthic community (Rhoads and Young, 1970; Brenchley, 1978).

Many species directly and indirectly rely on eelgrass (Heck et al., 1989; Lazzari and Stone, 2006; Lazzari, 2008). Eelgrass provides breeding grounds, nursery grounds, habitat and food for fish and crustaceans, and protection from predation and physical factors (Harlin, 1980; Heck et al., 1989; Lazzari and Tupper, 2002). Kindblon (1991) characterized *Zostera* beds as larval traps because their presence drastically increased the settlement of larval and juvenile blue mussels (*Mytilus edulis*). Similarly, Peterson et al. (1984) found that the concentration of clams (*Merceneria merceneria*) was greater within *Zostera* beds than over a nearby sand flat and that the *Zostera* bed contained

larger individuals on average than the sand flat. More than 100 species of marine invertebrates have been reported as epiphytic on *Zostera* blades (Harlin, 1980).

Few grazers can directly digest eelgrass because it contains a high percentage of cellulose (Klumpp et al., 1992). As detritus, it provides ecosystems with many nutrients (Vizzini et al., 2002) and has been shown to retain a similar ^{13}C signal to live plants (Stephenson et al., 1986). The physical breakdown of seagrasses and other macroalgae into detritus does not affect the characteristic isotopic signature of species, however, the microbial breakdown of seagrasses can alter the ^{13}C of seagrasses (Zieman et al., 1984).

Eelgrass in the GoM has been declining over the last century due to environmental factors (grazing, disease, rise in sea level) and direct anthropogenic factors (nutrient and sediment loading, pollution, dredging, boating, etc.) (Orth et al., 2006). Eelgrass has high light requirements and is thus susceptible to damage from increased water turbidity caused by algal blooms (resulting from increased nutrient inputs) and suspended sediment (Zimmerman, 2006). Under these conditions, eelgrass is easily outcompeted by algal species such as kelp. A study in southern New England showed that fish abundance, biomass, and species richness decreased with decreasing eelgrass habitat complexity in a series of bays over an 11-year period (Hughes et al., 2002).

Kelp (*Laminaria* spp.) colonizes rocky shorelines in cool, coastal waters at depths of 15 to 40 m (Jackson and Winant, 1983). Kelp forests are structurally complex, highly productive ecosystems that are common between 40° and 60° latitudes (Steneck et al., 2002). During the growing season, *Laminaria longicruris* in Cobscook Bay, Maine had production rates of 2.3 g C $m^{-2}day^{-1}$ (Vadas et al., 2004). Kelp species are known for their rapid growth rates and can reach blade lengths of 5-15 m in 3-5 years. *Laminaria* spp. in

the North Atlantic are prostrate kelps that cover the benthic environment with their fronds. The lifespan of individual kelps is approximately 25 years (Steneck and Dethier, 1994). Kelp beds and forests include kelp plants, which provide structural habitat for many organisms, and associated organisms that can include up to 10 phyla— Chordata, Arthropoda, Annelida, Echinodermata, Bryozoa, Cnidaria, Mollusca, Platyhelminthes, Brachiopoda, and Porifera. Marine mammals, fishes, crabs, sea urchins, mollusks, and other algal species and epiphytic biota are common in kelp forests (Mann, 1973).

Kelp forests have significant effects on the local environment. Like eelgrass, their canopies dampen waves, which reduces flow within canopies, increasing sedimentation, larval recruitment, and ultimately, production (Duggins et al., 1990). Canopies also reduce the amount of light that reaches benthic communities, which favors species that are adapted to low-light environments and can affect interspecific competition (Dayton, 1985). Kelp beds also provide sessile species with substrate (Duggins, 1980) and provide mobile invertebrates and fish with nursery habitat and refuge from predation (Anderson et al., 1997; Steneck et al., 2002).

1.2.3 Consumers in Seagrass Beds and Kelp Forests

Temperate seagrass beds experience significant herbivory, although marine grazing pressure is heaviest in tropical seagrass beds (MacArthur and Hyndes, 2007; Prado et al., 2007). Juvenile and small fish and urchins are the most common grazers in temperate seagrass beds (Heck and Valentine, 2006). Grazing pressure by both fish (Tomas et al., 2005b) and sea urchins (Eklof et al., 2008) has been shown to exceed seagrass growth rates in some systems, resulting in a loss of seagrass biomass, although this is a relatively rare phenomenon. Epiphytic algae in grass beds, however,

have similar ^{13}C values to the seagrass itself, and is common and readily consumed by herbivores (Hoshiko et al., 2006).

Kelp breaks down more quickly than eelgrass and is directly consumed by more organisms (Harrison, 1989). Herbivores generally consume less than 10% of kelp biomass (Mann, 2000), thus the amount of macroalgal detritus generated within kelp canopies is large and forms an important nutritional source for coastal ecosystems (Duggins et al., 1989). Detritivores, herbivores, and suspension feeders consume carbon originating from kelp fronds when kelp is broken down by bacteria. Filter feeders in kelp beds can derive up to 85% of their carbon from kelp detritus (Duggins et al., 1989). Some species, such as specialized limpets and the sea hare, *Aaplysia punctata*, appear to feed directly on kelp fronds (Hayward et al., 1995; Bustamante et al., 1995). Consequently, kelp forests concentrate secondary production, which supports complex food webs (Duggins et al., 1989: Mann, 2000).

In theory, the carbon isotopic composition of the primary producers, such as eelgrass and kelp, in the GoM will be transferred to the herbivores and detritivores that forage in marine systems, so that the ^{13}C signal of primary producers is reflected in the signal of secondary producers. Stable C isotopic analysis has been used to determine that seagrass carbon plays a moderate, but significant role in the food webs of a North Carolina *Zostera marina* bed **(**Thayer et al., 1978), an Australian seagrass meadow (Hyndes and Lavery, 2005), and Alaska seagrass beds (McConnaughey and McRoy, 1979). The importance of seagrass carbon to secondary consumers in temperate environments is less clear. A recent review by Heck et al. (2008) concludes that "seagrass ecosystems provide a large subsidy to both near and distant locations through the export of particulate organic matter and living plant and animal biomass", although

they note that algal carbon probably supports more production by small animals that inhabit seagrass beds.

Stephenson et al. (1986) examined the ^{13}C signal of several consumers (including grazers, filter feeders, and carnivores) in adjacent *Laminaria longicruris* and *Zostera marina* beds in Nova Scotia, Canada. They found that only a small herbivorous snail (*Lacuna vincta*) differed significantly in ^{13}C between the two habitats, although 4 of the 7 species examined were more enriched in ^{13}C from the *Zostera marina* bed (Stephenson et al., 1986). *Lacuna vincta* was observed feeding directly on both kelp and eelgrass in the field. The authors hypothesize that phytoplankton C was more important as a carbon source to this temperate system than *Zostera marina* because most consumer ^{13}C values were more depleted than *Zostera marina* blades and detritus (Stephenson et al., 1986), although the relative importance of phytoplankton compared to kelp was difficult to assess because the ^{13}C range of these groups tends to overlap (Fry and Sherr, 1984; Stephenson et al., 1984). In a study employing stable C isotopic analysis in a similar manner, Hyndes and Lavery (2005) found that seagrass was unlikely the main C source for benthic invertebrates except for harpacticoid copepods and some species of polychaetes.

Several recent studies employing stable C isotopic analysis have shown that the ^{13}C signature of *Laminaria* kelp species is recorded in tissues of the primary consumers that inhabit these kelp forests. For example, Fredriksen (2003) examined the ^{13}C and ^{15}N composition of invertebrates, fish, and birds from a *Laminaria hyperborea* forest in western Norway to determine if their main carbon source was kelp or phytoplankton. The ^{13}C composition of many species, such as the gastropods *Helcion pellucida* and *Lacunta vincta*, and several filter feeders, showed that these animals relied heavily on kelp as a carbon source. In addition, the ^{13}C of cod caught in the kelp forest was significantly

more enriched (a difference of 2.5‰) than that of cod caught in open ocean areas, which are presumably more dependent on phytoplankton as a C source, although cod did not differ in trophic level (Fredriksen, 2003).

Schaal et al. (2009) also used stable C analysis to demonstrate that *Laminaria digitata* is an important C source for herbivores and detritivores in rocky areas surrounding Batz Island, France. Kelp is a particularly important C source in sheltered environments where kelp detritus was shown to be more protein-rich (Schaal et al., 2009). Similarly, Duggins et al. (1989) showed that C from *Laminaria* and *Alaria* beds is reflected in the ^{13}C of nearshore food webs in the Bering Sea.

1.3 Previous Isotopic Studies on Fish Tissues

The isotopic composition of different fish tissues provides information on the individual's diet over different time scales (Fogel and Cifuentes, 1993). Bulk organic matter, as opposed to specific amino acids, produces an integrative signal that indicates processes acting on the individual over part of its life (Fogel and Cifuentes, 1993). Bone collagen provides a signal of an individual's diet up to the last year; muscle, up to a few months; liver, a few weeks; and blood, a few days. These differences are mostly determined by the turnover rate of the tissue and the rate of new tissue growth (Tieszen et al., 1983).

Elsdon et al. (2010) examined the ^{13}C and ^{15}N of fish muscle and otoliths after conducting a controlled feeding experiment in which mummichogs were fed five diets that differed in ^{13}C. They found that fish muscle was enriched in ^{13}C and ^{15}N relative to the fishes' diet, although the magnitude of this increase varied between diets, and concluded that the isotopic signature of muscle can be used to assess foraging behavior

of fish. They also found that otoliths were enriched in ^{13}C and ^{15}N relative to the fishes' diet. The isotopic signal of otoliths likely records differences in the isotopic composition of the individual's diet, however, the authors note that there are many variables that affect the ^{13}C of otoliths, which must be further studied before such conclusions can be made confidently (Elsdon et al., 2010).

McMahon et al. (2010) performed a similar controlled feeding experiment on mummichogs, which were raised on 4 isotopically distinct diets, and examined the diet-muscle ^{13}C fractionation of bulk tissue and individual amino acids (AA) in fish muscle tissue. They concluded that the ^{13}C of essential AAs, which experienced virtually no fractionation, are a good indicator of basal carbon source. Non-essential AAs from fish muscle, however, were more enriched in ^{13}C than the diet ^{13}C. Similar to the conclusions of Elsdon et al. (2010), this study found that the fractionation between bulk muscle tissue and non-essential AAs is variable and depends on the diet of fish (McMahon et al., 2010).

Field studies have concluded that the ^{13}C and ^{15}N of fish muscle reflect the isotopic signature of their diets. Sherwood et al. (2007) compared the C isotopic composition of Atlantic cod from several regions offshore from Newfoundland and Labrador, which differ in a number of population characteristics including growth rates and condition factor. Differences in ^{13}C between populations indicated that cod from Labrador and northeast Newfoundland, which grow more slowly and have lower condition factors, consume mainly northern shrimp and have a benthic ^{13}C signature. Cod from the south coast of Newfoundland rely on a greater variety of prey items, including zooplankton, crabs, and capelin. The ^{13}C of these cod was indicative of a pelagic lifestyle (Sherwood et al., 2007).

Fry (1988) analyzed C, N, and S isotopes of invertebrate and fish species and particulate organic matter from Georges Bank to determine that ^{15}N was a better indicator of trophic level than ^{13}C or ^{34}S. He concluded that Georges Bank supports a minimum of four trophic levels (Fry, 1988). In the same system, Wainright et al. (1993) used C and N isotopic analysis of fish scales from Georges Bank to examine changes to fish diets and food webs from the 1930s to the 1990s. The ^{13}C of most consumers decreased by 1.5‰ from 1929 to 1960, and then increased slightly from 1960 to 1987. The isotopic decrease until 1960 may indicate the ^{13}C value of phytoplankton changed or the main prey items shifted from fish to lower trophic level invertebrates during the study period. They also concluded that haddock fed at a higher trophic level in 1987 than in 1929 based on increased ^{15}N values (Wainright et al., 1993).

In addition to determining modern foraging ecology, stable isotope analysis is also a useful tool for studying prehistoric temporal and spatial trends. In some cases, archaeological fish bone collagen has been used to identify the geographic origin of the fish. Barrett et al. (2008) examined the ^{13}C and ^{15}N of cod bone collagen from the 9th to the 15th century AD in the North Sea, during which time the cod trade was active in medieval Europe. They found that the ^{13}C and ^{15}N of archaeological cod bone collagen was indicative of their region of catch in the North Sea, Black Sea, and Kattegat. The authors note their conclusions are limited by the unknown role that variations in time, space, and fish size may play (Barrett et al., 2008).

Another study examined C and N isotopes in bone collagen from archaeological middens in an Aleutian archipelago to determine temporal trends (Misarti et al., 2009). The authors analyzed fish and mammal bone samples from 4,500 years ago to the present. All species examined, except cod, were depleted in ^{13}C during modern times relative to their prehistoric C values. The authors tie this trend to climate trends,

hypothesizing that a decrease in regional primary productivity in the Gulf of Alaska (specifically the loss of ice algae, which is more enriched in ^{13}C than phytoplankton) resulted in ^{13}C depletion of modern ^{13}C values (Misarti et al., 2009). Modern pacific cod, however, were approximately 0.6‰ enriched in ^{13}C relative to archaeological cod after modern samples were corrected for the Oceanic Suess Effect. No changes in cod ^{13}C or ^{15}N were statistically significant in the last 4,500 years (Misarti et al., 2009).

1.4 Archaeological Overview of Penobscot Bay

More than 500 shell middens have been found in Maine and the surrounding New England states. They date from 5,000 to 400 years before present (BP). These middens primarily contain remnants of clams, oysters, and other marine organisms, implying that their inhabitants relied heavily on marine sources. Penobscot Bay contains many archaeological sites on its islands, which were excavated and studied in the 1970s and 1980s. The excavation of 40 sites produced 10,000 artifacts and many more faunal remains (Bourque et al., 2008). The Turner Farm site, located on North Haven Island, has been the most extensively studied (Bourque, 1995; Spiess and Lewis, 2001).

Native populations have inhabited Maine since the last glaciers retreated approximately 12,000 years ago, revealing a treeless tundra environment. The Paleoindians occupied sites from 11,500 to 9,000 BP. The Archaic Period followed from 9,000 BP to approximately 3,000 BP. The first indication of human occupation of Penobscot Bay is projectile points whose style is attributed to the Early and Middle Archaic period approximately 8,500 to 6,000 BP (Bourque, 2001). Small Stemmed Points discovered on the Maine coast date to approximately 5,000 BP (Bourque, 1995). The Moorehead Phase followed the Small Stemmed Point tradition and dates to

approximately 3,800 BP. Their subsistence was derived from maritime sources (mainly cod and swordfish) and some terrestrial hunting.

The Susquehanna Tradition quickly followed after the Moorehead Phase disappeared in 3,800 BP and likely represents the arrival of a new group of people in the Maine coast (Bourque et al., 2008). Although this phase was longer-lived in other places in New England, it persisted in Maine for only about 300 years. Little is known about the period from the disappearance of the Susquehanna Tradition until midden accumulation began again at approximately 2,800 BP.

The Ceramic Period, named for the introduction of pottery remains in the archaeological record, dates from 2,500 to 500 BP. Turner Farm and other middens in Penobscot Bay were occupied more or less continuously from the start of the Ceramic Period until the end of the prehistoric period (Bourque, 2001). More archaeological sites in Maine are attributed to the Ceramic Period than any other archaeological time period, which indicates that indigenous populations grew in number and expanded during this period (Bourque, 2001). These sites are found in greatest numbers on Maine's coast where evidence of a subsistence style based on shell-fish gathering, fishing, and some terrestrial hunting has accumulated (Bourque, 1995).

Material artifacts excavated from the Ceramic Period strata at the Turner Farm site include lobate-stemmed points, narrow-stemmed points, triangle points and notched points among other bifaces (Bourque, 1995). Artifacts made of bone include points probably used on thrusting weapons (i.e. spears), tools made from beaver teeth, barbed spears and harpoons, and small and large fishing hooks. Large fishhooks were likely used to fish for cod, and small fishhooks and were likely used to catch flounder. This suite of tools indicates that sustenance from marine sources was very important to this culture (Bourque, 1995).

Several styles of pottery can be distinguished in Ceramic Period strata at Turner Farm. Vinette I, the earliest style, is characterized by dense tempering with coarse grit, evidence of coiled construction, and cord impressions on both surfaces. Pseudo-Scallop-Shell-Stamped pottery enters the archaeological record at around the same time as Vinette I. Pseudo-Scallop-Shell stamps and other decorative motifs distinguish this style. A thicker, more coarsely tempered style of pottery, called Dentate-Rocker-Stamped (D-R-S) is representative of the Middle Ceramic Period. The final pottery style representative of the Late Ceramic Period is Cord-Wrapped-Stick-Impressed pottery, which is darker in color than D-R-S pottery and characterized by cord impressions on the outside surface of pottery (Bourque, 1995).

The Contact Period dates from 500 to 250 BP when European fishermen and explorers reached Maine's coast. Europeans reached the Gulf of St. Lawrence by 400 BP (during the 16th century) and were soon established as a consistent presence (Bourque, 1995). This period is characterized by the exchange of ideas and material goods, such as animal pelts, shell beads, and tools, between indigenous people and Europeans. The Fox Islands, including North Haven Island, were considered part of the French colony of Acadia during the 17th century and early 18th century, although no French settlements were established on these islands (Bourque, 1995). Indigenous populations along Maine's coast begin to decline because of epidemic diseases and new villages that formed inland from the coast (Bourque, 1995).

1.4.1 Previous Research at Turner Farm

Turner Farm is a shell-midden attributed to the Red Paint People and other Native American groups (Bourque, 1995). These middens are refuse piles from the

people who historically inhabited North Haven Island. Turner Farm is recognized as preserving one of the most complete archaeological records in the Gulf of Maine coast (Bourque, 1995). Animal remains from several strata have been radiocarbon dated, indicating the strata range in age from 4,500 to 500 BP. Thus the midden provides a record of local population diets from 4,500 years ago until the era of sustained European contact (~400 years ago) (Bourque, 1995).

1.4.2 Human Impacts on Marine Ecosystems

Western North Atlantic fish populations are commonly assumed to have been unaffected by anthropogenic factors until European contact some 500 years ago. The arrival of Europeans and the development of commercial fisheries for specific fish species on Maine's coast are thought to be the catalyst for the collapse of certain fish stocks (Jackson et al., 2001; Lotze et al., 2006). Evidence has accumulated, however, that suggests indigenous populations affected the diversity and abundance of their natural ecosystems (Jackson et al., 2001; Lotze and Milewski, 2004; Bourque et al., 2008). This research shows that hunter-gatherer populations may alter the dynamics of their local marine and aquatic ecosystems. This phenomenon has been reported in several systems such as the Aleutian Islands in Alaska (Simenstad et al., 1978) the California coast (Erlandson et al., 2005), and the Caribbean (Wing and Wing, 2001).

Until recently, nearshore ecosystems in the GoM were thought to have remained in a relatively stable state, dominated by benthic macroalgae (kelp forests), sea urchins, and apex fish predators, mainly cod, from 4,000 years to approximately 1,000 years ago (Steneck et al., 2004). In this stable state, mesopredators such as flounder, tomcod, and lobsters did not play a large role in ecosystem functioning (Steneck et al., 2004). This

balance was significantly affected by early 20th century advances in fishing technology and by the sea urchin fishery that developed in the 1980s (Steneck et al., 2004).

A recent archaeological study of fish bones from the Turner Farm middens suggests that some apex predators experienced declines in abundance long before Europeans arrived (Bourque et al., 2008). Between 4,500 and 500 BP the majority of bone fragments at Turner Farm shift from higher to lower trophic levels (Bourque et al., 2008). This shift may indicate that apex predators such as cod, swordfish, and dogfish have been overfished, releasing predation pressure on mesopredators, such as flounder, sturgeon, and sculpin, whose populations increased accordingly.

Isotopic data from Turner Farm fish bones show that cod, flounder, and sculpin diets have changed significantly over the last 4,000 years (Bourque et al., 2008). The ^{13}C of fish organic matter is more depleted in samples younger than 1,300 years old, with the greatest rate of change occurring over the last 400 years. This apparent dietary shift seems to have occurred approximately 2,000 years after a significant decrease in apex predators and increase in mesoscale predators and has been attributed to the loss of eelgrass and/or kelp biomass over the last 300 years (Bourque et al., 2008).

Faunal and isotopic analyses from Turner Farm suggests that humans have had an impact on aquatic ecosystems for thousands of years. The exact timing, magnitude, and spatial extent of these isotopic shifts remains in question.

1.5 Purpose

The purpose of this study was to determine if the apparent changes to nearshore ecosystems indicated by analysis of fish bones from Turner Farm (i.e. prehistoric decline in apex predators and loss of eelgrass (Bourque et al., 2008)) is a local phenomenon

specific to Turner Farm or if evidence for these changes exists in other shell middens in Penobscot Bay. The stable C and N isotopic composition of archaeological fish bone collagen from the Ceramic Period of human occupation from multiple sites in midbay, Penobscot Bay were analyzed. These results were compared to modern fish tissues collected from Penobscot Bay. These analyses allow the timing and extent (magnitude and scale) of changes to the main autotrophs that support nearshore food webs and the trophic level of characteristic demersal fishes to be elucidated. Three fishes were examined, including Atlantic cod (*Gadus morhua*), winter flounder (*Pseudopleuronectes americanus*), and longhorn sculpin (*Myoxocephalus octodecemspinosus*). These benthic fishes all occupy mid-high trophic levels, feed opportunistically, and increase trophic level slowly with size. They are also relatively well represented in the Penobscot Bay middens over the last 2,400 years.

1.6 Modern Feeding Ecology of Study Species

Atlantic cod, an opportunistic generalist, lives in marine and estuarine systems from 10-250m deep. Cod have a diverse diet that changes ontogenetically (Methven, 1999; Sherwood et al., 2007). There is a general shift from benthivory to piscivory with increasing body length (Link and Garrison, 2002a), but cod of all life-history stages and ages consume zooplankton, shrimp, and benthic invertebrates (Sherwood et al., 2007; Link et al., 2009). Juvenile and small cod consume mainly small crustaceans, including mysids, amphipods, euphausiids, and small shrimp. Medium-sized cod consume mainly larger crustaceans and small planktivorous fish, including capelin, sand lance, and juvenile gadoids. Large cod consume crabs, small fish and medium-sized demersal fish. Cod also consume other taxa, such as ctenophores, cnidarians, polychaetes, gastropods, bivalves, and echinoderms, but in much smaller quantities (Link et al., 2009).

Until capelin populations declined drastically in the last decade, these fish were an important component of the diet of north Atlantic cod (Sherwood et al., 2007).

In the GoM and Georges Bank ecosystems, cod tend to feed on the same prey items even when local habitat type varies (Link and Garrison, 2002a). Their diet usually consists of the most abundant, benthic species present. Although cod are still among the top 10 fish predators in Georges Bank, they consume less than one-third of the biomass they consumed historically, having been replaced by increasing numbers of elasmobranchs and other gadoids (Link and Garrison, 2002b). Cod populations have decreased dramatically over the last century; this decline is attributed to climate change to some extent, but more strongly to fishing pressures (Mieszkowska et al., 2010). Currently, cod comprise only 5-10% of the biomass in the GoM-Georges Bank ecosystem (Serchuk et al., 1994).

Winter flounder are benthic feeders that are found in the northwest Atlantic from North Carolina to Labrador, Canada (Kendall, 1909). They are found in shallow water, 1-100m deep. They are common on Georges Bank and in the GoM region (Klein-MacPhee, 2002). Flounder from Georges Bank are generally larger than flounder from more inshore populations, possibly due to more favorable temperature conditions (Lux et al., 1970).

Flounder are sight feeders that require adequate light to forage (Able, 1999), thus they feed mainly during the day and are inactive at night (Olla et al., 1969). They also reduce feeding during winter months or stop feeding altogether (Levings, 1974). The feeding habits of flounder vary with size and life history stage (Pearcy, 1962). The number of taxa found in stomach contents increases with growth. Young-of-the-year and yearling flounder consume mostly copepods, amphipods, and polychaetes. Large juveniles and adults are omnivorous opportunists (Pereiera et al., 1999). Adults can

reach 58cm in length and live over 15 years (Pereira et al., 1999). Their dominant prey items are polychaetes and crustaceans, mostly amphipods (Carlson et al., 1997). The diet of adults reflects the common benthic species present in the flounder's habitat and includes bivalves, capelin eggs, and fish.

Longhorn sculpin inhabit the same environment as winter flounder, shallow waters 1-100m deep. Sculpin can tolerate marine and estuarine conditions and are found in harbors and shallow coastal waters (Bigelow and Schroeder, 2002; Hyndman and Evans, 2009). Their range in the northwest Atlantic extends from Virginia to the Gulf of St. Lawrence in Canada. In the warm summer months and cold winter months, sculpin move to deeper water (down to 120m) to avoid extreme water temperatures (Bigelow and Schroeder, 2002). Longhorn sculpin are the most abundant species of sculpin in the GoM. They have remained ubiquitous in the GoM, Georges Bank region even though their numbers have declined in recent decades (Fogarty and Murawski, 1998).

Sculpin are omnivorous, opportunistic, benthic feeders that differ from flounder in their frequent consumption of detritus, in addition to other food sources. Common prey items include crustaceans, mollusks, worms, squid and many fishes, including herring, mackerel, smelt, sand lance, silversides, alewives, mummichogs, and tomcods (Scott and Scott, 1988). The diet of sculpin shifts ontogenetically because older, larger individuals can consume larger prey items. Rock crabs and other crustaceans were the dominant stomach contents of adult sculpin from Atlantic waters near Block Island Sound in Rhode Island (Link and Almeida, 2002). Adults reach an average length of 25cm, live approximately 11 years (Robins and Ray, 1986), and are mid- to high-trophic level predators (Scott and Scott, 1988).

2. Methods

2.1 Site Descriptions and Chronology

Archaeological bones were collected from seven coastal middens located on islands within Penobscot Bay (**Table 2, Figure 5**). Two of these middens were stratified, indicating that the site was occupied multiple times. The middens sampled represent ages between 340 and 2,400 calibrated radiocarbon years BP. The age of each midden or midden stratum was determined either by radiocarbon dating of associated organic matter (**Table 3**) or by determining the age of associated archaeological artifacts (**Table 4**). Radiocarbon dates were calibrated using the intcal09.14c calibration data set on Calib 6.0 calibration software (Reimer et al., 2004). The 2-sigma range (1.00 relative probability) is reported for each sample, although only the midpoint of the calibrated age in years BP is displayed in all other tables and figures hereafter. (The chronologies presented in the introduction were in ^{14}C years BP. All radiocarbon dates presented hereafter will be in calibrated years BP).

Inner Bay

The Asbornsen site is located on the northwestern tip of Little Deer Island in the inner Penobscot Bay. This site had one stratum, which contained cod, flounder, and sculpin bones and dates to approximately 340 BP based on historical records. This site is attributed to the Late Ceramic culture at the start of the Contact Period

Outer Bay

The Bar Island site is located on the southern tip of Bar Island, one of several small islands located at the western entrance to Penobscot Bay. It contained one

Table 2. Location of Coastal Archaeological Middens
Latitude and longitude of coastal middens in Penobscot Bay.

Site Name	Latitude (N)	Longitude (W)
Asbornsen	44° 17' 50.52"	68° 44' 12.00"
Bar Island	43° 59' 2.05"	69° 50' 8.81"
Bull Rock	44° 8' 40.52"	68° 49' 14.44"
Butter Island	44° 13' 36.51"	68° 47' 14.04"
Crocker	44° 7' 46.22"	68° 53' 15.58"
Oak Hill	44° 11' 0.59"	68° 49' 23.37"
Turner Farm	44° 8' 27.17"	68° 50' 55.02"

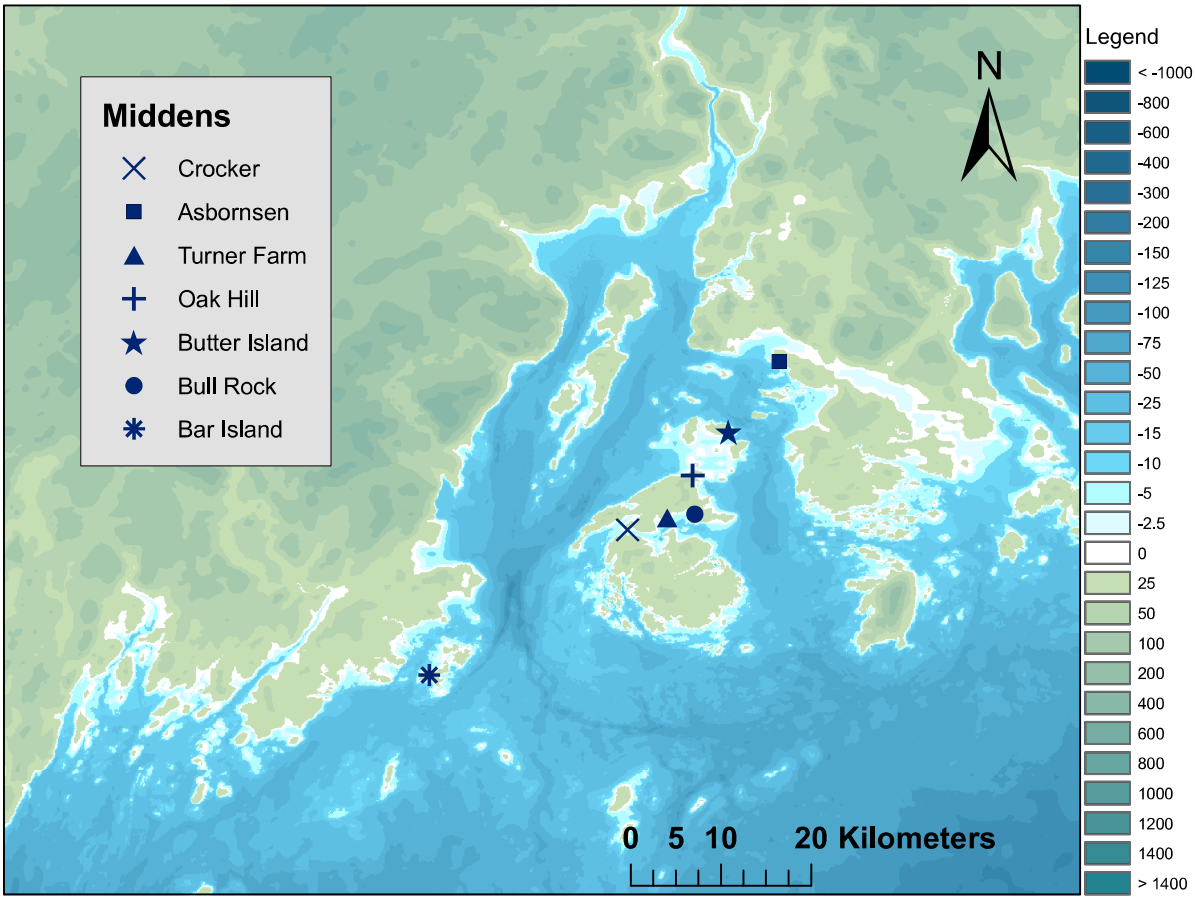

Figure 5. Site Map of Penobscot Bay
Symbols indicate the location of all archaeological middens sampled in Penobscot Bay.

Table 3. Radiocarbon Chronology Summary

Calibrated radiocarbon dates in years BP and calendar years BC/AD from organic matter isolated from various horizons in 5 archaeological middens from Penobscot Bay, Maine. Radiocarbon dates were calibrated using the intcal09.14c calibration data set on Calib 6.0 calibration software (Reimer et al., 2004). The 2-sigma range (1.00 relative probability) is listed for each sample.

Site	Site Number	Culture	Sample	^{14}C Age ± SD	Sample No.	Lab No.	95.4% (2s) cal age ranges	Midpoint	95.4% (2s) cal age ranges	Midpoint
Bar Island	18.4	MC	Bone	1710 ± 30		OS-84352	BP 1546-1697	1622 BP	253-404 AD	329 AD
Bar Island	18.4	MC	Bone	1710 ± 35		OS-84380	BP 1541-1702	1622 BP	248-409 AD	329 AD
Bull Rock	29.94	LC	Wood Char.	470 ± 90	26	RL-1300	BP 312-649	480 BP	1301-1638 AD	1469 AD
Bull Rock	29.94	LC	Wood Char.	520 ± 100	32	RL-1299	BP 318-672	495 BP	1278-1632 AD	1455 AD
Butter Island	29.159	MC	Wood Char.	1850 ± 70	138	BETA-5916	BP 1608-1945	1776 BP	5-342 AD	173 AD
Butter Island	29.159	MC	Wood Char.	1950 ± 100		BETA-5917	BP 1690-2149	1920 BP	200 BC- 260 AD	230 AD
Butter Island	29.159	MC	Wood Char.	2010 ± 150		BETA-5918	BP 1688-2337	2013 BP	388 BC- 262 AD	63 BC
Crocker	29.81	LC	Wood Char.	1290 ± 40	431	GX-29244-AMS	BP 1167-1297	1232 BP	653- 783 AD	718 AD
Crocker	29.81	LC	Wood Char.	1780 ± 40	435	GX-29243-AMS	BP 1601-1820	1711 BP	130-349 AD	240 AD
Crocker	29.81	LC	Bone	755 ± 45	58	GX-21381	BP 652-765	709 BP	1185-1298 AD	1242 AD
Crocker	29.81	LC	Human Bone	810 ± 40	434	GX-22242-AMS	BP 673-790	732 BP	1160-1277 AD	1219 AD
Crocker	29.81	LC	Human Bone	830 ± 40	433	GX-29240-AMS	BP 676-797	737 BP	1153-1274 AD	1214 AD
Crocker	29.81	LC	Human Bone	840 ± 40	432	GX-29246-AMS	BP 679-799	739 BP	1049-1084 AD	1067 AD
Turner Farm	29.9	EC	Wood Char.	2275 ± 130	173	SI-2398	BP 1992-2710	2351 BP	761-43 BC	402 BC
Turner Farm	29.9	EC	Shell	2575 ± 75	160	GX-2463	BP 2364-2842	2603 BP	893-415 BC	654 BC

Table 4. Archaeological Artifacts Summary
Estimated age of archaeological artifacts isolated from two archaeological middens in Penobscot Bay. Source: B. Bourque, Personal Communication.

Site	Sample	Age (years BP)
Asbornsen	French Medals	340
Oak Hill	Pottery Record	1,500-2,000

stratum, which is attributed to the Middle Ceramic culture and dates to approximately 2,400 BP. Cod, flounder, and sculpin bones were analyzed from this site.

Middle Bay

The Turner Farm site is a shell midden on the southern coast of North Haven Island (Bourque, 1995). Covering over 2,000 m^2, the stratified site reaches depths of 1.5m; the deepest stratum of which correlates to approximately 4,000 BP. Cod, flounder, and sculpin bones from the second gravel floor stratum, which dates to approximately 2,400 BP were analyzed in this study. This horizon is attributed to the Early Ceramic culture.

The Crocker site is located on the southern coast of North Haven Island, approximately 2.9 km west and 1.2 km south of Turner Farm. Cod, flounder, and sculpin bones analyzed from this midden are approximately 1,000 BP. The Crocker site is attributed to the Late Ceramic culture.

The Bull Rock site is located on North Haven Island, approximately 2.3km east of Turner Farm on the island's southern coast. Cod, flounder, and sculpin bones were sampled from two strata of this midden dating to approximately 480 and 495 BP, respectively. Although these bones came from two depositional events, the ages of these strata are not significantly different, and bones from the two strata were combined in all analyses and considered to be 500 BP. Both strata are attributed to the Late Ceramic culture.

The Oak Hill site is located on the northern tip of North Haven Island, approximately 4 km due north of the Bull Rock site. This midden was one of two sites (see Butter Island below) that contained only sculpin bones. This site dates to 1,800 BP and is attributed to the Early/Middle Ceramic culture.

The Butter Island site is located on the southern coast Butter Island, a smaller island in the middle of Penobscot Bay, approximately 8 km northeast of North Haven Island. This midden only contained sculpin bones and dates to 2,000 BP. This site is attributed to the Middle Ceramic culture.

2.2 Collection Methods

2.2.1 Archaeological Samples

A total of 90 archaeological bone samples were obtained from the 7 middens examined (**Table 5**). All archaeological bone samples had previously been excavated from the sites over the years between 1971 and 1992, identified to the lowest possible taxonomic group by Arthur Spiess and Robert Lewis, and stored in the Maine State Museum in Augusta, ME (B. Bourque, Personal Communication). Bone samples were labeled with the quadrat, stratum, and depth from which they were recovered. Samples chosen for analysis were always selected from the same stratum to ensure they were of similar age.

Most bones analyzed were bones specific to each fish species being investigated (i.e. head bones from cod and diagnostic spines from flounder and sculpin) to ensure that a single fish was not sampled multiple times. Two to six cod, flounder, and sculpin bones were selected for analysis from each site, or in the case of Bull Rock, from each horizon being analyzed at the site. In many cases, sample size was limited by the availability of appropriate specimens at each site.

Table 5. Archaeological Bone Samples
Approximate age and number of bones analyzed from each archaeological midden. Ages are given in calibrated (cal) BP years except for Asbornsen and Oak Hill which were dated based on cultural artifacts, and whose age is given in estimated years before present.

Location	Site Name	Cod	Flounder	Sculpin	Total	Age (cal Years BP)
Inner Bay	Asbornsen	6	6	6	18	340
Outer Bay	Bar Island	6	2	6	14	1600
Middle Bay	Bull Rock	5	6	6	17	500
	Crocker	6	5	6	17	1000
	Oak Hill	-	-	6	6	1800
	Butter Island	-	-	4	4	2000
	Turner Farm	4	5	5	14	2400

2.2.2 Modern Samples

Modern cod, flounder, and sculpin samples were collected between 2008 and 2010. Fish from both nearshore locations within Penobscot Bay and between 20-30km offshore in the GoM were analyzed (**Table 6, 7**). Nearshore fish samples were caught in close proximity to Vinalhaven Island in the middle of Penobscot Bay in August 2010. Offshore cod and flounder were purchased from the Harbor Fish Market in Portland, Maine in June 2009, and only the approximate catch location is known.

2.3 Laboratory Methods

2.3.1 Preparing modern fish tissues for analysis

Three cod and three flounder caught in the same region of Georges Bank were purchased from the Harbor Fish Market in Portland, Maine. The length of each fish was recorded, and all fish were dissected to remove individual vertebrae, which were subsequently picked clean of organic matter. Up to three vertebrae from each fish were analyzed for stable C and N isotopic composition.

Two cod, three flounder, and three sculpin were caught near Vinalhaven Island in Penobscot Bay. The length of each fish was recorded and all fish were dissected to remove small bones extending from the vertebrae, which were subsequently picked clean of organic matter. One spine from each fish was analyzed for stable C and N isotopic composition.

Table 6. Modern Fish Samples

Total length and body depth of all modern fish samples. Nearshore samples were caught near Vinalhaven Island in Penobscot Bay. Offshore samples were caught 20-30 km offshore in the Gulf of Maine.

System	Species	Bates College Sample ID	Total Length (cm)	Body Depth (cm)
Nearshore	Cod	6979	55.0	11.0
		6980	44.5	9.0
	Flounder	6976	25.0	11.0
		6977	33.0	14.5
		6978	33.5	14.0
	Sculpin	7644	29.0	6.5
		7645	31.0	9.0
		7646	27.5	6.0
Offshore	Cod	5676	63.5	-
		5677	61.0	-
		5678	66.0	-
	Flounder	5728	42.0	-
		5729	43.5	-

Table 7. Modern Bone Samples

The number of individual fish and bones analyzed from two modern samples. Nearshore samples were caught near Vinalhaven Island in Penobscot Bay. Offshore samples were caught 20-30 km offshore in the Gulf of Maine.

		Cod	Flounder	Sculpin	Total
Nearshore	**No. Fish Sampled**	2	3	3	8
	Total No. Bones Samples	2	3	3	8
Offshore	**No. Fish Sampled**	3	2	-	5

2.3.2 Preparing bone samples for isotopic analysis

A 20-30 mg piece of bone was removed from each sample to prepare for isotopic analysis. All of the archaeological bone samples were first scoured with a dremel tool to remove their outer layer. Next, modern and archaeological samples were demineralized in 0.2 M HCl to completion (2-10 days) and rinsed extensively in reverse osmosis (RO) water (see Burton et al., 2001). Archaeological bones were then extracted in 0.25 M NaOH to remove the humic acids that accumulate in bone samples over time and thoroughly rinsed in RO water again. Finally, modern and archaeological samples were lyophilized.

2.3.3 Isotopic Analysis

A 0.5-1.0 mg subsample of each lyophilized, demineralized bone was weighed into a tin boat. Samples were analyzed for ^{13}C and ^{15}N on a Costech Elemental Analyzer (EA) coupled with a Conflo III combustion interface to a Finnigan Delta Plus Advantage stable isotope ratio mass spectrometer (IRMS) in the Environmental Geochemistry Laboratory at Bates College, Lewiston, Maine.

All isotope fractionations are reported in delta notation:

$$(‰) = ([R_{sample}/R_{standard}] - 1) \times 1000$$

where R= ^{13}C:^{12}C or ^{15}N:^{14}N. The carbon standard is Pee Dee Belemnite, and the nitrogen standard is atmospheric N_2 gas. Analytical precision was assessed using homogenized laboratory standards of acetanilide (n=28), cod meat (n=23), caffeine (n=22), organic millet flour (n=5), and corn husk (n=3) dispersed throughout each run. The standard deviation of ^{13}C and ^{15}N for each standard was <0.2‰ in every run.

2.3.4 Imaging Bones

Some archaeological and modern bones were selected to photograph to create a visual record of sample preparation. Bones were photographed before and after scouring with the dremel tool, after demineralization (wet) and finally after lyophilization. All photographs were taken on an Epson V750 Photo flatbed scanner in the Bates College Imaging Center.

2.4 Analysis Methods

2.4.1 Determining bone sample preservation

Bone collagen was chosen to be analyzed over other tissues because it can be well-preserved over time and quantitative measures exist to determine the quality of samples. The percent collagen recovered after demineralization, the molar C/N ratio of bones, and the presence of a collagen "ghost" were the three criteria used to determine the degree of sample preservation (after Deniro, 1985; Tuross et al., 1989; Ambrose, 1990). Bone samples were massed prior to demineralization and after lyophilization to determine the percent collagen by weight that remained for each sample. If the images showed the bone structure prior to demineralization was retained after lyophilization, the presence of a collagen "ghost" was confirmed. The molar C/N ratio, %C, and %N of samples were also monitored and compared to the accepted C/N range of 3.1-3.6.

2.4.2 Accounting for the Oceanic Suess Effect

The Oceanic Suess Effect (OSE) describes the modern carbon isotopic depletion of dissolved inorganic carbon (DIC) in the world's oceans since the start of the Industrial Revolution due to the increase of isotopically depleted CO_2 released to the atmosphere

when fossil fuels are burnt (first described by Suess, 1953). The magnitude of this depletion in DIC is estimated to be approximately 1.5‰ in the North Atlantic since 1953 (Kortzinger et al., 2003). All ^{13}C values reported for modern samples have been adjusted to account for the OSE by adding 1.5‰ to their ^{13}C value.

2.4.3 Statistical Analyses

2.4.3.1 Comparing Modern Samples

The ^{13}C and ^{15}N values of modern and offshore fish of each species were compared using unpaired, two sample t-tests. Statistical significance for all tests was determined at the $P<0.05$ level.

2.4.3.2 Detecting long-term trends from the bone collagen record

One-Way ANOVAs with Tukey's multiple-comparison post-hoc tests were used to determine the difference among the ^{13}C values of each species separately through time. The same procedure was used to determine the relationship among the ^{15}N of each species separately through time. Statistical significance for all tests was determined at the $P<0.05$ level. All groups (defined as the data for one stable isotope for one species through time) had equal variance (as determined with Levene's test for equal variance). All samples (defined as the data for one stable isotope for one species at one site), except for Bar Island cod ^{13}C and Turner Farm sculpin ^{13}C, passed the Kolmogorov-Smirnov test for normality. Because the One-Way ANOVA test is robust to deviations from normality (Zar, 2010), and no more than one sample in each test was non-normally distributed, this parametric test was used.

One-Way ANOVAs with Tukey's multiple-comparison post-hoc tests were also used to determine the relationship among the ^{13}C and ^{15}N values for cod, flounder, and sculpin at every middle bay midden that contained all three species.

2.4.4 Determining Trophic Level

The trophic level (TL) of all individuals was calculated using the following equation (Hobson et al., 1995):

$$TL = [(D-X)/3.8]+1$$

where D= $^{15}N_{individual}$ and X= the ^{15}N of the base of the food web. Modern POM values from Maquoit Bay, a relatively pristine *Zostera marina* bed in Brunswick, ME, were used as the base of the food web (**Table 8**).

Trophic level calculations from the ^{15}N signal of a fish bone are based on several assumptions. 1) The trophic enrichment between food source and consumer is constant through time and constant among the study species. 2) The ^{15}N of POM at the bottom of the food web is constant through time. 3) All changes in ^{15}N to one species through time can be attributed to changes in trophic level.

Previous studies have shown that trophic enrichments between prey and consumer in terrestrial systems are constant from 19,000 BP to the present (Bocherens and Drucker, 2003), thus it is reasonable to assume the same is true for marine systems. Previous work has also shown that typical trophic enrichments for marine fish in cold, temperate environments are 3-4‰, which agree with the 3.8‰ enrichment used in the equation (Dickenson, 1986). Because POM from a pristine modern system that does not experience heavy anthropogenic inputs was used as the baseline value, this assumption

Table 8. Maquoit Bay POM

The ^{13}C and ^{15}N (mean ± SE) of POM from Maquoit Bay, Brunswick, Maine. *Indicates modern samples that have been corrected for the Oceanic Suess Effect (see Methods). Source: Flynn, unpublished data, 2011.

	^{13}C	$^{13}C^{*}$	^{15}N	n
POM	-19.7 ± 0.7	-18.2 ± 0.7	5.3 ± 0.2	3

is also reasonable. Therefore it is reasonable to apply this equation to fishes from nearshore systems in Penobscot Bay.

2.4.5 Determining Basal Carbon Source

The ^{13}C of the main basal carbon source of each individual was calculated using the following equations:

$$^{13}C_{food\ source} = {}^{13}C_{fish\ bone} - 5‰$$

This equation was applied to the raw ^{13}C data for all archaeological samples and the modern samples that had been corrected for the OSE. This equation accounts for the maximum reported isotopic shift (5‰) between food source tissues and consumers tissues as carbohydrates are converted to proteins (Fry and Sherr, 1984).

2.5 Spatial Differences within the Bay

The Asbornsen, Bar Island, and modern (offshore) samples were excluded from analyses that sought to elucidate long-term changes to food webs in Penobscot Bay. The Asbornsen and Bar Island sites are interesting and important sites that represent critical time periods in the archaeological record, however, they are located on islands at the mouth and innermost location of the bay. Because the degree of spatial homogeneity of the Penobscot Bay is currently unknown, including these samples in analyses of long-term trends would present problems because differences between the isotopic compositions of samples from these sites could either be caused either by factors acting over time, through space, or some combination of both. Therefore, samples from these sites were excluded in analyses conducted to determine long-term trends.

Similarly, the nearshore modern sample represents a better analog for the archaeological samples than the offshore modern sample. The indigenous groups that fished in Penobscot Bay likely rarely ventured more than 5-10 km from their islands (B. Bourque, personal communication), so it would be inappropriate to compare these samples to modern samples caught 20-30 km offshore in the GoM. Furthermore, offshore fish populations rely on different relative amounts of basal carbon sources (i.e. primary producers) than do nearshore fish populations, so conclusions about the autotroph that supports the most productivity in the GoM would be inaccurate if the offshore sample were used as a point of modern comparison.

To make inferences about possible changes to food webs over time from the isotopic data collected, several assumptions must be made. First, the foraging behavior of both these omnivorous fishes and the indigenous people that caught them is assumed to conform to optimal foraging theory (eg. Pyke,1984). Thus fish are assumed to feed in a manner that maximizes prey intake and minimizes energy expenditure. Their prey choices should reflect the prey items that are most abundant or easiest to capture. The fishing practices of indigenous people are similarly assumed to reflect which marine species were largest, most abundant, and/ or most easy to capture within 5-10 km of the islands they occupied. This practice would have allowed them to gain the most food for the least energy.

Second, changes in the isotopic record generated from midbay sites are assumed to be caused by factors acting over time rather than through space. Thus, the isotopic record generated from archaeological bones is treated as a long-term record of the same environment. Spatial variation in a number of factors (nutrient concentrations, salinity, water temperature, etc.) has the potential to affect the isotopic composition of primary producers (and thus higher trophic levels) (Peterson, 1999). This variation was

minimized, and potentially negated, by analyzing only sites that cluster tightly around North Haven Island, in the middle of Penobscot Bay.

3. Results

3.1 Bone Sample Preservation

Archaeological and modern bone collagen of cod, flounder, and sculpin all had similar C/N atomic ratios, %C data, and %N data, although modern bones had greater collagen recoveries by weight (**Table 9**). Archaeological bone collagen had mean C/N atomic ratios between 3.4 and 3.5, and modern bone collagen had mean C/N ratios between 3.1 and 3.7. Archaeological bone collagen of each species varied between 12.2 %N and 13.6 %N and between 28.9 %C and 39.1 %C. Modern bone collagen varied between 12.4 %N and 16.4 %N and between 36.9 %C and 48.3 %C. Archaeological bone collagen varied between 11.9% and 13.9% collagen recovered on average for each species. Modern bones of each species were between 30.5% and 32.6% collagen by weight on average. The collagen content of modern bones was more variable than that of archaeological samples, although this may be a reflection of smaller sample sizes for modern bones.

A subset of modern and archaeological bones was monitored for the presence of a collagen ghost using a series of photographs. All photographed bones possessed a collagen ghost after demineralization. Typical modern and archaeological cod bone samples are shown—in both cases the demineralized bone resembles the shape and size of the original bone sample (**Figure 6**).

The lower collagen recoveries of archaeological bones indicate that some collagen is lost over time. The C/N, %C, and %N data, however, show that carbon and nitrogen appear to be lost in equal proportions over time. Thus the amount of collagen in archaeological samples is reduced but its chemical composition remains intact. These

Table 9. Geochemical Measures of Bone Preservation
The C/N atomic ratios, %C, %N, and % collagen recovered by weight (mean ± SD) for modern and archaeological samples from Penobscot Bay.

	Archaeological			Modern		
	Cod	**Flounder**	**Sculpin**	**Cod**	**Flounder**	**Sculpin**
C/N (Molar)	3.5 ± 0.2	3.5 ± 0.1	3.4 ± 0.2	3.7 ± 0.1	3.6 ± 0.1	3.1 ± 0.03
%C	37.3 ± 4.9	28.9 ± 4.2	39.1 ± 5.0	36.9 ± 8.4	47.9 ± 3.6	48.3 ± 1.7
%N	12.2 ± 2.6	13.6 ± 1.9	13.6 ± 2.1	12.4 ± 3.3	14.4 ± 1.6	16.4 ± 0.5
% Collagen Recovered	13.9 ± 1.3	12.4 ± 0.7	11.9 ± 0.6	32.6 ± 7.3	30.5 ± 4.3	31.4 ± 6.8
n	26	23	37	9	8	3
No. Sites	6	6	8	2	2	1

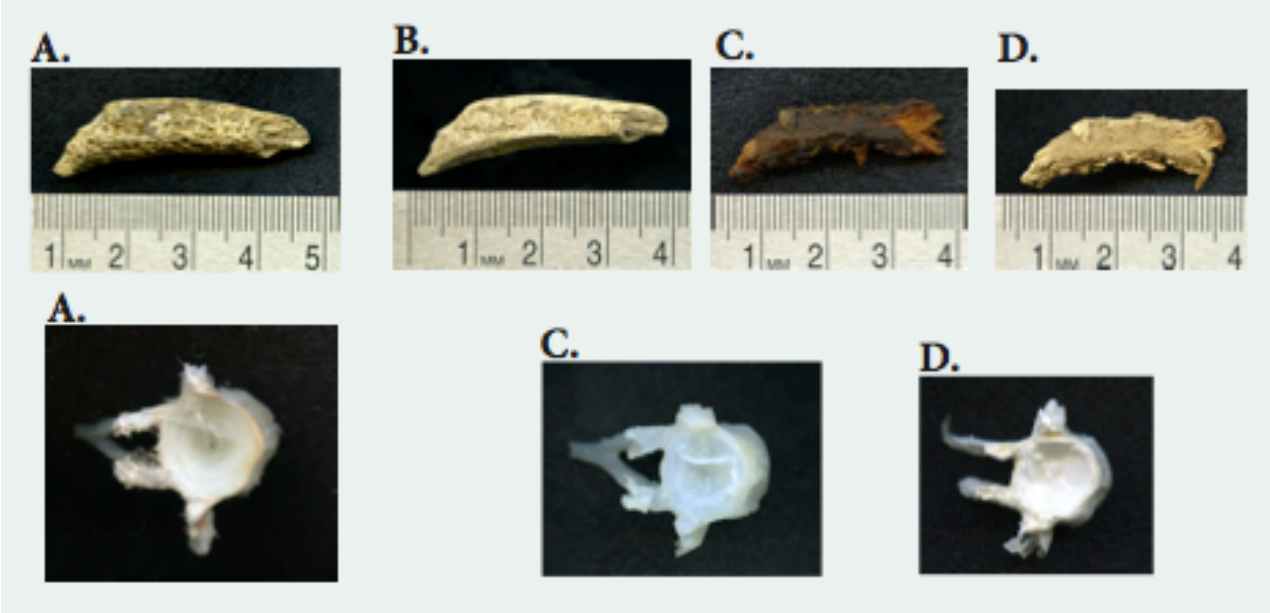

Figure 6. Photographic Record of Typical Modern and Archaeological Bones

The process of preparing bones for isotopic analysis was documented with an Epson V750 Photo flatbed scanner. Typical results are presented here. The first row shows a 2,400-year-old cod head bone from Turner Farm. The second row shows a modern cod vertebra from 20-30 km offshore in the GoM.

A) The original bone sample. B) The archaeological sample after scouring with the dremel tool. C) The bones after demineralization in hydrochloric acid; wet. D) The "collagen ghost"; demineralized bones after freeze-drying.

C/N values, % collagen recoveries, and the presence of collagen ghosts fulfill the requirements for good preservation put forward by Turross et al. (1989) and are in good agreement with other paleodietary studies (P. Koch, personal communication). Thus, the bone samples from archaeological middens appear to be well preserved and their isotopic composition should reflect the diets of animals living thousands of years ago. This high degree of preservation is likely a result of the presence of calcium carbonate ($CaCO_3$)-containing shells in the middens, which mitigates the effect of acid rain on bones (Bourque, 1995).

3.2 Isotopic Composition of Modern Samples

In both cod and flounder, the nearshore sample was more enriched in ^{13}C and ^{15}N than the offshore sample. The average ^{13}C of cod from the nearshore sample was 1.7‰ more enriched than the offshore sample after OSE correction ($t_{(7)}$=5.317, P<0.05) (**Table 10**). Cod from the nearshore sample was also more enriched in ^{15}N by about 1‰, although this difference was not statistically significant ($t_{(7)}$=1.231, P=0.258).

The average ^{13}C of flounder from the nearshore sample was 1.7‰ more enriched than the offshore sample after OSE correction ($t_{(6)}$=3.785, P<0.05). Flounder from the nearshore sample was also more enriched in ^{15}N by about 0.5‰, although this difference was not statistically significant ($t_{(6)}$=0.421, P=0.689).

No offshore sculpin were collected for this study. The ^{13}C of nearshore sculpin was -12.5‰ (after OSE correction), which is slightly more depleted than the nearshore cod. The ^{15}N of nearshore sculpin was 14.6‰, which is higher than any of the other modern samples, and equates to a trophic level of 3.4. There were no significant

Table 10. Isotopic Composition of Modern Bones

The ^{13}C and ^{15}N (mean ± SE) of bone collagen from all modern samples. * Indicates modern samples that have been corrected for the Oceanic Suess Effect (see methods). The trophic level and number of individual fish sampled (n) is also shown.

Species	**Location**	**^{13}C**	**^{13}C***	**^{15}N**	**Mean Trophic Level**	**n**
Cod	Nearshore	-13.7 ± 0.4	-12.2 ± 0.4	13.7 ± 0.6	3.2	2
	Offshore	-15.4 ± 0.4	-13.9 ± 0.4	12.8 ± 0.3	3.0	3
Flounder	Nearshore	-15.9 ± 0.2	-14.3 ± 0.2	12.2 ± 1.3	2.8	3
	Offshore	-17.5 ± 0.6	-16.0 ± 0.2	11.7 ± 0.1	2.7	2
Sculpin	Nearshore	-14.0 ± 0.1	-12.5 ± 0.1	14.6 ± 0.5	3.4	3

differences among nearshore cod, flounder, and sculpin in ^{13}C or ^{15}N (see Section 3.4.3 Relationship Among Study Species at each Time Horizon).

3.3 Isotopic Composition of Archaeological Samples

3.3.1 Middle Bay Sites

Cod Bone Collagen

In the middle Bay archaeological sites examined, the mean ^{13}C of cod ranged from -14.0‰ at Crocker to -12.2‰ at Bull Rock (**Table 11, Figure 7**). The mean ^{15}N ranged from 15.0‰ at Bull Rock to 15.7‰ at Turner Farm (**Figure 8**). The mean ^{13}C and ^{15}N of cod did not differ through time, although modern cod are 2‰ more depleted in ^{15}N than cod from 2400 BP (**Table 12**).

Flounder Bone Collagen

In the middle Bay archaeological sites examined, the mean ^{13}C of flounder ranged from -12.2‰ at Bull Rock to -10.3‰ at Turner Farm (**Table 13**). ^{13}C values decreased by 3.5‰ from 2,400 BP to the present. The mean ^{15}N of flounder ranged from 12.1‰ at Turner Farm to 13.4‰ at Bull Rock. The ^{13}C of flounder from Crocker was the most variable (SE=0.9) compared to flounder from other sites.

The mean ^{13}C of flounder bone collagen differed through time ($F_{(3,14)}$=4.774, P<0.05) (**Table 12**). The results of a Tukey's multiple-comparison post-hoc test are shown in **Figure 9**. The mean ^{15}N of flounder bone collagen did not differ through time (**Figure 10**).

Table 11. Isotopic Composition of Archaeological Cod Bones
The ^{13}C and ^{15}N (mean ± SE) of cod bone collagen from five archaeological samples. The trophic level of each sample, number of individual fish sampled (n) and approximate age of each site is also shown. Ages are given in cal BP years except for Asbornsen, which was dated based on cultural artifacts, and whose age is given in estimated years before present.

Location	**Site**	**^{13}C**	**^{15}N**	**Mean Trophic Level**	**n**	**Age of Site (cal Years BP)**
Inner Bay	Asbornsen	-11.3 ± 0.3	15.0 ± 0.4	3.5	6	400
Outer Bay	Bar Island	-12.5 ± 0.3	15.3 ± 0.3	3.6	6	1600
Middle Bay	Bull Rock	-12.2 ± 0.6	15.0 ± 0.5	3.6	5	500
	Crocker	-14.0 ± 0.4	15.1 ± 0.4	3.6	6	1000
	Turner Farm	-12.6 ± 0.6	15.7 ± 0.3	3.7	4	2400

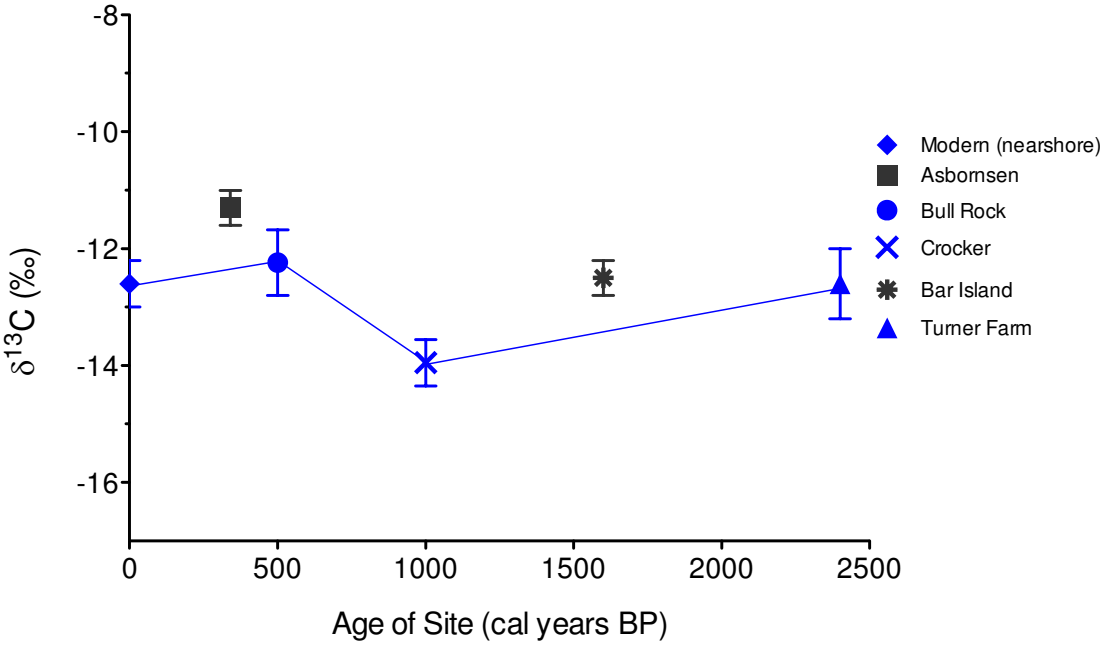

Figure 7. The $\delta^{13}C$ of cod bone collagen
The ^{13}C (mean ± SE) of cod bone collagen plotted against the age of the midden strata from which the bones were collected. Middle bay sites are shown in blue, sites from the inner and outer bay are shown in black. Lines connect archaeological sites from the middle bay to the modern nearshore sample.

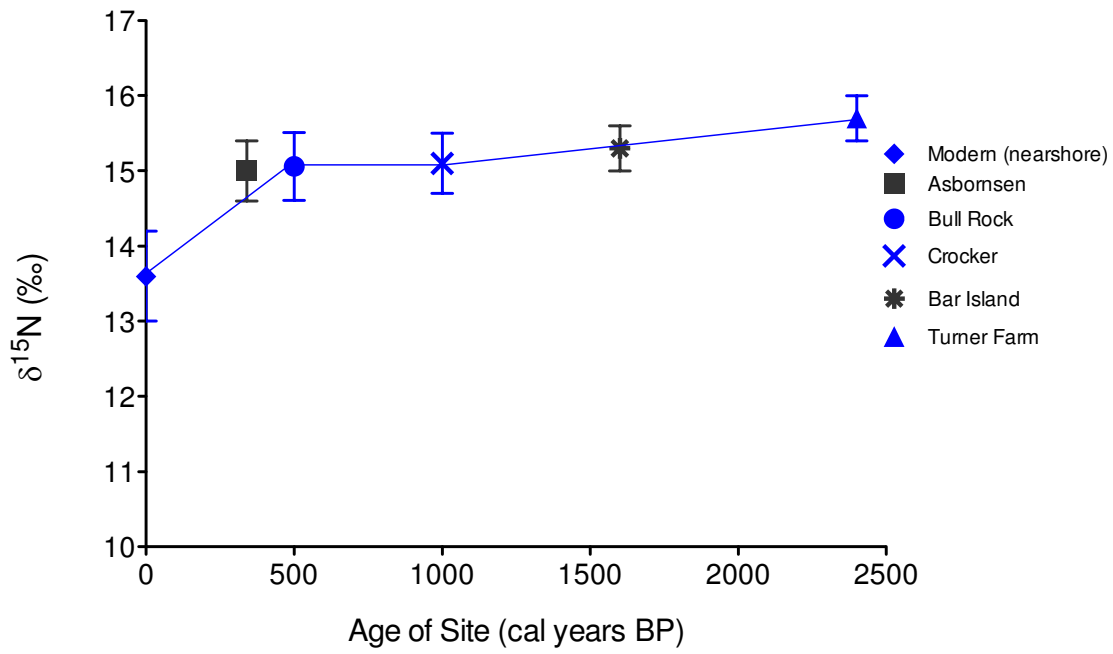

Figure 8. The $\delta^{15}N$ of cod bone collagen

The ^{15}N (mean ± SE) of cod bone collagen plotted against the age of the midden strata from which the bones were collected. Middle bay sites are shown in blue, sites from the inner and outer bay are shown in black. Lines connect archaeological sites from the middle bay to the modern nearshore sample.

Table 12. Statistical Results

Summary of the results of six 1-Way ANOVA tests with Tukey's multiple-comparison post-hoc tests. F-values, degrees of freedom (t=treatment, r=residual), and *P*-values for each test are shown. Only significant pair-wise comparisons ($P<0.05$) are listed.

Species	Groups (^{13}C)	F (d.f. $_t$, d.f. $_r$)	*P*-value	Groups (^{15}N)	F (d.f. $_t$, d.f. $_r$)	*P*-value
Cod	All (4)	2.937 (3,16)	0.0729	All (4)	2.224 (3,13)	0.134
Flounder	All (4)	4.774 (3,14)	0.017	All (4)	0.7069 (3,14)	0.564
	Modern vs. Crocker		<0.05			
	Modern vs. Turner Farm		<0.05			
Sculpin	All (6)	5.855 (5,14)	0.0011	All (6)	2.752 (5,24)	0.042
	Bull Rock vs. Oak Hill		<0.01			
	Crocker vs. Oak Hill		<0.01			
	Turner Farm vs. Oak Hill		<0.01			

Table 13. Isotopic Composition of Archaeological Flounder Bones
The ^{13}C and ^{15}N (mean ± SE) of flounder bone collagen from five archaeological samples. The trophic level of each sample, number of individual fish sampled (n) and approximate age of each site is also shown. Ages are given in cal BP years except for Asbornsen, which was dated based on cultural artifacts, and whose age is given in estimated years before present.

Location	Site	^{13}C	^{15}N	Mean Trophic Level	n	Age of Site (cal Years BP)
Inner Bay	Asbornsen	-10.8 ± 0.4	13.0 ± 0.2	3.0	6	400
Outer Bay	Bar Island	-10.7 ± 2.1	13.1 ± 0.1	3.0	2	1600
Middle Bay	Bull Rock	-12.2 ± 0.5	13.4 ± 1.0	3.1	6	500
	Crocker	-10.8 ± 0.9	13.1 ± 0.3	3.0	5	1000
	Turner Farm	-10.3 ± 0.8	12.1 ± 0.6	2.8	5	2400

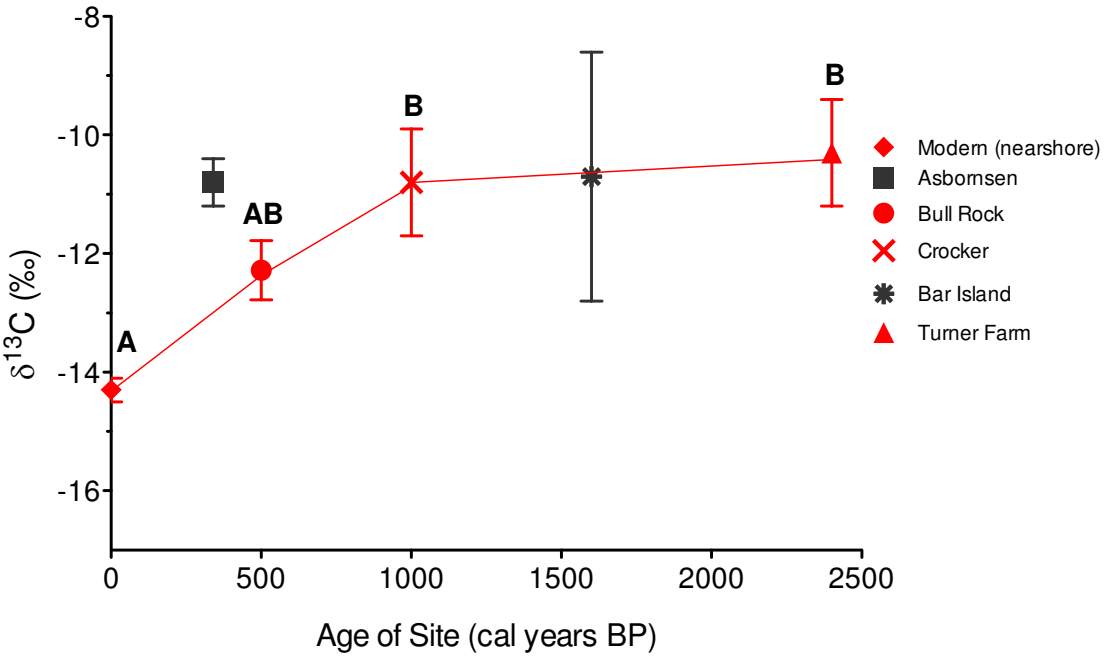

Figure 9. The $\delta^{13}C$ of flounder bone collagen

The ^{13}C (mean ± SE) of flounder bone collagen plotted against the age of the midden strata from which the bones were collected. Middle bay sites are shown in red, sites from the inner and outer bay are shown in black. Middle bay groups that do not share a letter are significantly different as determined with a 1-Way ANOVA with Tukey's multiple-comparison post-hoc test ($P<0.05$). Lines connect archaeological sites from the middle bay to the modern nearshore sample.

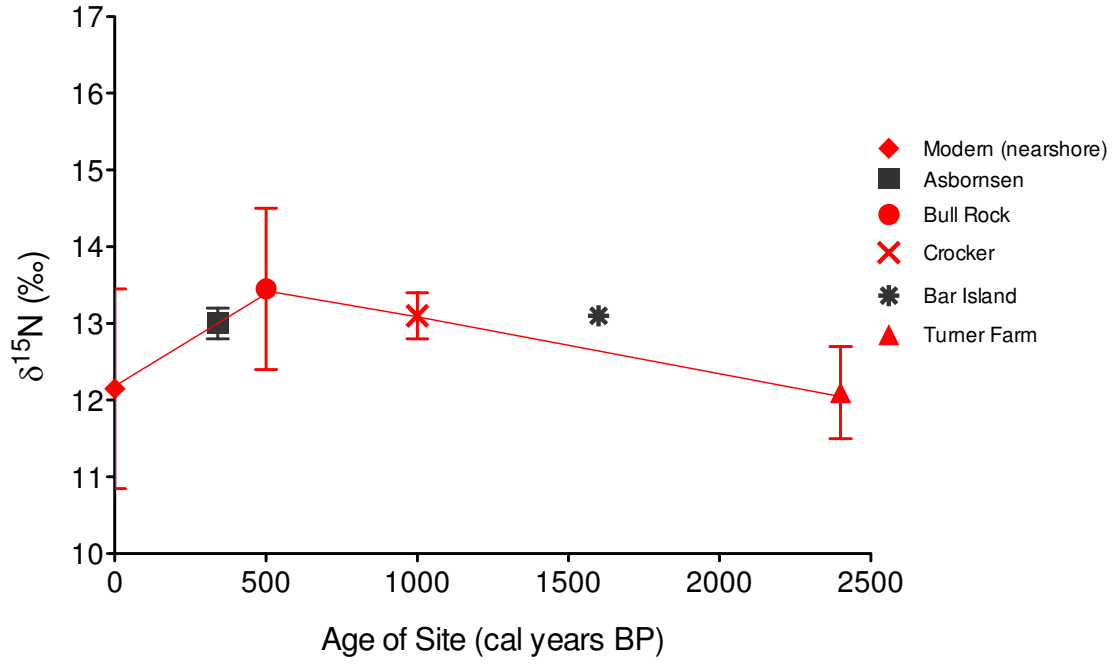

Figure 10. The $\delta^{15}N$ of flounder bone collagen

The ^{15}N (mean ± SE) of flounder bone collagen plotted against the age of the midden strata from which the bones were collected. Middle bay sites are shown in red, sites from the inner and outer bay are shown in black. Lines connect archaeological sites from the middle bay to the modern nearshore sample.

Sculpin Bone Collagen

In the middle bay archaeological sites examined, the mean ^{13}C of sculpin ranged from -11.5‰ at Turner Farm to -14.2 at Oak Hill (**Table 14**). The mean ^{15}N of sculpin ranged from 12.19‰ at Oak Hill to 14.9‰ at Bull Rock. Sculpin from Turner Farm was the most variable in both ^{13}C and ^{15}N.

The mean ^{13}C of sculpin bone collagen differed among all sites ($F_{(5,24)}$=5.855, *P*<0.05) (**Table 12**). The results of a Tukey's multiple-comparison post-hoc test are shown in **Figure 11**. The mean ^{15}N of sculpin bone collagen also differed among all sites ($F_{(5,24)}$=2.752, *P*<0.05), although no pairwise comparisons were significant (**Figure 12)**.

3.3.2 Inner and Outer Bay Sites

Cod Bone Collagen

Cod from Asbornsen site, in the inner Bay, had a mean ^{13}C of -11.3‰ and a mean ^{15}N of 15.0‰. Cod from Bar Island, in the outer Bay, had a mean ^{13}C of -12.5‰ and a mean ^{15}N of 15.3‰.

Flounder Bone Collagen

Flounder from Asbornsen site, in the inner Bay, had a mean ^{13}C of -10.8‰ and a mean ^{15}N of 13.0‰. Flounder from Bar Island, in the outer Bay, had a mean ^{13}C of -10.7‰ and a mean ^{15}N of 13.1‰. The ^{13}C of flounder from Bar Island was extremely variable (SE=2.1), which is likely because only two flounder bones were examined from this site.

Table 14. Isotopic Composition of Archaeological Sculpin Bones
The ^{13}C and ^{15}N (mean ± SE) of sculpin bone collagen from seven archaeological samples. The trophic level of each sample, number of individual fish sampled (n) and approximate age of each site is also shown. Ages are given in cal BP years except for Asbornsen and Oak Hill which were dated based on cultural artifacts, and whose age is given in estimated years before present.

Location	Site	^{13}C	^{15}N	Mean Trophic Level	n	Age of Site (cal Years BP)
Inner Bay	Asbornsen	-11.6 ± 0.4	14.4 ± 0.4	3.4	6	400
Outer Bay	Bar Island	-12.1 ± 0.5	14.8 ± 0.3	3.5	6	1600
Middle Bay	Bull Rock	-11.7 ± 0.3	14.9 ± 0.6	3.5	6	500
	Crocker	-11.8 ± 0.4	14.6 ± 0.5	3.4	6	1000
	Oak Hill	-14.2 ± 0.5	12.9 ± 0.1	3.0	6	1800
	Butter Island	-13.3 ± 0.3	13.2 ± 0.2	3.1	4	2000
	Turner Farm	-11.5 ± 0.6	14.3 ± 0.8	3.4	5	2400

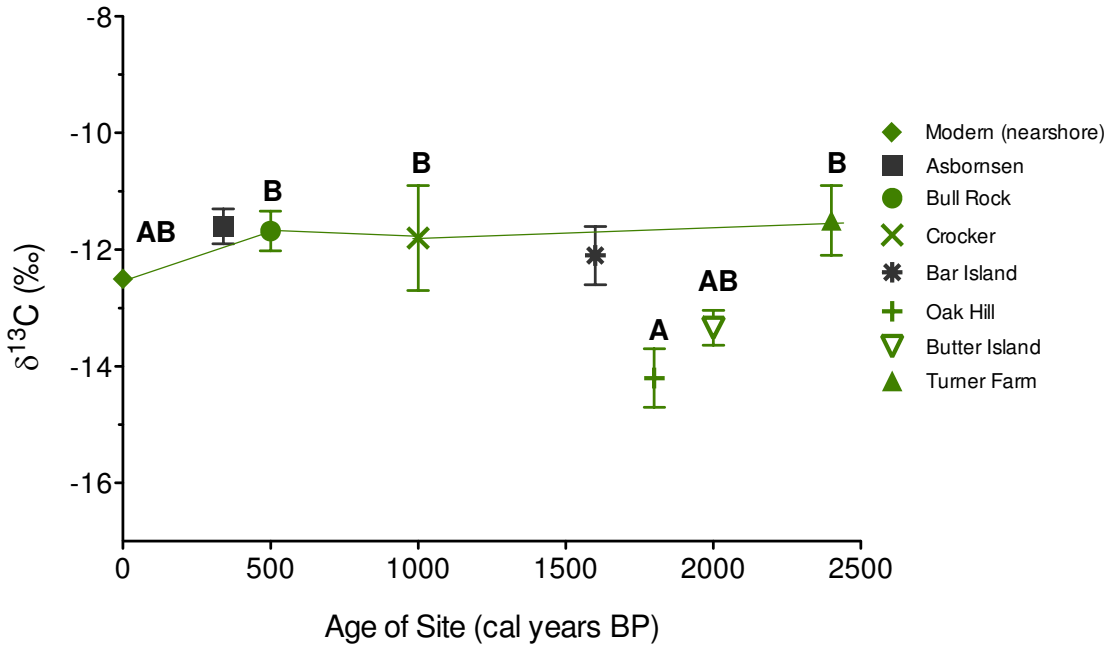

Figure 11. The $\delta^{13}C$ of sculpin bone collagen
The ^{13}C (mean ± SE) of sculpin bone collagen plotted against the age of the midden strata from which the bones were collected. Middle bay sites are shown in green, sites from the inner and outer bay are shown in black. Middle bay groups that do not share a letter are significantly different as determined with a 1-Way ANOVA with Tukey's multiple-comparison post-hoc test ($P<0.05$). Lines connect archaeological sites from the middle bay to the modern nearshore sample.

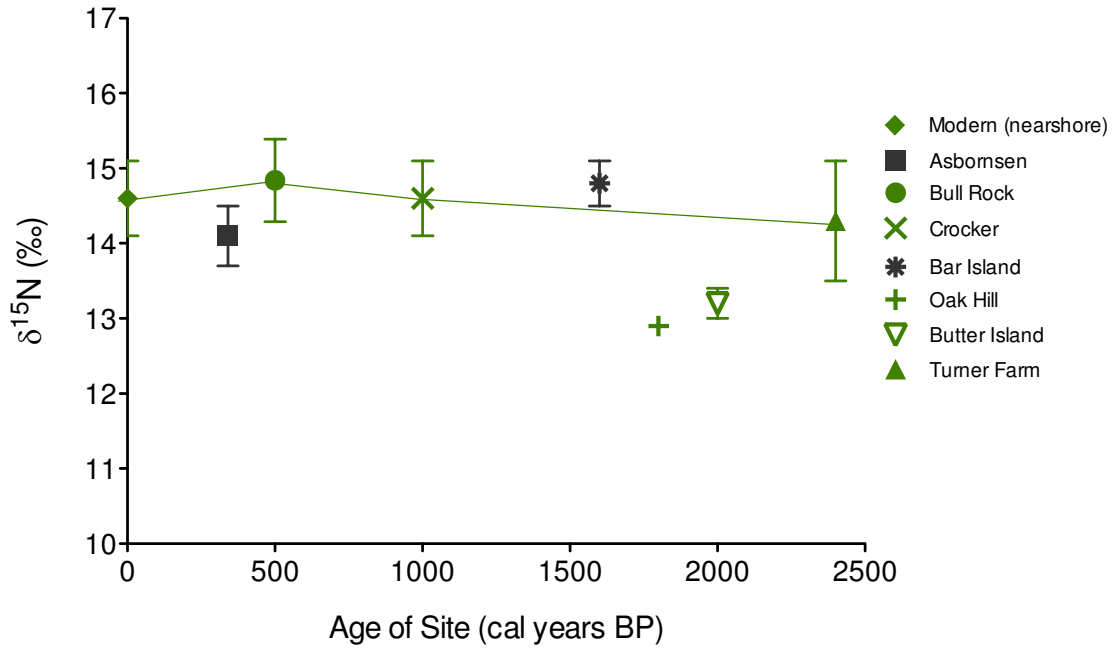

Figure 12. The $\delta^{15}N$ of sculpin bone collagen

The ^{15}N (mean ± SE) of sculpin bone collagen plotted against the age of the midden strata from which the bones were collected. Middle bay sites are shown in green, sites from the inner and outer bay are shown in black. Middle bay groups are significantly different, although no pairwise comparisons were significant. Lines connect archaeological sites from the middle bay to the modern nearshore sample.

Sculpin Bone Collagen

Sculpin from Asbornsen site, in the inner Bay, had a mean ^{13}C of -11.6‰ and a mean ^{15}N of 14.4‰. Sculpin from Bar Island, in the outer Bay, had a mean ^{13}C of -12.1‰ and a mean ^{15}N of 14.8‰.

Comparison to Middle Bay Sites

The isotopic signature of bones from the inner and outer bay sites in Penobscot Bay do not appear to fit with the ^{13}C and ^{15}N trends established in the middle bay sites (**Figures 7-12**). The samples from Asbornsen fall above the middle bay trend line for ^{13}C in all three species. Compared to the middle bay ^{15}N trend line, the signal from Asbornsen samples is more enriched for cod and more depleted for sculpin. The sculpin ^{15}N from Asbornsen falls on the middle bay trend line. Cod from Bar Island were more enriched in ^{13}C than the middle bay ^{13}C trend line predicts, but the ^{15}N of Bar Island cod fell exactly on the middle bay ^{15}N trend line. The flounder and sculpin samples from Bar Island appear to fit respective middle bay ^{13}C trend lines, however both were more enriched in ^{15}N than their middle bay ^{15}N trend lines predict.

As mentioned previously, it is not currently possible to control for spatial differences within the bay, so it is difficult to determine if these differences represent changes to nearshore ecosystem dynamics through time or simply spatial heterogeneity within the bay.

3.4 Determining Long-term Trends

Isotopic data from the midbay regions over the period of time between 2,000 BP and 1,600 BP only exist for sculpin (Oak Hill and Butter Island) (**Figures 11 and 12**). While it is possible to infer a more ^{13}C-depleted basal carbon source and a reduction in

trophic level for sculpin for this time period, it is impossible to determine if these shifts are specific to sculpin or are experienced more widely through the ecosystem.

3.4.1 Carbon Isotopes

Temporal shifts in ^{13}C values are most significant in flounder (4‰ decrease in ^{13}C values over the last 2,400 years) (**Figure 13**). The most rapid shift appears to begin after 1,000 BP. Cod vary by approximately 2‰ through time, with the most depleted values occurring at 1,000 BP and the most enriched values occurring between 500 BP and the present. Sculpin vary by approximately 2.5‰ through time and are the most depleted at 1,800 BP and the most enriched at 500 BP. Between 500 BP and present, the ^{13}C of all species decreases although the magnitude of this shift is greatest for flounder (2.1‰), followed by cod (0.9‰) and sculpin (0.8‰).

3.4.2 Nitrogen Isotopes

Temporal shifts in ^{15}N values are most pronounced in cod and sculpin, each of which vary by approximately 2‰ over the last 2,400 years (**Figure 14**). Flounder varies by approximately 1.3‰ over the last 2,400 years. Cod become more depleted over time, with the most rapid decrease occurring between 500 BP and the present. Flounder and sculpin exhibit the same trend at time horizons that contain data for both species. The ^{15}N of flounder and sculpin increase from 2,400 BP to 500 BP. Between 500 BP and the present the ^{15}N of flounder and sculpin both decrease.

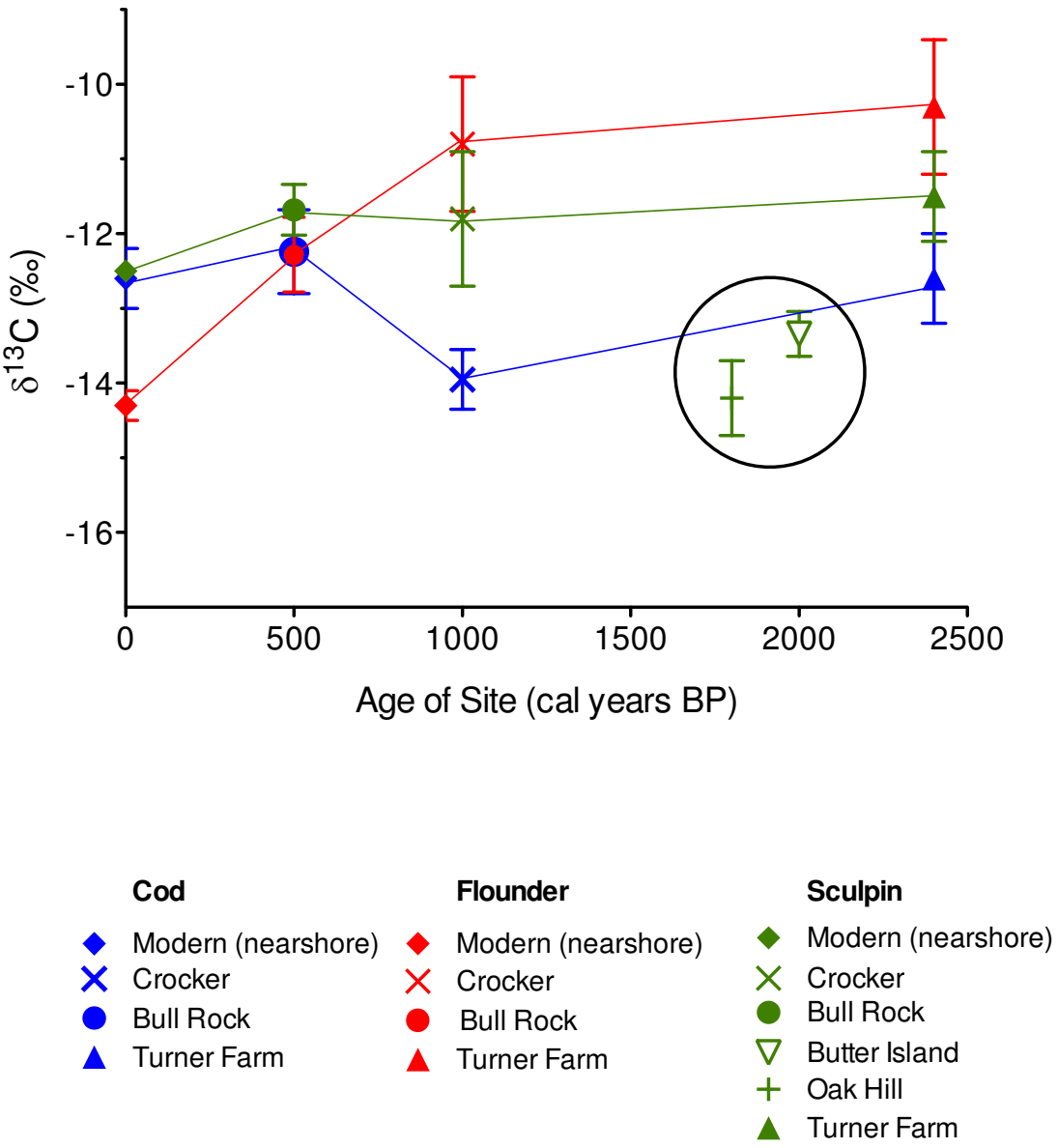

Figure 13. The $\delta^{13}C$ of Middle Bay Sites

The ^{13}C (mean ± SE) of modern (nearshore) and archaeological bone collagen from cod, flounder, and sculpin are plotted against the age of the midden strata from which the bones were collected. Only data from sites in the middle of the bay are shown. Data from middens that only contained sculpin bones are circled and were not included in further analyses because there were no corresponding data from cod or flounder with which to compare these samples.

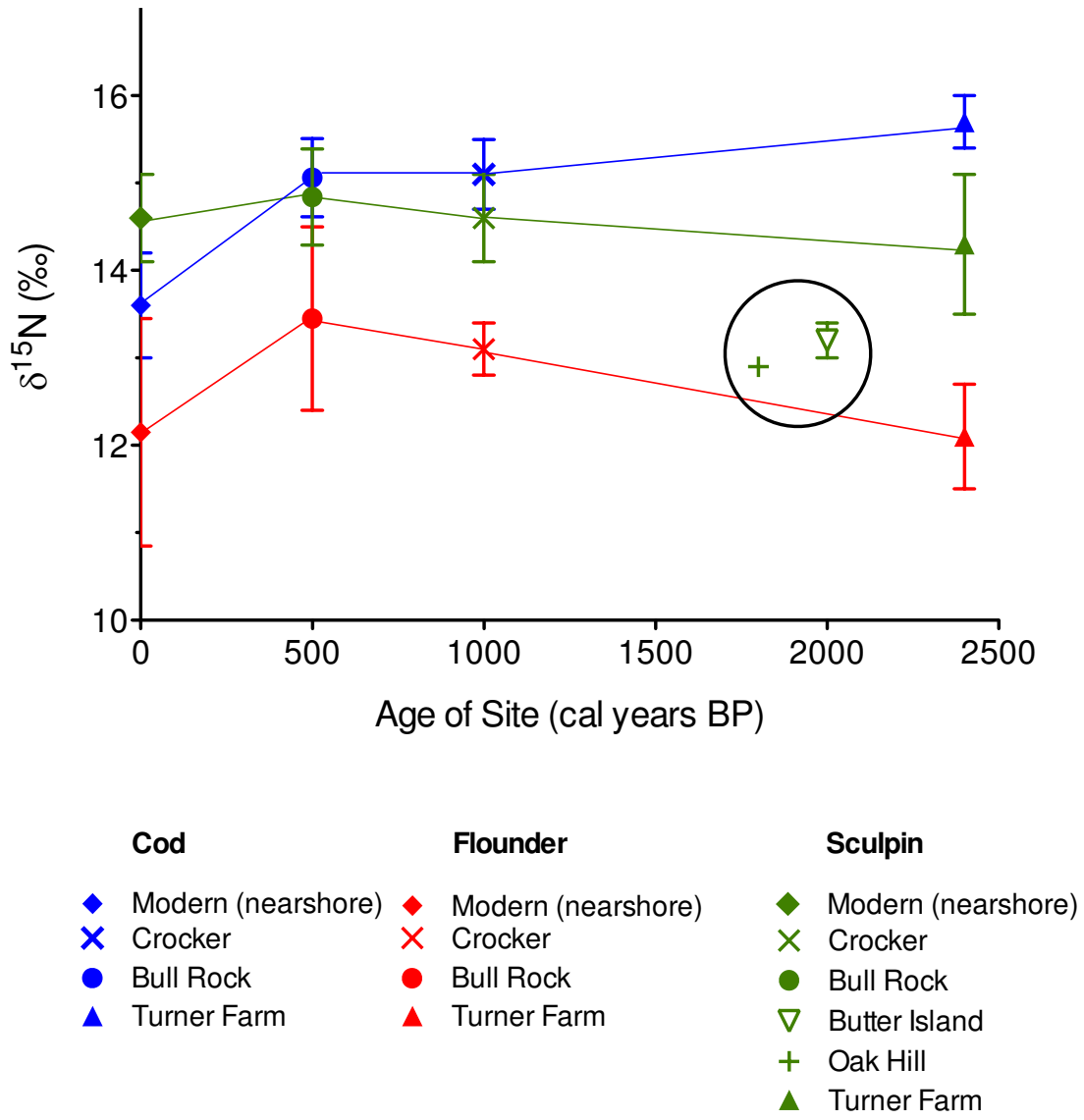

Figure 14. The $\delta^{15}N$ of Middle Bay Sites

The ^{15}N (mean ± SE) of bone collagen from modern (nearshore) and archaeological cod, flounder, and sculpin from the middle of Penobscot Bay are plotted against the age of the midden strata from which the bones were collected. Only data from sites in the middle of the bay are shown. Data from middens that only contained sculpin bones are circled and were not included in further analyses because there was no corresponding data from cod or flounder with which to compare these samples.

3.4.3 Relationship Among Study Species at each Time Horizon

A comparison of carbon and nitrogen isotope data among all three fish species at each time horizon and then examining changes to these patterns over time, has the potential to reveal information on ecosystem-wide changes that might have occurred, such as changes to ecological niche width.

The ^{13}C and ^{15}N offset between cod, flounder, and sculpin at each time horizon is not constant, although cod tend to be the most enriched in ^{15}N followed by sculpin and flounder (**Figure 15**). At 2,400 BP and 500 BP, there was no difference among the ^{13}C of study species (2,400 BP: $F_{(2,11)}=2.679$, $P=0.113$, 500 BP: $F_{(2,14)}=0.536$, $P=0.596$). At 1,000 BP, however, cod were more depleted in ^{13}C than flounder or sculpin ($F_{(2,14)}=7.928$, $P<0.05$). In modern nearshore systems, flounder are more depleted than cod or flounder ($F_{(2,5)}=27.21$, $P<0.05$).

The relationship among ^{15}N values of each species is the same at 2,400 years and 1,000 years ago. Cod is more enriched than flounder, and sculpin is not significantly different from either other species (2,400 BP: $F_{(2,11)}=8.772$, $P<0.05$, 1,000 BP: $F_{(2,14)}=5.623$, $P<0.05$). Sometime after 1,000 BP this relationship is disturbed and ^{15}N values do not differ among species at either 500 BP ($F_{(2,14)}=1.331$, $P=0.296$) or in modern nearshore systems ($F_{(2,5)}=2.207$, $P<0.206$).

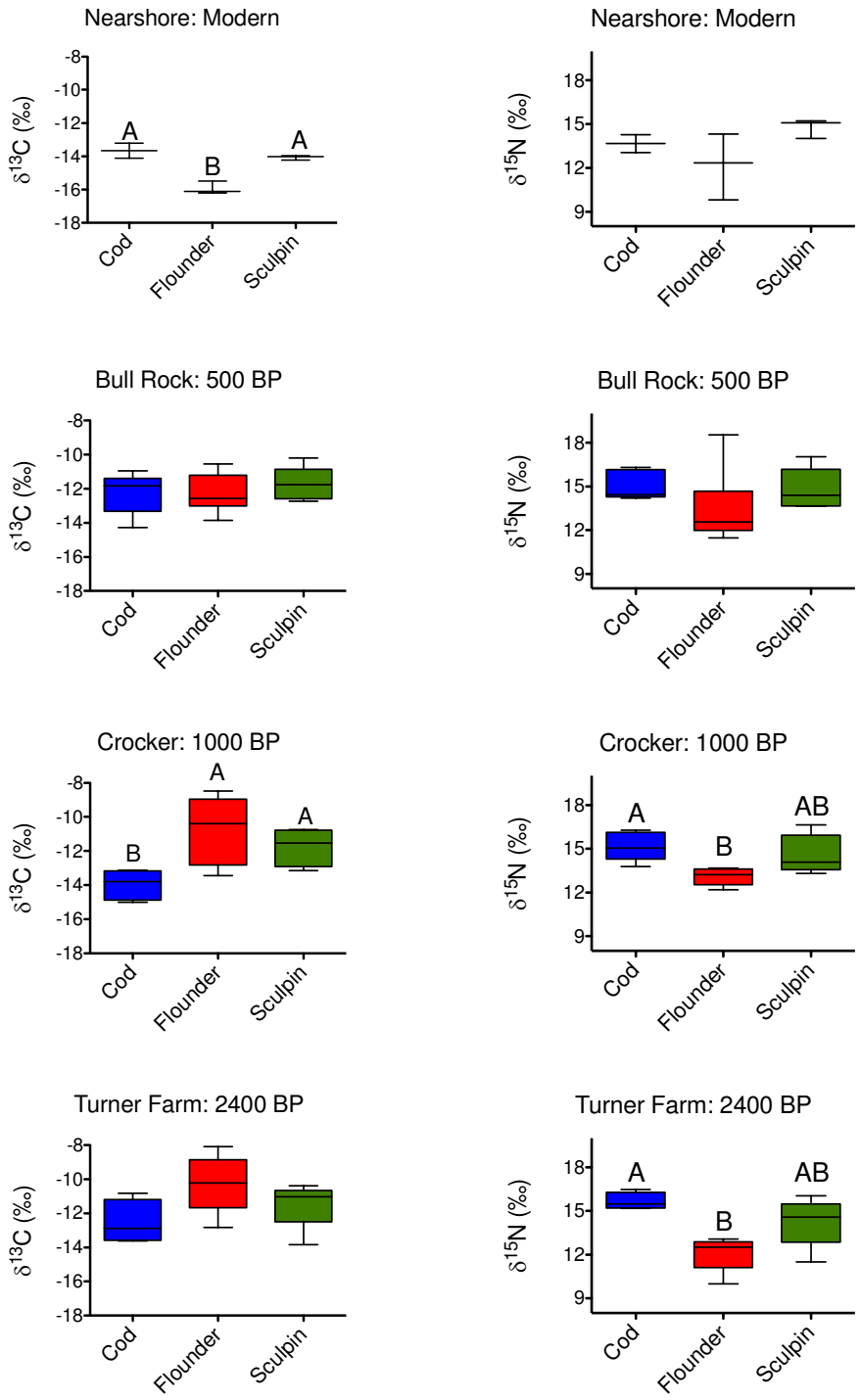

Figure 15. Relationship between $\delta^{13}C$ and $\delta^{15}N$ of Study Species at Middle Bay Sites
The ^{13}C and ^{15}N of cod, flounder, and sculpin at each midden. Whiskers show the minimum and maximum value, boxes enclose the first and third quartile when appropriate (when groups consisted of more than 3 data points) and the line shows the mean. The ^{13}C and ^{15}N of each species at each site was compared with a 1-Way ANOVA and Tukey's multiple-comparison post-hoc test. Lettered groups that do not share a particular letter differ significantly ($P<0.05$). If no letters are given, there are no significant among between species.

4. Discussion

4.1 Modern GoM System

Modern offshore samples of cod and flounder were more depleted in ^{13}C than nearshore samples of the same species, which agrees with findings of previous studies (Hobson et al., 1997; Burton and Koch, 1999; Sherwood and Rose, 2005). This difference likely results from differences in the ^{13}C of primary producers that are propagated to higher trophic levels (Michener and Schell, 1994; Hobson et al., 1997). Benthic macrophytes contribute greater amounts of production in shallow, nearshore areas than in offshore areas (Michener and Schell, 1994). Kelp and eelgrass (which are both more enriched in ^{13}C than phytoplankton) are more important to nearshore food webs in shallow areas of the GoM.

Variation in phytoplankton ^{13}C caused by species composition (Fry and Wainright, 1991), the concentration of CO_2 in the water column (Rau et al., 1992b), and nutrient levels (France, 1995) may contribute to the depletion of offshore samples. Phytoplankton in nearshore areas generally grow faster than phytoplankton in offshore areas because coastal upwelling provides nearshore systems with high nutrient supplies. Phytoplankton in areas of high productivity have more enriched ^{13}C values than in areas of lower productivity (Laws et al., 1995).

In both cod and flounder, the nearshore samples were more enriched in ^{15}N than offshore samples, although this difference was not statistically significant. This enrichment likely reflects anthropogenic inputs to coastal waters rather than implying that nearshore samples feed at a higher trophic level than offshore samples (Aguilar et al., 2008). Wastewater and artificial fertilizer, which enter coastal waters via runoff, are both more enriched in ^{15}N than natural N sources (Macko and Ostrom, 1994; Vander

Zanden et al., 2005). These anthropogenic nutrient inputs are incorporated into primary producers tissues, which are consumed by higher trophic levels. Thus the heavy N signal is propagated up food webs.

Modern cod, flounder, and sculpin from nearshore systems all range from -12.2‰ to -14.3‰ for ^{13}C and from 12.2‰ to 14.6‰ for ^{15}N. These data agree well with published N isotopic data on these species. Literature ^{13}C values for these species were often more depleted for cod and flounder and more enriched for sculpin. Atlantic cod bone collagen from other systems in the Northwest Atlantic was slightly more depleted in ^{13}C (-14.5‰ to -18.5‰ after OSE correction) and had similar ^{15}N values (12.6‰ to 15.1‰) (Fry, 1988; Hobson and Montevecchi, 1991; Sherwood and Rose, 2005; Sherwood et al., 2007). Winter flounder bone collagen from nearshore Newfoundland and Georges Bank ranged from -16.8‰ to -18.9‰ for ^{13}C (after OSE correction) and from 11.1‰ to 13.4‰ for ^{15}N (Fry 1988; Lesage et al., 2001). Bone collagen from a different species of sculpin in the *Cottidae* family in the Gulf of St. Lawrence was more enriched in ^{13}C (~-16.5‰ after OSE correction) and in ^{15}N (~16‰) than the Longhorn sculpin from Penobscot Bay (Lesage et al., 2003). Moustache sculpin (*Triglops murrayi*) from Newfoundland, Canada were also more enriched in ^{13}C (-18.5‰ after OSE correction) than the sculpin from Penobscot Bay, although their ^{15}N (13.8‰) agreed with that of this study (Sherwood and Rose, 2005).

The enrichment of Penobscot Bay flounder and cod relative to members of the same species caught in similar temperate environments may be reflecting the increased presence of aquatic macrophytes in the bay relative to the other system studies. Seagrasses and kelp are more common in shallow systems than in deeper offshore waters. This enrichment could also reflect higher productivity rates in Penobscot Bay, which, as previously mentioned, are associated with more ^{13}C-enriched phytoplankton

(Laws et al., 1995). Because there are no isotope values published on Longhorn sculpin to my knowledge, it is impossible to determine why the sculpin from Penobscot Bay are more depleted in ^{13}C than other species of sculpin, although it is likely related to foraging habits.

4.2 Changes to Nearshore Mid Bay Systems Through Time

4.2.1 Evidence from Stable C Analysis

Possible Loss of Eelgrass

Inferences about changes to the relative importance of each primary producer in the GoM can be made by examining the calculated ^{13}C of food sources that support each fish species through time (**Figure 16**). Although it appears that the majority of samples plot at or near the average ^{13}C range for kelp, it is unlikely that 100% of these fishes' diets are ultimately supported by kelp production. Kelp forests in the GoM are estimated to contain significantly less biomass than they did a century ago (Steneck et al., 2002), and are incapable of supporting the entire nearshore ecosystem of Penobscot Bay.

Phytoplankton production is known to support approximately 50% of nearshore net primary production (O'Reilly et al., 1987; Duarte and Cebrián, 1999). It is likely that phytoplankton contributed less, but still were a significant component of nearshore production in prehistoric times as well. Therefore, for fish bones to have intermediate

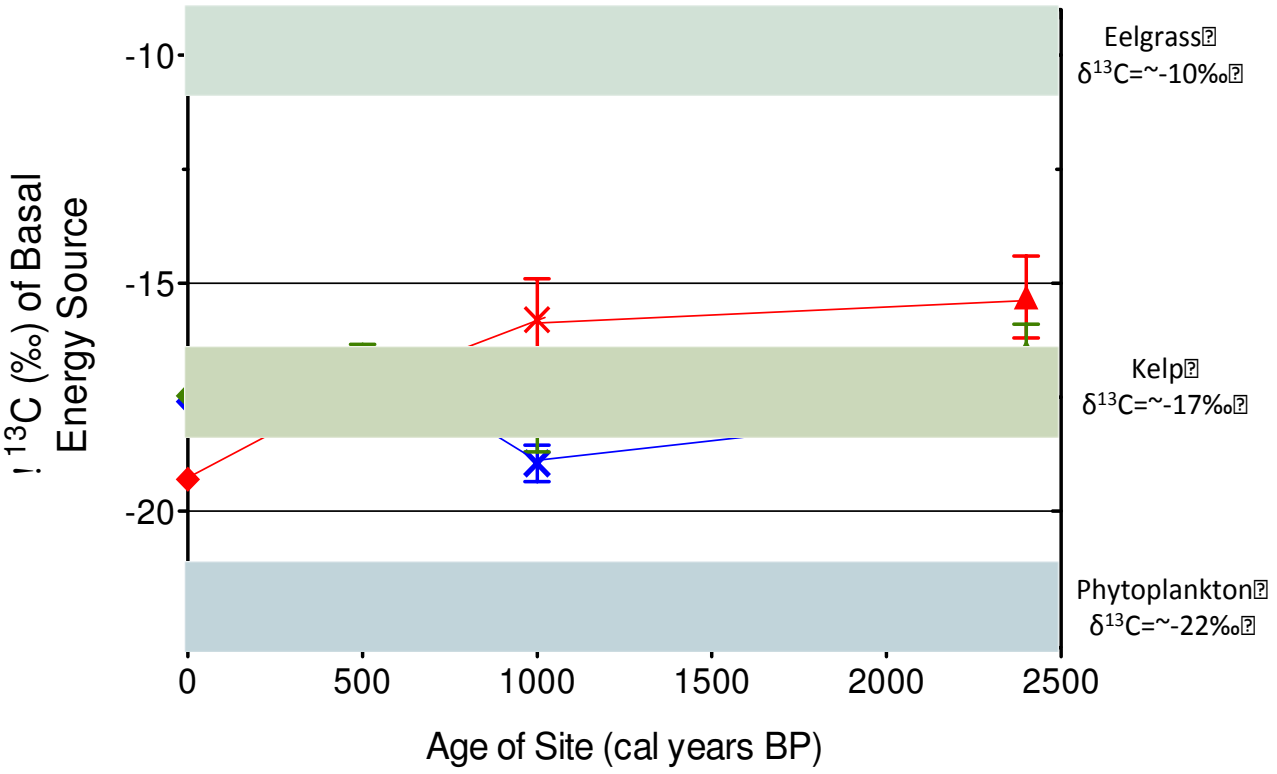

Figure 16. The $\delta^{13}C$ of Basal Energy Sources in Middle Bay Sites
The ^{13}C (mean ± SE) of the main carbon/ energy source of modern and archaeological cod (blue symbols), flounder (red symbols), and sculpin (green symbols). Data are plotted against the age of the midden strata from which the bones were collected. The colored bands represent ^{13}C (mean ± 1‰) of eelgrass, kelp, and phytoplankton (see Table 1). Only data from sites in the midbay that contained all three study species are shown.

^{13}C values, a more ^{13}C enriched food source, such as eelgrass, must also be an important carbon source. It follows that eelgrass was probably an important energy source in paleo environments, when fish bones were more ^{13}C-enriched, and that eelgrass plays a more minor role in modern ecosystems.

An overall decrease in ^{13}C of the baseline carbon source is evident in all three study species over last 500 years. This depletion may reflect a loss of eelgrass in Penobscot Bay (**Figure 17**), which contains at least 50% less eelgrass cover than it did a century ago (Muehlstein, 1989). As eelgrass cover is reduced, phytoplankton and kelp, which are more ^{13}C-depleted, likely became a more important C source to higher trophic levels.

The C isotopic signature of flounder may be the best indicator of the status of eelgrass in Penobscot Bay. Flounder rely on eelgrass for predation refuge and foraging habitat to a greater extent than cod or sculpin, although sculpin rely on eelgrass more than cod. The ^{13}C data of the three species through time support this theory; the more enriched values of flounder and sculpin indicate eelgrass likely contributed more energy to these fish than to cod. Modern research shows that eelgrass beds are important habitats for larval and juvenile flounder. Flounder young-of-the-year sampled along Maine's coast were more abundant in *Zostera marina* beds than in kelp (*Laminaria longicruris*), drift algae (*Phyllophora* spp.), or over bare substrate (sand or mud) (Lazzari, 2008). Adult cod are also more pelagic than either flounder or sculpin, and so are likely supported to a greater degree by phytoplankton (Link et al., 2009).

The ^{13}C of flounder declined rapidly between 1,000 BP and 500 BP and between 500 BP and the present, probably indicating a loss of eelgrass in Penobscot Bay. Eelgrass decline in North Atlantic systems over the last century has been well

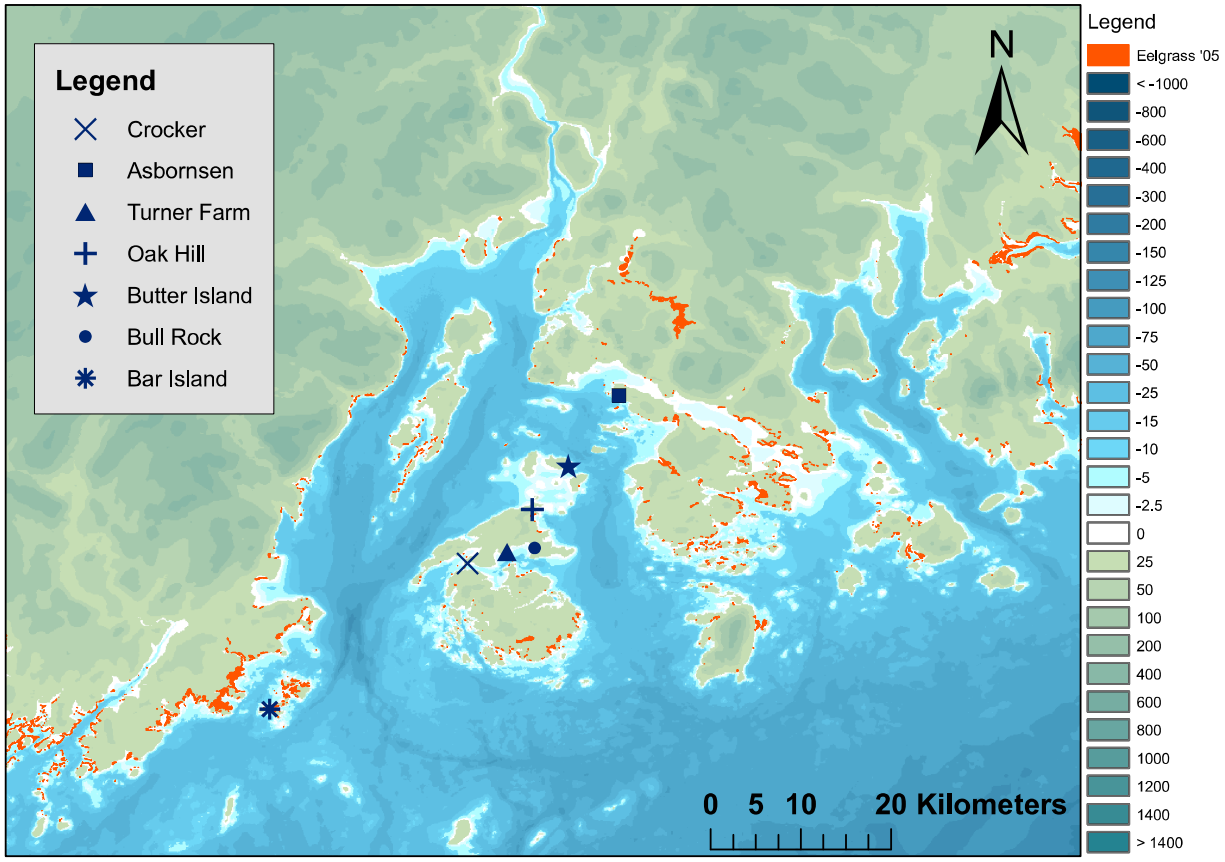

Figure 17. Modern Eelgrass Cover in Penobscot Bay
The approximate extent of eelgrass (*Zostera marina*) in 2005.

documented (ex. Orth et al., 2006). Causes of this decline include eutrophication (Short and Wylie-Echeverria, 1996), physical disturbances such as dredging, boating, and shell-fishing (Neckles et al., 2005), and wasting disease, which began in the 1930s (Short et al., 1986). Estimates suggest wasting disease reduced eelgrass cover in the North Atlantic by as much as 90% (Muehlstein, 1989).

The timing of the ^{13}C decrease in flounder, however, indicates that eelgrass in Penobscot Bay may have begun to decline between 1,000 BP and 500 BP. This decline in eelgrass before the arrival of Europeans could be the result of natural or anthropogenic factors. Seagrasses are extremely sensitive to water quality changes such as nutrient loading, which are often caused by human activities (Short and Wylie-Echeverria, 1996). It is possible that increased nutrient inputs to the Penobscot River from maize agriculture at inland locations reached Penobscot Bay. Indigenous groups on the northeast coast of America often burned areas of forest to create clearings for maize cultivation and this practice transferred nutrients and organic matter to rivers (Bourque, 2001). These inputs, which would have eventually reached Penobscot Bay could trigger the start of eutrophication events, to which eelgrass is extremely sensitive. It is also possible that the decline was caused by natural factors, such as a water-borne pathogen like the one hypothesized to cause wasting disease (Ralph and Short, 2002).

The exact carbon/ energy contribution of each primary producer to higher trophic level fish cannot currently be assessed. Mixing models are often used to evaluate the contribution of isotopically distinct primary producers to a given environment (see Post, 2002b). This technique generally requires data from isotopes numbering one less than the number of autotrophs in the system. Although the ^{13}C and ^{15}N of the main primary producers in the GoM have been quantified, there is little variation in ^{15}N among each autotroph and each species has a wide ^{15}N range. The average ^{15}N of kelp, eelgrass,

and phytoplankton all vary between 6-8‰ (McMillan, 1980; Fry, 1988; Fredriksen, 2003). To perform a mixing model analysis, the fish bones would need to be analyzed for the composition of a third stable isotope, such as sulfur, which is known to differ among primary producers (Connolly et al., 2004).

Ontogenic Effects

Changes in the ^{13}C of fish species through time could also be the result of changes in the size of fish being caught. All three study species are known to change their diet as they get older and larger. Sherwood et al. (2007) demonstrated that the ^{13}C of cod muscle increases with the size of the source fish. The magnitude of this increase is approximately 1-1.5‰ as fish increased from 20 to 70 cm. The ^{13}C of fish muscle appeared to remain relatively constant in fish greater than 70 cm. The exact size of the fish from archaeological sites is unknown, although the size and style of fishing hooks found in the middens suggest that they were specialized to catch large fish (Bourque, 1995). It is possible that recent decreases to the fish size in the GoM account for a small portion of the ^{13}C decline observed between 500 BP and the present, although this would only affect the magnitude, not the direction, of the trends observed.

4.2.2 Evidence from Stable N Analysis

Prehistoric Decline of Apex Predators, Rise of Mesopredators

The modern trophic level of all species produced from the given equation agrees with literature values for the trophic levels of all three species (Pereira, 1999; Link and Almeida, 2002; Link et al., 2009). The trophic level of cod has been declining since 2,400 BP, with the most rapid decline occurring over the last 500 years. From 2,400 BP to 500

BP, the trophic level of flounder and sculpin increased, and both species experienced a decline in trophic level over the last 500 years (**Figure 18**). Changes to trophic level for all three species may result from diet shifts that are related to changes in fish size. Larger demersal fish consume large fish and benthic invertebrates and smaller fish consume fewer fish, smaller invertebrates such as polychaetes, and more zooplankton (Sherwood et al., 2007 Pearcy, 1962 Link and Almeida, 2002).

It is most likely that the trophic level trends observed from 2,400 BP to 500 BP in the study species was caused by the fishing practices of the various groups of people who inhabited the Penobscot Bay coast and islands. In the western North Atlantic region, indigenous peoples have exploited cod by hook and line fishing for thousands of years (Bourque 1995; Bourque, 2001; Steneck, 1997), which explains why cod experience a decrease in trophic level 2,000 years earlier than sculpin or flounder. The magnitude of cod's trophic shift between 2,400 BP and 500 BP is smaller than the shift from 500 BP to the present likely because indigenous population densities were smaller and because their fishing methods were less efficient than modern day otter trawls and gillnets, so their effect on ecosystems was mitigated.

The abundance of cod in the Penobscot Bay likely began to decline when prehistoric fisheries targeted these populations. The reduction of cod, an apex predator, would release mesopredator populations (such as sculpin and flounder) from predation pressure and allow their numbers to expand (Steneck, 1997). Thus the removal of cod probably allowed mesopredators to grow in abundance and, likely, in size, which is suggested by the trophic level increases in flounder and sculpin observed in this study

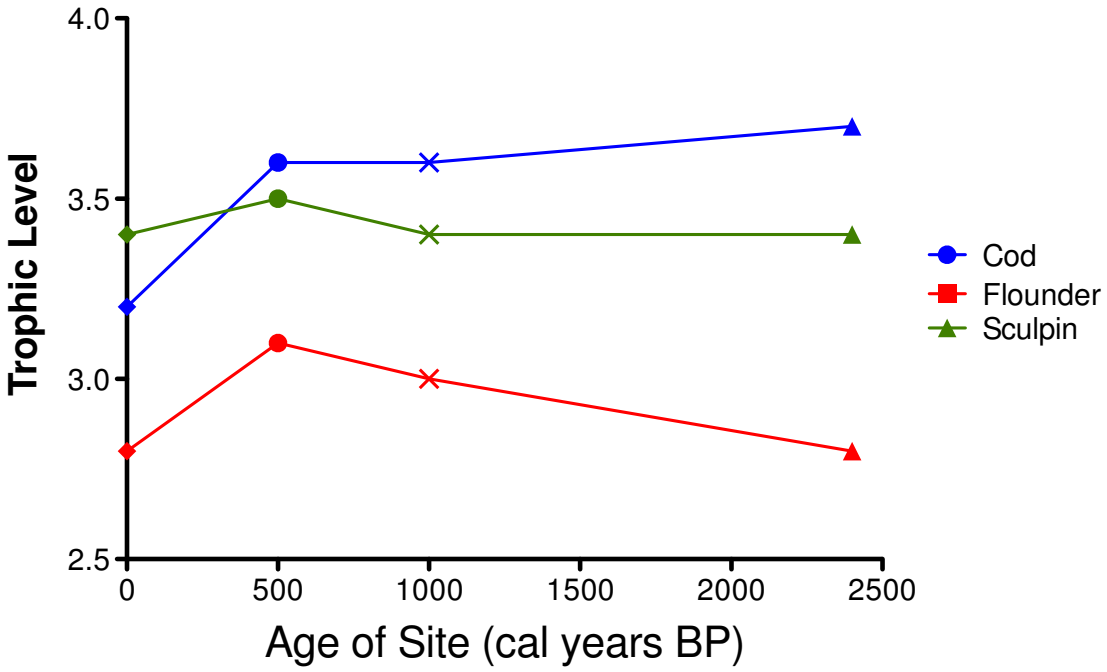

Figure 18. Mean Trophic Level of Study Species in Middle Bay Sites
The mean trophic level of modern and archaeological cod, flounder, and sculpin from the middle of Penobscot Bay are plotted against the age of the midden strata from which the bones were collected. Only data from sites in the middle bay that contained all three study species are shown.

from 2,400 BP to 500 BP. These isotopic data support conclusions from Bourque et al. (2008), which quantified changes to the relative amount of apex predator, mesopredator, and herbivore bone fragments found in each stratum at the Turner Farm site over the last 5,000 years. Changes in relative abundance for each trophic level likely reflect changes to nearshore systems and are readily apparent in the three species examined in the present study (**Figure 19**). Over time from 4,500 BP to 500 BP there was a dramatic reduction in the relative amount of apex predator bone fragments and a corresponding increase in the amount of mesopredator bones (specifically flatfish such as flounder and American dab, although sculpin increase as well) (Bourque et al., 2008).

The decrease in cod bones and increase in sculpin and flounder bones appears to have started by 4,000 BP. This rapid change, which is attributed to indigenous fishing practices, may have been caused by the immigration of a new group of people or by technological/ methodological advances that increased fishing efficiency (Bourque, 1995). For example, the Susquehanna Tradition begins in 3,800 BP, just after these apparent changes to ecosystem structure, and is accepted as marking the arrival of a new group of people to Maine's coast (Bouque, 1995).

Recent Decline of Mesopredators

Overfishing may have caused the rapid trophic level decline of cod, flounder, and sculpin between 500 BP and the present. European settlers arrived to the Atlantic coast by 400 BP and began to target large marine consumers (high trophic levels), whose abundance quickly declined. The magnitude of this fishing pressure was greater than that of local populations because of a large commercial market that supplied dried

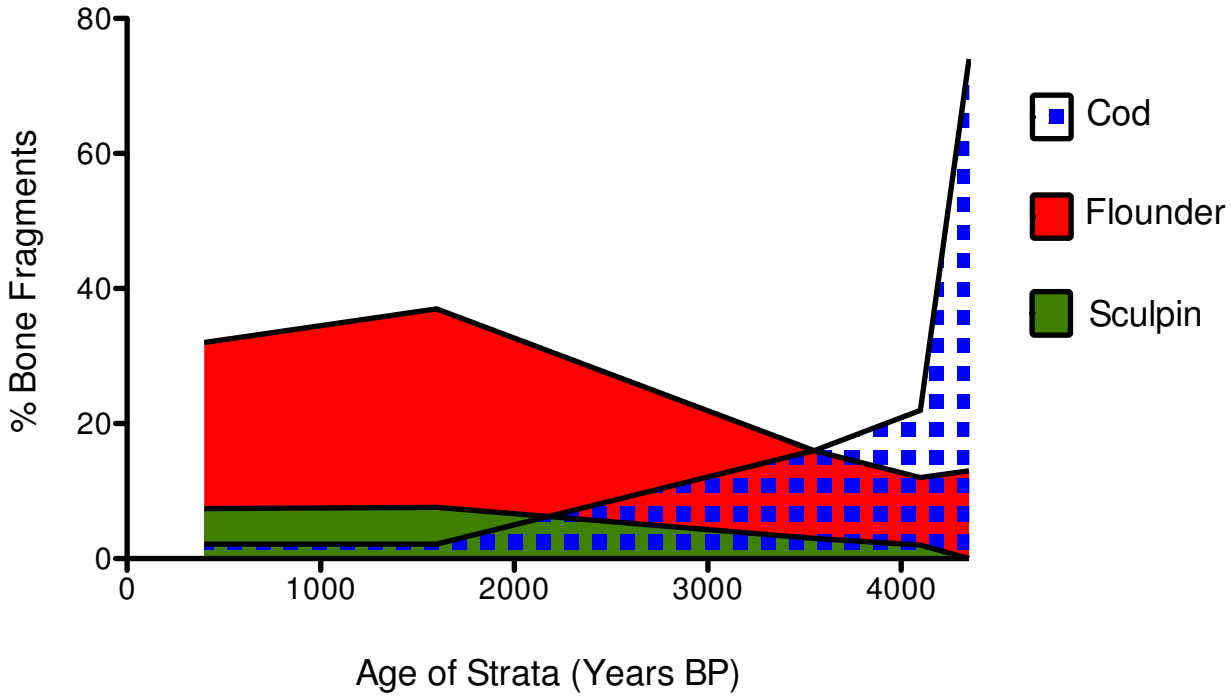

Figure 19. Percent Bone Fragments in the Turner Farm Midden
The proportion of cod, flounder, and sculpin bone fragments in Turner Farm archaeological midden from strata with median ages from 4,350 BP to 400 BP. Modified from Bourque et al., 2008.

and salted cod to Europe, where it had become a diet staple. By 1600 AD (~400 BP), 650 European vessels were fishing for cod along the Atlantic coast and shipping approximately 350,000 pounds of cod to Europe each year (Hendrickson et al., 2006).

This practice led to several local extinction events and the global extinction of 9 species (Lotze and Milewski, 2004). By the mid 1800s skates and dogfish were the most abundant demersal fish in Georges Bank and small sculpin and cunner had become dominant in nearshore systems (Lotze and Milewski, 2004). In the 1930s, the introduction of mechanized fishing technology and refrigeration on fishing vessels drastically increased the annual catch of cod (Conkling and Ames, 1996). The abundance and size of cod rapidly decreased, and smaller species like sculpin, which have less commercial value, became more abundant (Steneck, 1997).

During the late 19th century, commercial fisheries for cod collapsed or drastically diminished. At this time, populations of flounder, sculpin, lobster, sea scallop, and periwinkles were thriving (Steneck et al., 2004). As soon as humans recognized the potential value of these species, however, commercial fisheries developed for most mesopredators in the GoM (Lotze and Milewski, 2004). Annual commercial landings of flounder steadily increased from the 1900s until the 1980s when the peaked at 3,000 metric tons (Hendrickson et al., 2006).

Previous research shows that the general size of all predatory and mesopredatory fish has decreased significantly in the modern GoM compared to prehistoric systems (Jackson et al., 2001; Rosenberg et al., 2004; Hendrickson et al., 2006). Fewer and fewer flounder above age 6 are caught commercially and recreationally in the GoM each year, suggesting that the majority of flounder belong to younger (and smaller) cohorts (Hendrickson et al., 2006). Both this decrease in fish size and the decrease in the total number of trophic levels supported in the GoM can account

for the decrease in ^{15}N of all study species. The diet of all fish species shifts ontogenetically, with larger fish able to consume larger invertebrates that may represent higher trophic levels. Therefore, the present trophic level of cod, flounder, and sculpin is reduced because individual fish are smaller and because the prey items available, such as small crustaceans and benthic worms, inhabit low trophic levels.

A commercial fishery for sculpin in GoM never developed, because sculpin are spiny and produce less-appealing meat for human consumption than other demersal fish (Link and Almeida, 2002). This may explain why sculpin inhabit the highest trophic level out of the three study fish only in modern times. Because commercial or recreational fisheries never targeted sculpin, they are one of the most abundant fish in the GoM (although their numbers have decreased recently) and individual fish in these populations have probably not decreased in size to the extent that cod and flounder have (Link and Almeida, 2002).

4.2.3 Possible Ecological Niche Reduction

The offset among the ^{13}C of cod, flounder, and sculpin at a single time horizon and the range (distance between maximum and minimum value) within the ^{13}C of each species decreases over time. The range in ^{15}N has steadily declined in sculpin and cod, but increased in flounder, over time. Similarly, at 2,400 BP and 1000 BP, the offset among ^{15}N of cod and flounder was large and these groups were statistically different, but at 500 BP and in modern times there were no differences among study species. These changes may reflect the compression of the ecological niche inhabited by the study species over time (as in Bearhop et al., 2004), in agreement with Bourque et al. (2008).

This reduction in niche width may be caused by a decrease in the diversity of prey items available, the evenness of prey items, or the range of trophic levels inhabited by prey items (Bearhop et al., 2004). Food web studies focused on the North Atlantic have concluded that faunal diversity and primary producer diversity has decreased over the last century (Steneck et al., 1997; Sherwood et al., 2007; Mountain and Kane, 2010). The current GoM system contains only one trophic level, herbivores, with crabs and lobsters acting as apex predators (Steneck et al., 2004). Cod are considered to be ecologically extinct in this system (Estes et al., 1989). Four trophic levels (predators, mesopredators, herbivores, and autotrophs) were supported before commercial fisheries developed in the early 20th century (Steneck et al., 2004). This decrease in trophic level variety in the GoM may, in part, explain the decrease in range of ^{15}N values over time.

Other Factors that Influence ^{13}C and ^{15}N

Changes to the isotopic composition of fish species could be caused by a number of variables besides changes to trophic level and basal carbon source. These factors include changes to environmental factors (temperature, nutrient sources, nutrient concentrations, etc.), and fish migration from other depths or latitudes (Wainright et al., 1993; Burton and Koch, 1999; Aguilar et al., 2008; Asante et al., 2010).

Temperature changes over the last 2,400 years are unlikely to have caused large changes in the isotopic record of archaeological fish bones. Cooler temperatures caused by the Little Ice Age occurred at the same time as the apparent decrease in apex predators reported in this study. Cooler temperatures are more favorable for fish growth and, in the absence of other factors, would be expected to increase ^{13}C and ^{15}N-

enrichment. Because the opposite trend is evident in the archaeological record at this time, temperature changes likely did not affect the trends observed in the isotopic record.

It is possible that changes in the source fish population that indigenous people fished from could account for some changes to ^{13}C and ^{15}N of cod, flounder, and sculpin over time. The movement of fish populations, however, has not been assessed in prehistoric times, and cannot be discounted as a source of error. At this time it is not possible to determine conclusively that all fish caught by the inhabitants of these coastal archaeological sites came from one location or source population. Even if indigenous populations fished from the same general area, the fish populations they sampled from may have migrated from other locations in Penobscot Bay or the GoM.

4.3 Conclusions

Penobscot Bay is one of the more productive areas in the GoM and provides many ecosystem services. For example, it provides vital nurseries for commercially important fish species such as cod and flounder (Lazzari, 2008). It is important to understand how the Penobscot Bay system has changed over time and whether the driving force for these changes is natural or anthropogenic. By considering the isotopic data generated in this study and information about the lifestyles of indigenous coastal people, inferences about the extent and cause (i.e. environmental versus anthropogenic) of ecosystem alteration can be made.

It appears that both the loss of eelgrass and the decline of apex predators in Penobscot Bay had begun by 1,000 BP, approximately 500 years before the arrival of western Europeans to Maine's coast. The apparent decrease of cod's trophic level and increase in that of sculpin and flounder, combined with published data on the relative

abundance of these species in the diets of indigenous people (Bourque et al., 2008), suggest strongly that indigenous populations exerted fishing pressures strong enough to affect their nearshore ecosystem. Similarly, the C isotopic record, particularly of flounder, indicates that eelgrass in Penobscot Bay began to decline well before the arrival of Europeans. At this time, however, it is not possible to determine if this decline in eelgrass was caused by natural or anthropogenic factors.

Future research should focus on generating greater temporal and spatial resolution in the fish bone collagen isotopic record in Penobscot Bay. Increased temporal resolution will allow the timing of the decline in apex predators and of the loss of eelgrass to be determined more precisely. Increased spatial resolution will allow the question of spatial variation within the bay to be addressed. Future work should also include an attempt to analyze the bone samples used in this study for sulfur isotopes to apply a mixing model that would allow the relative contribution of eelgrass, kelp, and phytoplankton in Penobscot Bay to be accurately assessed. It would also be helpful to confirm that the isotopic signal of the main prey items for cod, flounder, and sculpin, such as benthic worms, small crustaceans, and small fish, reflects the isotopic composition of the main autotroph in the prey items' habitat (i.e. eelgrass, kelp, or phytoplankton).

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6. Appendices

Appendix A. Archaeological Data.

Bates College Sample ID	Site	Sample Info	Species
6825	Asbornsen	TP-4 0-45cm	Cod
6826	Asbornsen	L.9	Cod
6827	Asbornsen	L.10	Cod
6828	Asbornsen	L.7	Cod
6829	Asbornsen	L.7 35-40cm	Cod
6830	Asbornsen	L.5 25-30cm	Cod
6831	Asbornsen	L.6 30-35cm	Flounder
6832	Asbornsen	L.5 25-30cm	Flounder
6833	Asbornsen	L.7 35-40cm	Flounder
6834	Asbornsen	L.3 15-20cm	Flounder
6835	Asbornsen	L.2 10-15cm	Flounder
6836	Asbornsen	L.7 25-40cm	Flounder
6837	Asbornsen	L.5 25-30cm	Sculpin
6838	Asbornsen	L.1 0-10cm	Sculpin
6839	Asbornsen	L.6 30-35cm	Sculpin
6840	Asbornsen	L.5 25-30cm	Sculpin
6841	Asbornsen	L.4 20-25cm	Sculpin
6842	Asbornsen	L.4 20-25cm	Sculpin
6703	Bar Island	BI-75	Cod
6704	Bar Island	BI-57	Cod
6705	Bar Island	BI-64	Cod
6706	Bar Island		Cod
6707	Bar Island	BI-58	Cod
6708	Bar Island	BI-70	Cod
6709	Bar Island	BI-70	Flounder
6735	Bar Island	BI-65	Flounder
6710	Bar Island	BI-70	Sculpin
6711	Bar Island	BI-77	Sculpin
6712	Bar Island	BI-76	Sculpin
6713	Bar Island	BI-65	Sculpin
6714	Bar Island	BI-4	Sculpin
6715	Bar Island	BI-86	Sculpin
6659	Bull Rock Site	BR-25 (0-25cm)	Cod
6660	Bull Rock Site	BR-25 (0-25cm)	Cod
6661	Bull Rock Site	BR-25 (0-25cm)	Cod
6668	Bull Rock Site	BR-34 (20-30cm)	Cod
6669	Bull Rock Site	BR-34 (20-30cm)	Cod
6670	Bull Rock Site	BR-34 (20-30cm)	Cod
6665	Bull Rock Site	BR-25 (0-25cm)	Flounder
6666	Bull Rock Site	BR-25 (0-25cm)	Flounder

6667	Bull Rock Site	BR-25 (0-25cm)	Flounder
6674	Bull Rock Site	BR-34 (20-30cm)	Flounder
6675	Bull Rock Site	BR-34 (20-30cm)	Flounder
6676	Bull Rock Site	BR-34 (20-30cm)	Flounder
6662	Bull Rock Site	BR-25 (0-25cm)	Sculpin
6663	Bull Rock Site	BR-25 (0-25cm)	Sculpin
6664	Bull Rock Site	BR-25 (0-25cm)	Sculpin
6671	Bull Rock Site	BR-34 (20-30cm)	Sculpin
6672	Bull Rock Site	BR-34 (20-30cm)	Sculpin
6673	Bull Rock Site	BR-34 (20-30cm)	Sculpin
6821	Butter Island	N0 W1 section B	Sculpin
6822	Butter Island	N0 W1 section B	Sculpin
6823	Butter Island	N0 W1 section A	Sculpin
6824	Butter Island	N0 W1 section E	Sculpin
6568	Crocker	CR-3	Cod
6569	Crocker	CR-63	Cod
6570	Crocker		Cod
6571	Crocker	CR-63	Cod
6572	Crocker	CR-64	Cod
6573	Crocker	CR-64	Cod
6574	Crocker	CR-63	Flounder
6575	Crocker	CR-63	Flounder
6576	Crocker	CR-34	Flounder
6577	Crocker	CR-34	Flounder
6578	Crocker	CR-42	Flounder
6579	Crocker	CR-3	Sculpin
6580	Crocker	CR-3	Sculpin
6581	Crocker	CR-41	Sculpin
6582	Crocker	CR-41	Sculpin
6583	Crocker	CR-58	Sculpin
6584	Crocker	CR-58	Sculpin
5676	Modern Fish Market	-	Cod
5677	Modern Fish Market	-	Cod
5678	Modern Fish Market	-	Cod
5728	Modern Fish Market	-	Flounder
5729	Modern Fish Market	-	Flounder
6979	Modern Pen Bay	-	Cod
6980	Modern Pen Bay	-	Cod
6976	Modern Pen Bay	-	Flounder
6977	Modern Pen Bay	-	Flounder
6978	Modern Pen Bay	-	Flounder
6729	Oak Hill	E0 S26 W1/2	Sculpin
6730	Oak Hill	E0 S26 W1/2	Sculpin
6731	Oak Hill	E0 S26 W1/2	Sculpin
6732	Oak Hill	E2 S15	Sculpin
6733	Oak Hill	E2 S15	Sculpin
6734	Oak Hill	E2 S15	Sculpin
6680	Turner Farm	C66	Cod
6681	Turner Farm	B616	Cod
6682	Turner Farm	C210	Cod
6683	Turner Farm	B448	Cod

6684	Turner Farm	E1682	Cod
6685	Turner Farm	E1565	Cod
6686	Turner Farm	B637	Flounder
6687	Turner Farm	B420	Flounder
6688	Turner Farm	A860	Flounder
6689	Turner Farm	C228	Flounder
6690	Turner Farm	E1862	Flounder
6691	Turner Farm	C251	Flounder
6692	Turner Farm	E1803	Sculpin
6693	Turner Farm	C79	Sculpin
6694	Turner Farm	B586	Sculpin
6695	Turner Farm	A860	Sculpin
6696	Turner Farm	A865	Sculpin
6697	Turner Farm	B662	Sculpin

Appendix B. Isotope Data.

One flounder sample (6676) was removed from analysis, because its ^{15}N signal was anomalously high relative to other archaeological flounder samples. It is likely that this bone was misidentified and is actually a yellow-tail flounder bone (Source: B. Bourque, Personal Communication).

Analysis	Sample BC ID	Sample Type	Site	Mass (mg)	% N	umoles N	^{15}N (‰)	%C	umoles C	^{13}C (‰)	C/N (atomic)	Date Run
6050	Bypass	Acetanilide Standard		0.839	10.37	6.21	-1.64	72.84	50.62	-29.78	8.20	6/22/09
6052	1. 2991	Acetanilide Standard		0.554	10.36	4.14	-1.56	71.09	33.83	-29.86	8.01	6/22/09
6053	1. 2992	Caffeine Standard		0.263	28.98	5.50	-12.61	49.83	11.26	-30.64	2.01	6/22/09
6054	5677	Cod vertebrae 1	Modern Fish Market	0.711	14.07	7.23	11.87	41.36	25.26	-15.38	3.43	6/22/09
6055	5677	Cod vertebrae 2	Modern Fish Market	0.648	12.56	5.88	12.32	37.27	20.74	-15.93	3.46	6/22/09
6056	5677	Cod vertebrae 3	Modern Fish Market	0.619	14.00	6.26	11.98	40.83	21.71	-15.55	3.40	6/22/09
6061	1. 3002	Corn Husk Standard		1.031	0.84	0.63	-3.05	41.74	36.97	-11.38	57.91	6/22/09
6064	2. 2992	Caffeine Standard		0.24	28.09	4.87	-12.67	47.95	9.88	-30.53	1.99	6/22/09
6065	3. 2992	Caffeine Standard		0.203	27.98	4.10	-12.64	47.80	8.34	-30.54	1.99	6/22/09
6066	2. 3002	Corn Husk Standard		1.118	0.89	0.71	-1.47	41.17	39.54	-11.36	54.26	6/22/09
6067	3. 3002	Corn Husk Standard		1.016	0.89	0.65	-1.70	40.95	35.74	-11.32	53.55	6/22/09
6068	2. 2991	Acetanilide Standard		0.462	10.13	3.38	-1.40	69.34	27.52	-29.82	7.99	6/22/09
6069	3. 2991	Acetanilide Standard		0.559	10.18	4.11	-1.36	69.51	33.38	-29.81	7.97	6/22/09
6249	Bypass	Acetanilide Standard		1.438	10.21	10.88	0.29	68.88	80.76	-30.55	7.43	8/5/09
6251	1. 2991	Acetanilide Standard		0.296	10.36	2.17	-0.11	71.09	17.61	-30.36	8.13	8/5/09
6257	1. 4075	Organic Millet Flour Standard		1.464	1.54	1.59	4.22	40.69	49.85	-13.80	31.27	8/5/09
6258	1. 2992	Caffeine Standard		0.243	28.15	4.83	-12.61	48.91	9.95	-31.09	2.06	8/5/09
6259	2. 2991	Acetanilide Standard		0.516	10.40	3.79	0.01	70.37	30.39	-30.41	8.02	8/5/09
6265	2. 4075	Organic Millet Flour Standard		1.477	1.54	1.61	4.02	40.97	50.64	-14.17	31.46	8/5/09

6266	2. 2992	Caffeine Standard		0.301	28.64	6.09	-12.37	49.16	12.38	-31.13	2.03	8/5/09
6267	3. 2991	Acetanilide Standard		0.603	10.61	4.52	0.20	70.75	35.70	-30.32	7.90	8/5/09
6273	2. 4075	Organic Millet Flour Standard		1.556	1.52	1.67	3.92	41.15	53.59	-14.07	32.14	8/5/09
6274	3. 2992	Caffeine Standard		0.273	27.97	5.39	-12.40	48.46	11.07	-31.10	2.05	8/5/09
6275	4. 2991	Acetanilide Standard		0.441	10.19	3.17	-0.35	71.03	26.21	-30.31	8.26	8/5/09
6276	5728	Flounder vertebrae 1	Modern Fish Market	0.66	12.98	6.05	11.44	44.32	24.48	-17.41	4.04	8/5/09
6279	5728	Flounder vertebrae 2	Modern Fish Market	0.492	13.93	4.84	11.43	47.28	19.47	-17.32	4.02	8/5/09
6282	5729	Flounder vertebrae 1	Modern Fish Market	0.659	13.38	6.23	11.81	48.39	26.69	-18.38	4.28	8/5/09
6283	5729	Flounder vertebrae 2	Modern Fish Market	0.845	14.00	8.36	11.98	45.16	31.94	-17.58	3.82	8/5/09
6284	5729	Flounder vertebrae 3	Modern Fish Market	0.72	14.77	7.51	12.05	43.75	26.36	-16.65	3.51	8/5/09
6285	5. 2992	Caffeine Standard		0.25	28.56	5.04	-12.24	49.55	10.37	-30.98	2.06	8/5/09
6292	2991	Acetanilide Standard		0.665	10.81	5.08	0.37	70.36	39.16	-30.49	7.71	8/6/09
6741	Bypass	Acetanilide Standard		0.249	10.41	1.86	0.43	72.15	14.78	-29.58	7.94	8/31/09
6743	1. 2991	Acetanilide Standard		0.341	10.36	2.55	0.12	71.09	20.40	-30.27	8.00	8/31/09
6746	5676	Cod vertebrae 1	Modern Fish Market	0.638	14.83	6.83	12.94	43.78	23.50	-15.63	3.44	8/31/09
6747	5676	Cod vertebrae 2	Modern Fish Market	0.694	14.01	7.02	13.65	40.75	23.80	-15.08	3.39	8/31/09
6748	5678	Cod vertebrae 1	Modern Fish Market	0.657	14.72	6.98	12.83	41.59	22.99	-15.15	3.29	8/31/09
6749	5678	Cod vertebrae 2	Modern Fish Market	0.611	13.77	6.07	14.17	41.92	21.55	-14.92	3.55	8/31/09
6751	1. 2992	Caffeine Standard		0.303	29.61	6.48	-12.21	49.90	12.72	-31.05	1.96	8/31/09
6752	2. 2991	Acetanilide Standard		0.589	10.40	4.42	0.18	69.58	34.49	-30.30	7.79	8/31/09
6757	1. 4075	Organic Millet Flour Standard		1.714	1.37	1.70	3.75	40.73	58.74	-14.65	34.64	8/31/09
6758	2. 2992	Caffeine Standard		0.213	28.18	4.33	-12.10	48.69	8.73	-30.67	2.01	8/31/09
6759	2. 2991	Acetanilide Standard		0.554	6.81	2.72	-0.14	47.64	22.21	-30.28	8.15	8/31/09
6766	2. 4075	Organic Millet Flour Standard		1.561	1.32	1.48	3.83	40.53	53.25	-14.16	35.86	8/31/09
6767	3. 2992	Caffeine Standard		0.299	28.97	6.25	-12.33	49.79	12.53	-31.08	2.00	8/31/09
6768	3. 2991	Acetanilide Standard		0.453	10.00	3.27	-0.18	70.35	26.82	-30.26	8.20	8/31/09
6777	4. 2991	Acetanilide Standard		0.661	16.31	7.78	-0.10	107.00	59.52	-30.37	7.65	8/31/09
6781	5. 2991	Acetanilide Standard		0.608	10.22	4.49	-0.31	70.30	35.97	-30.34	8.02	8/31/09

1530	Bypass	Acetanilide Standard		1.271	10.34	8.75	0.27	70.44	72.70	-29.61	8.31	8/1/10
1532	2991.1	Acetanilide Standard		0.622	10.36	4.50	-0.11	71.09	36.59	-30.06	8.12	8/1/10
1533	2992.1	Caffeine Standard		0.35	28.33	6.93	-12.17	48.15	13.94	-31.01	2.01	8/1/10
1534	5676.1	Cod Meat Standard		0.509	14.31	5.09	13.56	44.91	18.91	-18.67	3.72	8/1/10
1536	6688	Flounder	Turner Farm	0.584	13.66	5.58	12.68	40.47	19.55	-12.84	3.51	8/1/10
1537	6692	Sculpin	Turner Farm	0.647	14.37	6.50	14.58	41.53	22.23	-10.38	3.42	8/1/10
1538	6693	Sculpin	Turner Farm	0.576	5.97	2.40	11.51	19.20	9.15	-13.84	3.81	8/1/10
1545	2991.2	Acetanilide Standard		0.475	10.65	3.54	-0.24	72.60	28.53	-30.23	8.07	8/1/10
1546	2992.2	Caffeine Standard		0.392	29.28	8.02	-12.38	50.11	16.25	-31.09	2.03	8/1/10
1547	5676.2	Cod Meat Standard		0.456	14.75	4.70	13.30	46.43	17.52	-18.88	3.73	8/1/10
1553	2992.3	Caffeine Standard		0.577	29.26	11.80	-12.38	50.62	24.17	-31.46	2.05	8/1/10
1554	5676.3	Cod Meat Standard		0.454	14.68	4.66	13.34	46.09	17.31	-18.95	3.72	8/1/10
1555	2991.3	Acetanilide Standard		0.624	10.74	4.68	-0.12	73.30	37.84	-30.36	8.08	8/1/10
1915	Bypass	Acetanilide Standard		0.821	10.16	6.03	-0.31	73.12	49.57	-29.89	8.22	8/16/10
1917	2991.1	Acetanilide Standard		0.609	10.36	4.55	-0.13	71.09	36.85	-30.30	8.10	8/16/10
1918	2992.1	Caffeine Standard		0.428	28.84	8.90	-12.18	48.66	17.72	-31.18	1.99	8/16/10
1919	5676.1	Cod Meat Standard		0.509	13.95	5.12	13.37	43.66	18.91	-18.82	3.69	8/16/10
1920	6825	Cod	Asbornsen	0.55	11.25	4.46	14.56	33.22	15.55	-11.53	3.49	8/16/10
1921	6826	Cod	Asbornsen	0.676	13.53	6.59	14.66	37.11	21.35	-10.57	3.24	8/16/10
1922	6827	Cod	Asbornsen	0.795	9.30	5.33	15.30	28.73	19.44	-10.95	3.65	8/16/10
1923	6828	Cod	Asbornsen	0.846	12.15	7.41	13.75	34.85	25.09	-12.33	3.39	8/16/10
1924	6829	Cod	Asbornsen	0.586	10.59	4.47	15.39	33.24	16.58	-11.60	3.71	8/16/10
1925	6830	Cod	Asbornsen	0.578	11.79	4.91	16.58	34.49	16.96	-10.67	3.45	8/16/10
1926	6831	Flounder	Asbornsen	0.806	14.22	8.26	12.01	40.20	27.57	-9.50	3.34	8/16/10
1927	6832	Flounder	Asbornsen	0.647	10.45	4.88	13.31	32.01	17.62	-12.64	3.61	8/16/10
1928	6833	Flounder	Asbornsen	0.627	13.10	5.92	12.52	37.93	20.24	-10.72	3.42	8/16/10
1929	6834	Flounder	Asbornsen	0.655	13.52	6.39	13.11	37.91	21.13	-10.48	3.31	8/16/10
1930	6835	Flounder	Asbornsen	0.692	12.56	6.27	13.35	36.21	21.32	-11.22	3.40	8/16/10

1931	6836	Flounder	Asbornsen	0.61	14.23	6.26	13.52	40.55	21.05	-10.40	3.36	8/16/10
1932	2991.2	Acetanilide Standard		0.719	10.35	5.36	-0.05	69.90	42.77	-30.28	7.97	8/16/10
1933	2992.2	Caffeine Standard		0.407	28.87	8.47	-12.39	47.99	16.62	-31.20	1.96	8/16/10
1934	5676.2	Cod Meat Standard		0.394	14.01	3.98	13.44	43.29	14.52	-18.91	3.65	8/16/10
1935	6837	Sculpin	Asbornsen	0.904	13.18	8.59	15.12	36.85	28.35	-11.04	3.30	8/16/10
1936	6838	Sculpin	Asbornsen	0.638	14.92	6.86	14.58	41.02	22.27	-11.53	3.25	8/16/10
1937	6839	Sculpin	Asbornsen	0.631	13.92	6.33	15.06	38.68	20.77	-10.29	3.28	8/16/10
1938	6840	Sculpin	Asbornsen	0.826	13.69	8.15	13.69	39.24	27.59	-11.67	3.38	8/16/10
1939	6841	Sculpin	Asbornsen	0.622	13.90	6.23	13.41	39.33	20.82	-13.02	3.34	8/16/10
1940	6842	Sculpin	Asbornsen	0.762	14.37	7.90	14.34	39.68	25.73	-12.02	3.26	8/16/10
1944	6683	Cod	Turner Farm	0.624	14.80	6.66	16.47	41.09	21.82	-10.83	3.28	8/16/10
1945	6730	Sculpin	Oak Hill	0.715	14.80	7.63	12.78	41.51	25.26	-13.82	3.31	8/16/10
1946	6731	Sculpin	Oak Hill	0.634	10.75	4.91	12.56	34.60	18.67	-15.99	3.80	8/16/10
1947	2991.3	Acetanilide Standard		0.565	9.96	4.06	-0.08	66.62	32.03	-30.35	7.89	8/16/10
1948	2992.3	Caffeine Standard		0.396	28.33	8.09	-12.49	47.25	15.92	-31.13	1.97	8/16/10
1949	5676.3	Cod Meat Standard		0.426	14.00	4.30	13.28	43.16	15.65	-18.77	3.64	8/16/10
1950	6732	Sculpin	Oak Hill	0.689	13.16	6.54	13.05	41.67	24.44	-15.42	3.74	8/16/10
1951	6733	Sculpin	Oak Hill	0.647	12.97	6.05	12.58	37.64	20.73	-13.66	3.43	8/16/10
1952	6734	Sculpin	Oak Hill	0.672	14.79	7.17	13.39	41.57	23.77	-13.23	3.32	8/16/10
1953	6703	Cod	Bar Island	0.773	15.22	8.48	15.20	42.02	27.64	-11.85	3.26	8/16/10
1954	6704	Cod	Bar Island	0.624	14.58	6.56	14.03	40.35	21.43	-12.10	3.27	8/16/10
1955	6705	Cod	Bar Island	0.755	12.88	7.01	15.82	37.90	24.35	-13.37	3.47	8/16/10
1956	6706	Cod	Bar Island	0.617	13.76	6.12	15.33	40.86	21.46	-13.72	3.51	8/16/10
1957	6707	Cod	Bar Island	0.699	15.51	7.82	16.51	42.71	25.41	-12.07	3.25	8/16/10
1958	6711	Sculpin	Bar Island	0.783	16.13	9.11	15.70	42.96	28.63	-10.27	3.14	8/16/10
1959	6712	Sculpin	Bar Island	0.818	12.91	7.61	14.88	36.40	25.34	-12.53	3.33	8/16/10
1960	6713	Sculpin	Bar Island	0.753	12.87	6.99	14.37	36.52	23.40	-13.06	3.35	8/16/10
1961	6714	Sculpin	Bar Island	0.504	12.40	4.50	13.49	37.00	15.87	-13.35	3.52	8/16/10

1962	6715	Sculpin	Bar Island	0.574	14.98	6.20	14.61	40.92	19.99	-11.58	3.22	8/16/10
1976	Bypass	Acetanilide Standard		0.977	10.55	7.30	0.17	73.46	58.60	-29.95	8.03	8/25/10
1978	2991.1	Acetanilide Standard		0.55	10.36	4.05	-0.21	71.09	32.52	-30.28	8.02	8/25/10
1979	2992.1	Caffeine Standard		0.282	28.68	5.75	-12.49	48.78	11.44	-31.10	1.99	8/25/10
1980	5676.1	Cod Meat Standard		0.654	14.25	6.63	13.43	45.18	24.58	-18.78	3.71	8/25/10
1984	6708	Cod	Bar Island	1.068	14.70	11.17	14.87	41.56	36.91	-12.10	3.30	8/25/10
1985	6735	Flounder	Bar Island	0.789	11.85	6.65	13.06	36.49	23.95	-12.79	3.60	8/25/10
1988	2991.2	Acetanilide Standard		0.289	10.39	2.14	-0.28	70.64	16.98	-30.29	7.95	8/25/10
1989	2992.2	Caffeine Standard		0.967	28.72	19.76	-12.11	49.82	40.07	-31.27	2.03	8/25/10
1990	5676.2	Cod Meat Standard		0.908	14.32	9.25	13.54	45.68	34.50	-18.85	3.73	8/25/10
1998	2991.3	Acetanilide Standard		0.279	10.37	2.06	-0.14	70.73	16.41	-30.22	7.97	8/25/10
1999	2992.3	Caffeine Standard		0.66	28.59	13.42	-12.38	49.20	27.01	-31.23	2.01	8/25/10
2000	5676.3	Cod Meat Standard		0.652	14.32	6.64	13.32	45.34	24.59	-18.85	3.70	8/25/10
2009	2991.4	Acetanilide Standard		0.598	10.37	4.41	-0.14	71.20	35.42	-30.39	8.03	8/25/10
2010	2992.4	Caffeine Standard		0.659	28.80	13.50	-12.32	49.71	27.25	-31.13	2.02	8/25/10
2011	5676.4	Cod Meat Standard		0.368	14.31	3.75	13.23	45.01	13.78	-18.87	3.68	8/25/10
2327	Bypass	Acetanilide Standard		0.727	9.45	5.30	-0.11	73.84	39.96	-29.87	7.54	9/29/10
2329	2991.1	Acetanilide Standard		0.564	10.36	4.17	-0.21	71.09	31.54	-30.17	7.57	9/29/10
2330	2992.1	Caffeine Standard		0.378	28.43	7.66	-12.30	48.00	14.27	-30.89	1.86	9/29/10
2331	5676.1	Cod Meat Standard		0.521	14.36	5.34	13.42	45.53	18.66	-18.74	3.50	9/29/10
2347	2991.2	Acetanilide Standard		0.796	10.47	5.94	-0.03	78.81	49.34	-30.42	8.30	9/29/10
2348	2992.2	Caffeine Standard		0.387	29.66	8.19	-12.36	54.47	16.58	-31.16	2.02	9/29/10
2349	5676.2	Cod Meat Standard		0.597	14.37	6.12	13.47	49.31	23.15	-18.82	3.78	9/29/10
2363	2991.3	Acetanilide Standard		0.564	10.44	4.20	-0.22	81.21	36.02	-30.51	8.58	9/29/10
2364	2992.3	Caffeine Standard		0.505	29.28	10.55	-12.29	56.62	22.49	-31.42	2.13	9/29/10
2365	5676.3	Cod Meat Standard		0.511	14.34	5.23	13.29	51.46	20.68	-18.94	3.96	9/29/10
2366	6976	Flounder	Modern Pen Bay	0.872	14.19	8.83	9.80	49.28	33.80	-16.20	3.83	9/29/10
2367	6977	Flounder	Modern Pen Bay	0.47	17.33	5.81	12.34	53.23	19.68	-16.12	3.39	9/29/10

2368	6978	Flounder	Modern Pen Bay	0.657	16.56	7.76	14.31	52.51	27.13	-15.49	3.50	9/29/10
2369	6979	Cod	Modern Pen Bay	0.826	6.14	3.61	14.29	20.53	13.34	-13.22	3.69	9/29/10
2370	6980	Cod	Modern Pen Bay	0.547	7.10	2.77	13.05	24.39	10.49	-14.10	3.79	9/29/10
2413	2992.1	Caffeine Standard		0.52	34.16	10.63	-12.13	58.68	20.96	-31.21	1.97	10/8/10
2414	5676.1	Cod Meat Standard		0.425	14.30	4.45	13.17	45.24	16.16	-18.90	3.63	10/8/10
2422	6669	Cod	Bull Rock (upper)	0.829	12.07	7.33	15.98	37.71	26.27	-11.81	3.59	10/8/10
2423	6670	Cod	Bull Rock (upper)	0.905	10.83	7.18	14.38	34.66	26.35	-12.34	3.67	10/8/10
2424	6671	Sculpin	Bull Rock (upper)	0.545	13.80	5.50	13.67	39.61	18.14	-11.42	3.30	10/8/10
2425	6672	Sculpin	Bull Rock (upper)	0.63	14.14	6.52	14.22	40.30	21.33	-12.74	3.27	10/8/10
2426	6673	Sculpin	Bull Rock (upper)	0.713	13.91	7.26	13.64	40.15	24.06	-12.55	3.31	10/8/10
2427	6674	Flounder	Bull Rock (upper)	0.67	13.03	6.39	12.24	39.00	21.96	-11.43	3.44	10/8/10
2428	6675	Flounder	Bull Rock (upper)	0.8	12.86	7.53	13.39	38.44	25.84	-10.55	3.43	10/8/10
2429	*6676	Flounder	Bull Rock (upper)	0.676	12.64	6.25	18.53	38.36	21.79	-12.65	3.48	10/8/10
2433	2991.2	Acetanilide Standard		0.764	10.18	5.69	-0.01	70.86	45.49	-30.28	7.99	10/8/10
2434	2992.2	Caffeine Standard		0.351	27.46	7.06	-12.20	47.68	14.06	-31.03	1.99	10/8/10
2435	5676.2	Cod Meat Standard		0.635	14.11	6.56	13.31	45.21	24.13	-18.79	3.68	10/8/10
2442	2991.3	Acetanilide Standard		0.654	10.14	4.85	-0.04	70.62	38.81	-30.30	7.99	10/8/10
2443	2992.3	Caffeine Standard		0.507	28.22	10.48	-12.48	49.13	20.93	-31.07	2.00	10/8/10
2444	5676.3	Cod Meat Standard		0.743	13.73	7.47	13.48	45.26	28.26	-18.76	3.78	10/8/10
2453	2991.4	Acetanilide Standard		0.786	10.00	5.75	0.04	69.82	46.11	-30.28	8.01	10/8/10
2454	2992.4	Caffeine Standard		0.536	27.86	10.93	-12.75	48.64	21.91	-31.19	2.00	10/8/10
2455	5676.4	Cod Meat Standard		0.444	13.78	4.48	13.35	44.48	16.60	-18.88	3.71	10/8/10
2476	Bypass	Acetanilide Standard		0.99	10.86	7.93	-0.05	72.02	59.98	-30.24	7.57	10/11/10
2478	1. 2991	Acetanilide Standard		0.758	10.36	5.18	-0.02	71.09	42.17	-30.36	8.14	10/11/10
2479	1. 2992	Caffeine Standard		0.297	30.74	6.02	-12.38	52.44	12.19	-31.14	2.02	10/11/10
2480	1. 5676	Cod Meat Standard		0.644	15.47	6.57	13.55	49.03	24.71	-18.92	3.76	10/11/10
2481	6729	Sculpin	Oak Hill	0.719	15.43	7.32	13.16	45.04	25.34	-13.07	3.46	10/11/10
2482	6709	Flounder	Bar Island	1.363	13.07	11.76	13.19	38.78	41.36	-8.54	3.52	10/11/10

2483	6710	Sculpin	Bar Island	0.853	15.21	8.56	15.61	42.66	28.48	-11.63	3.33	10/11/10
2484	6680	Cod	Turner Farm	1.132	15.24	11.39	15.69	43.62	38.64	-12.29	3.39	10/11/10
2485	6682	Cod	Turner Farm	0.785	15.59	8.07	15.18	43.67	26.83	-13.47	3.32	10/11/10
2487	6685	Cod	Turner Farm	1.001	13.77	9.10	15.28	41.21	32.28	-13.62	3.55	10/11/10
2489	2. 2991	Acetanilide Standard		0.349	11.08	2.55	-0.01	76.67	20.94	-30.20	8.21	10/11/10
2490	2. 2992	Caffeine Standard		0.535	30.31	10.70	-12.41	52.61	22.03	-31.12	2.06	10/11/10
2491	2. 5676	Cod Meat Standard		0.38	15.67	3.93	13.07	49.55	14.73	-18.74	3.75	10/11/10
2492	6687	Flounder	Turner Farm	0.944	15.24	9.49	13.08	44.44	32.83	-10.22	3.46	10/11/10
2493	6689	Flounder	Turner Farm	0.861	15.53	8.82	12.24	44.37	29.89	-8.08	3.39	10/11/10
2494	6690	Flounder	Turner Farm	1.164	15.42	11.85	10.01	44.32	40.37	-9.64	3.41	10/11/10
2495	6691	Flounder	Turner Farm	0.779	15.70	8.07	12.52	44.16	26.92	-10.50	3.34	10/11/10
2496	6694	Sculpin	Turner Farm	1.182	6.36	4.96	14.20	19.37	17.92	-10.93	3.61	10/11/10
2498	6696	Sculpin	Turner Farm	0.98	15.14	9.79	16.05	44.55	34.16	-11.02	3.49	10/11/10
2499	6697	Sculpin	Turner Farm	0.921	15.45	9.39	14.92	44.18	31.85	-11.13	3.39	10/11/10
2500	3. 2992	Caffeine Standard		0.469	30.90	9.56	-12.33	53.05	19.47	-31.10	2.04	10/11/10
2501	3. 5676	Cod Meat Standard		0.614	15.62	6.33	13.40	49.38	23.73	-18.84	3.75	10/11/10
2502	3. 2991	Acetanilide Standard		0.626	11.28	4.66	-0.07	77.33	37.88	-30.36	8.13	10/11/10
2503	Bypass	Acetanilide Standard		1.048	10.52	7.88	0.00	72.19	62.77	-30.03	7.97	10/12/10
2505	2991.1	Acetanilide Standard		0.572	10.36	4.23	-0.33	71.09	33.74	-30.24	7.97	10/12/10
2506	2992.1	Caffeine Standard		0.544	29.30	11.27	-12.42	49.48	22.26	-31.15	1.98	10/12/10
2507	5676.1	Cod Meat Standard		0.664	14.75	6.93	13.39	46.26	25.40	-18.81	3.67	10/12/10
2515	6824	Sculpin	Butter Island	0.971	14.09	9.67	12.99	40.47	32.49	-13.45	3.36	10/12/10
2516	6823	Sculpin	Butter Island	0.72	14.28	7.27	13.18	40.87	24.33	-13.08	3.35	10/12/10
2517	6822	Sculpin	Butter Island	0.841	14.30	8.50	13.83	40.60	28.24	-12.61	3.32	10/12/10
2518	6821	Sculpin	Butter Island	0.686	13.53	6.56	12.68	39.98	22.68	-14.23	3.45	10/12/10
2519	6572	Cod	Crocker	0.946	9.66	6.46	13.78	31.02	24.27	-14.30	3.76	10/12/10
2520	6574	Flounder	Crocker	0.654	13.87	6.42	13.23	40.47	21.89	-8.48	3.41	10/12/10
2521	6569	Cod	Crocker	0.849	10.74	6.45	16.26	33.76	23.70	-15.00	3.68	10/12/10

2522	6570	Cod	Crocker	0.714	14.56	7.35	16.10	40.54	23.94	-13.17	3.26	10/12/10
2523	6584	Sculpin	Crocker	0.84	14.49	8.60	13.31	40.79	28.33	-13.15	3.29	10/12/10
2524	6580	Sculpin	Crocker	0.815	14.79	8.52	16.64	42.11	28.38	-10.75	3.33	10/12/10
2525	6579	Sculpin	Crocker	0.752	15.01	7.98	13.82	42.14	26.21	-10.86	3.28	10/12/10
2526	6583	Sculpin	Crocker	0.878	14.00	8.69	14.35	40.05	29.08	-10.78	3.35	10/12/10
2527	2991.2	Acetanilide Standard		0.507	10.47	3.75	-0.17	71.67	30.05	-30.33	8.01	10/12/10
2528	2992.2	Caffeine Standard		0.479	29.11	9.86	-12.24	49.40	19.57	-31.14	1.98	10/12/10
2529	5676.2	Cod Meat Standard		0.498	15.00	5.28	13.36	47.35	19.50	-18.85	3.69	10/12/10
2530	6582	Sculpin	Crocker	0.832	12.37	7.28	15.67	38.41	26.43	-12.20	3.63	10/12/10
2531	6581	Sculpin	Crocker	0.798	14.15	7.98	13.63	40.83	26.94	-12.82	3.38	10/12/10
2532	6578	Flounder	Crocker	0.664	13.54	6.36	13.50	39.61	21.75	-10.40	3.42	10/12/10
2533	6577	Flounder	Crocker	0.912	12.92	8.33	12.90	37.49	28.27	-13.45	3.39	10/12/10
2534	6571	Cod	Crocker	0.943	8.82	5.88	15.19	27.63	21.55	-14.84	3.66	10/12/10
2535	6568	Cod	Crocker	1.766	8.39	10.48	14.48	27.30	39.87	-13.28	3.81	10/12/10
2536	6576	Flounder	Crocker	0.922	11.67	7.61	13.68	37.58	28.65	-12.17	3.77	10/12/10
2537	6575	Flounder	Crocker	0.752	14.81	7.87	12.20	41.98	26.11	-9.43	3.32	10/12/10
2538	6573	Cod	Crocker	1.137	13.76	11.06	14.90	40.65	38.22	-13.13	3.46	10/12/10
2540	6660	Cod	Bull Rock (lower)	0.861	13.90	8.46	14.45	40.73	29.00	-10.95	3.43	10/12/10
2541	6661	Cod	Bull Rock (lower)	0.79	12.08	6.75	14.20	39.10	25.54	-14.28	3.78	10/12/10
2542	6662	Sculpin	Bull Rock (lower)	0.861	12.28	7.47	17.05	36.69	26.12	-11.06	3.50	10/12/10
2543	6663	Sculpin	Bull Rock (lower)	0.677	15.06	7.21	15.89	41.12	23.02	-10.19	3.19	10/12/10
2544	6664	Sculpin	Bull Rock (lower)	0.74	13.06	6.83	14.57	39.14	23.95	-12.10	3.50	10/12/10
2545	6665	Flounder	Bull Rock (lower)	0.681	12.94	6.23	12.17	39.04	21.99	-12.73	3.53	10/12/10
2546	6666	Flounder	Bull Rock (lower)	0.792	13.67	7.65	12.89	39.90	26.13	-12.48	3.41	10/12/10
2548	6667	Flounder	Bull Rock (lower)	0.904	7.74	4.95	11.46	24.64	18.42	-13.85	3.72	10/12/10
2549	6668	Cod	Bull Rock (upper)	0.966	12.07	8.24	16.32	37.23	29.74	-11.83	3.61	10/12/10
2550	2992.3	Caffeine Standard		0.317	28.55	6.40	-12.29	49.34	12.93	-31.19	2.02	10/12/10
2551	5676.3	Cod Meat Standard		0.776	14.16	7.77	13.43	44.98	28.86	-18.84	3.72	10/12/10

2552	2991.3	Acetanilide Standard		0.652	10.28	4.74	-0.07	70.86	38.20	-30.39	8.06	10/12/10
4927	Bypass	Acetanilide Standard		0.963	7.02	7.57	-0.15	135.90	55.66	-30.13	7.36	3/14/11
4929	2991.1b	Acetanilide Standard		0.508	10.36	3.27	-0.08	71.09	23.49	-30.40	7.19	3/14/11
4930	2992.1	Caffeine Standard		0.275	32.52	5.55	-12.60	55.19	9.87	-31.14	1.78	3/14/11
4931	5676.1	Cod Meat Standard		0.77	13.74	6.57	13.18	43.63	21.85	-18.86	3.33	3/14/11
4938	2991.1b	Acetanilide Standard		0.841	6.75	3.53	0.04	46.49	25.43	-30.33	7.21	3/14/11
4939	2992.1	Caffeine Standard		0.902	8.22	4.60	-12.47	13.84	8.12	-31.09	1.76	3/14/11
4940	5676.1	Cod Meat Standard		0.664	16.99	7.00	13.19	54.21	23.41	-18.85	3.34	3/14/11
4953	7644	Sculpin	Modern Pen Bay	0.615	17.01	6.49	15.09	50.22	20.09	-14.23	3.09	3/14/11
4954	7645	Sculpin	Modern Pen Bay	0.879	16.03	8.75	15.23	47.73	27.29	-13.97	3.12	3/14/11
4955	7646	Sculpin	Modern Pen Bay	0.84	16.28	8.49	14.03	46.90	25.63	-14.01	3.02	3/14/11
4956	2991.1b	Acetanilide Standard		0.957	6.36	3.78	0.26	44.05	27.42	-30.36	7.25	3/14/11
4957	2992.1	Caffeine Standard		0.74	12.28	5.64	-12.14	20.66	9.94	-31.08	1.76	3/14/11
4958	5676.1	Cod Meat Standard		0.891	11.99	6.63	13.58	38.17	22.12	-18.79	3.34	3/14/11