2008

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Recommended Citation

Bourque, B. J., Johnson, B.J., and Steneck, R., 2008. Possible prehistoric fishing effects on coastal marine food webs in the Gulf of Maine. In Human Impacts on Ancient Marine Ecosystems (eds., T.C. Rick and J.M. Erlandson), University of California Press, Berkley, p. 165-185.

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Possible Prehistoric Fishing Effects on Coastal Marine Food Webs in the Gulf of Maine

Bruce J. Bourque, Beverly J. Johnson, and Robert S. Steneck

THE GULF OF MAINE is one of the world's most productive marine ecosystems. Its coastal codfish stocks attracted European colonists, including the Pilgrims at Plymouth, Massachusetts, on the shores of the then appropriately named Cape Cod. Today, however, Atlantic cod *(Gadus morhua)* and virtually all large-bodied fishes are rare and "ecologically extinct" (sensu Estes et al. 1989) from coastal zones of the Gulf of Maine. The decline of cod and other groundfishes is widely believed to be the result of overfishing (Jackson et al. 2001). Further, because cod were the dominant predator in Gulf of Maine waters (Steneck and Carlton 2001) their functional absence affects the entire ecosystem. Declines in apex predators release prey species at lower trophic levels, so mesopredators and herbivores often increase in abundance, becoming new fisheries targets (Jackson et al. 2001; Steneck and Sala 2005; Steneck et al. 2004). This process is known as "fishing down marine food webs" (Pauly et al. 1998).

Conventional wisdom assumes that fish stocks remained "pristine" until targeted by commercial fishing fleets to supply foreign markets, thus initiating a historical process of fishing down the marine food web (e.g., Jackson et al. 2001; Lotze et al. 2006). Thus, in the western North Atlantic a pristine state—one unaffected by human activity—is assumed to have persisted until European contact (Jackson et al. 2001; Lotze and Milewski 2004). Archaeological studies in the Aleutians (Simenstad et al. 1978), California (Erlandson et al. 2004, 2005), and the Caribbean (Wing and Wing 2001), however, have presented compelling evidence for prehistoric declines of apex predators due to fishing. If such prehistoric effects were widespread, then perhaps we will have to reset our timeline for when coastal ecosystems first departed from their pristine baseline (Erlandson and Fitzpatrick 2006; see also Erlandson and Rick, this volume).

In this chapter, we present archaeological and isotope data from a coastal site in Maine that suggests localized fishing down of nearshore coastal food webs may have begun thousands of years before European colonization. Specifically, we report on changes in the relative abundance of faunal remains in the well-preserved and best-studied midden in coastal Maine, the Turner Farm site in Penobscot Bay. We also use stable nitrogen and carbon isotope analysis of prehistoric and modern bone collagen of cod, sculpin, flounder, and humans to estimate relative trophic positions of each species and the degree to which coastal, kelp-derived organic matter supported the food web. We do this to provide long-term data on the magnitude and scale (spatial and temporal) of environmental change in nearshore coastal marine settings in the western North Atlantic to better understand when the region departed from pristine conditions, so managers can set realistic goals for ecosystem restoration.

GULF OF MAINE KELP FOREST ECOSYSTEM AND FOOD WEBS PAST AND PRESENT

Although the Gulf of Maine is highly productive, it has never been highly diverse (Steneck et al. 2002; Witman et al. 2004). This naturally low diversity results from three factors. First, the North Atlantic is relatively young and only recently inoculated with a subset of higher taxa from the eastern North Pacific (Vermeij 1991). Second, of the possible species relatively few could withstand the western North Atlantic's shallow water temperature extremes (Adey and Steneck 2001). Finally, North American glaciers expanded as recently as 18,000 BP (uncorrected radiocarbon years BP) to cover most of North America's rocky shores, resulting in local extinctions and biogeographic zone compression. As a result, the comparatively few species that lived in the Gulf of Maine were found in high abundance and provided key ecological services in the ecosystem.

The Gulf of Maine's coastal ecosystem comprises four dominant trophic levels: apex and mesopredators, herbivores, and algal primary producers (Figure 8.1). The algae include large structure-producing kelp such as *Laminaria* spp. (Steneck et al. 2002) and other algal forms. Kelp forests dominate nearshore rocky habitats from zero to 20–45 m deep, depending on water clarity (Vadas and Steneck 1988). Algae contribute significantly to the energy flow in nearshore food webs (Duggins et al. 1989; Mann 1973).

Most kelp forest ecosystems are sensitive to changes in herbivore populations, particularly the sea urchin *Strongylocentrotus droebachiensis* (Figure 8.1; Steneck et al. 2002). Strong interactions between adjacent trophic levels can create "trophic cascades" (sensu Paine 1980) in which predator declines release limits on herbivorous sea urchin population growth, resulting in urchin population explosions and widespread kelp deforestation (Steneck et al. 2002). Such sea urchin–induced algal deforestations are common globally and often result from the overfishing of predators (reviewed by Steneck et al. [2002]). However, in species-depauperate ecosystems such as the Gulf of Maine, there are so few species at each trophic level in the food web that population declines in a few key species can trigger significant changes throughout the system (Steneck et al. 2002).

Steneck et al. (2004) examined long-term ecological change in the Gulf of Maine and proposed that its coastal kelp forest ecosystem had remained relatively stable, dominated by apex predators and kelp for over 4,000 years (Figure 8.1). Evidence for this phase came from pooled archaeological records, mainly from the Penobscot Bay area of Maine, indicating a long-term abundance of large predatory fish, especially the demersal cod in nearshore waters beginning 4,200 to 4,000 years ago and ending early in the last century. Steneck et al. (2004) inferred the persistence of the three-trophic-level system of apex predators (primarily Atlantic cod), herbivores (the green sea urchin), and algae (mostly kelp) throughout that phase (Figure 8.1) with no hint of major changes in food webs. Mesopredators such as lobsters and crabs are generally not considered strong interactors. Then, in the last century, two significant ecosystem phase changes occurred. The first was a rapid, fisheries-induced decline in predatory finfish that began around AD 1930 with large-scale mechanized coastal trawling (Steneck and Carlton 2001). Affected species included cod and most other large-bodied, commercially important species such as haddock, hake, and halibut. Their decline allowed the

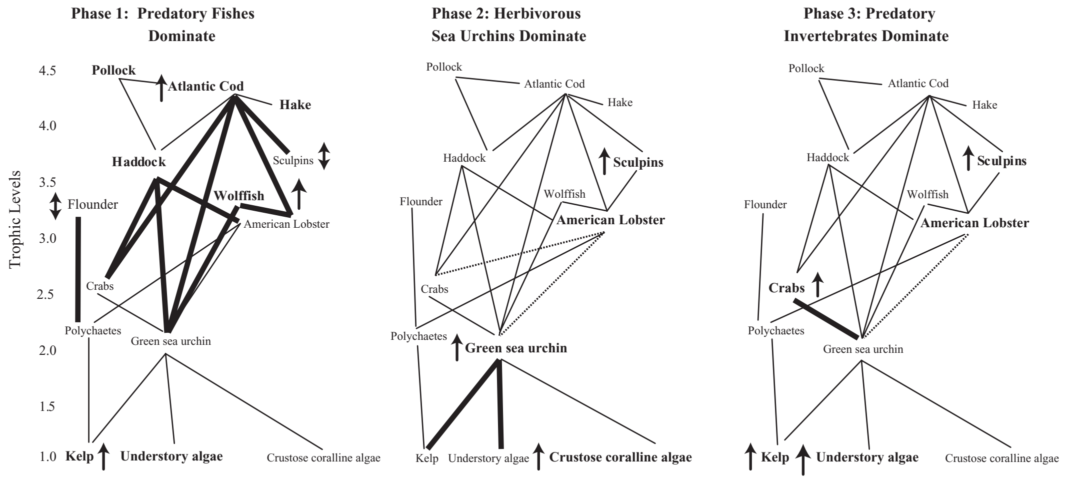

FIGURE 8.1. Three phases in marine food webs in coastal Maine over the past 5,000 years (modified from Steneck et al. 2004). All species determined to have been abundant at one time were plotted according to their assigned trophic level (Table 8.1). Only fully marine organisms are included; birds and terrestrial mammals (e.g., sea mink) were excluded. Abundant species are identified by larger font and boldface; rare or low-abundance species are shown in smaller regular type. Most trophic linkages (lines connecting species) have been demonstrated with ecological studies (see Steneck et al. 2004). Apex predators were all fish with a fractional above trophic level (TL) ≥ 4.They feed on mesopredators (TL >2, <4) and herbivores (TL ~2). Algae are primary producers in this system (TL 1). All TL values and scientific binomials are in Table 8.1. Interaction strengths correspond to the width of trophic linkage lines. Note that some species are weak interactors in this system. Lobsters' trophic linkages are weak despite their abundance in recent years because they feed primarily on lobster bait. Functionally dominant taxa at each trophic level are illustrated with an arrow indicating abundance. Double-headed arrows (pointing up and down) indicate taxa that fluctuate in importance during the identified phase.

expansion of prey species such as crabs, lobsters, and eventually sea urchins, which in turn caused a decrease in kelp forests, amounting to a functional phase shift in the system from three to two trophic levels (Figure 8.1b). The second sudden change was triggered by the unprecedented fishing of sea urchins, which began in AD 1987, peaked in AD 1993, and then quickly culminated in widespread stock collapse and another phase shift from two to one trophic level that persists to the present. Here kelp forests have expanded significantly, and crabs and lobster are the top predators (Figure 8.1c; Steneck et al. 2004).

These two recent phase shifts are examples of "trophic level dysfunction," where the abundance of organisms at a highly interactive trophic level declined to the point that they no longer limited the abundance of their prey, and their functional role was lost. The inability of the Gulf of Maine's coastal ecosystem to resist these phase shifts stems from its low biodiversity, which fails to provide ecologically equivalent species to buffer against trophic level dysfunction (Steneck at al. 2004). To date, no study has considered that such phase shifts may have occurred prehistorically. Such a consideration requires that we examine the archaeological record and cultural history of the region.

THE PENOBSCOT BAY ARCHAEOLOGICAL RECORD AND CULTURAL HISTORY

Penobscot Bay is centrally located on the Maine Coast within the Gulf of Maine. Most important archaeological sites in the bay are located on its many islands, including the Turner Farm site on North Haven Island (Figure 8.2). These sites have been the focus of archaeological research since 1970, and the bay now ranks among the better-studied archaeological regions of the western Atlantic Coast of North America. The number of excavated sites currently stands at over 40, the number of catalogued artifacts exceeds 10,000, and the number of faunal

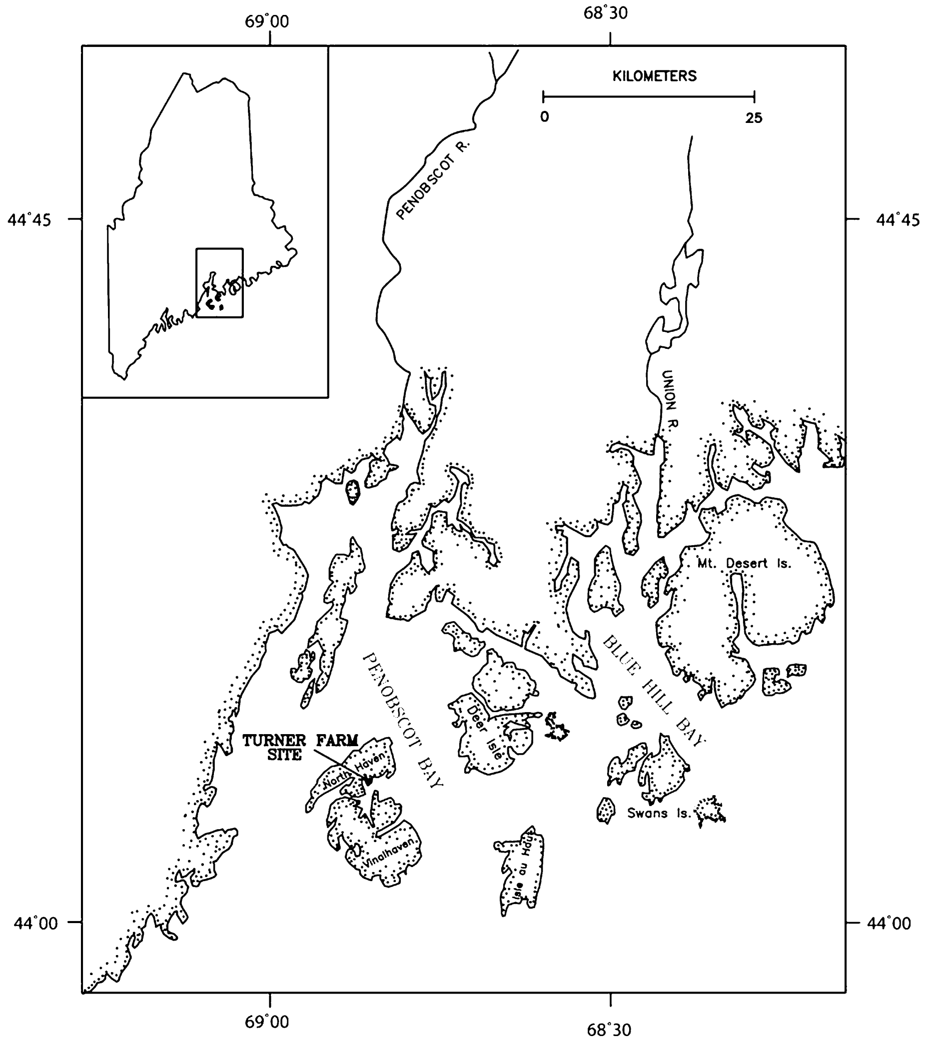

FIGURE 8.2. Map of the Penobscot Bay area showing North Haven Island on the outer coast of Maine, where most midden sites, including the Turner Farm site, were located.

specimens is exponentially larger. For purposes of this analysis, however, we focus on faunal samples from the Turner Farm site, a large, extensively analyzed shell midden on North Haven Island (see Bourque 1995; Spiess and Lewis 2001). The faunal samples from this site span, more or less continuously, the period from about 5000 to 400 BP. We grouped the samples into five occupation periods, although the record for the earliest and latest present problems. The faunal sample from the earliest occupation is very small, but we include it because it provides a glimpse of what early people ate in coastal Maine. The latest sample dates to around the time of first sustained European contact (~400 BP) but came from a stratum disturbed by historic agricultural plowing, Bourque's (1995) "plow zone" (Table 8.1). We include it in the present analysis despite the likelihood that it is to some extent contaminated by late prehistoric material because it exhibits trends we regard as significant. We use published chronostratigraphic dates (i.e., Bourque 1995) to show the overall trends, although the dates will likely be somewhat revised in the near future.

TABLE 8.1

Percent Bone Fragments from Turner Farm Site

COMMON NAME	SCIENTIFIC NAME	FRACTIONAL TROPHIC LEVEL	OCC. 1 4350 BP	OCC. 2 4100 BP	OCC. 3 3550 BP	OCC. 4 1600 BP	PLOW ZONE 400 BP
Atlantic cod	*Gadus morhua*	4.4	74.36	22.32	16.05	2.17	2.15
Flounder total	*Pleuronectes* sp.	3.2	12.82	12.02	16.36	37.68	31.79
Sea mink	*Mustela macrodon*	4.0	0.00	12.02	23.77	9.86	11.06
Fish unidentified	Class Actinopterygii	3.8	12.82	5.02	5.56	20.29	11.82
Flounder, winter	*Pleuronectes americanus*	3.2	0.00	6.61	9.10	14.76	17.62
Bivalve, softshell clams	*Mya arenaria*	2.1	0.00	12.95	15.12	1.50	10.74
Swordfish	*Xiphias gladius*	4.5	0.00	16.78	3.70	0.42	0.11
Sculpin	*Myoxocephalus* spp.	3.6	0.00	1.85	2.93	7.60	7.41
Atlantic sturgeon	*Acipenser oxyrhynchus*	3.4	0.00	1.59	1.39	1.16	2.04
Flounder, yellowtail	*Limanda ferruginea*	3.2	0.00	0.40	1.23	1.87	1.29
Atlantic tomcod	*Microgadus tomcod*	3.3	0.00	4.23	0.15	0.02	0.21
Seal, harbor	*Phoca vitulina*	4.0	0.00	0.79	0.93	0.39	0.64
Seal (unidentified)	*Phoca* sp.	4.0	0.00	0.13	1.70	0.74	0.00
Seal, gray	*Halichoerus grypus*	4.0	0.00	0.53	0.46	0.20	0.54
Flounder, American dab	*Hippoglossoides platessoides*	3.7	0.00	0.00	0.31	0.47	0.75
Spiny dogfish	*Squalus acanthias*	4.3	0.00	0.13	0.00	0.23	0.97
Cunner	*Tautogolabrus adsperus*	3.5	0.00	0.00	0.62	0.06	0.00
Atlantic herring	*Clupea harengus*	3.2	0.00	0.66	0.00	0.02	0.00
Blue mussel	*Mytilus edulis*	2.1	0.00	0.26	0.31	0.02	0.00
Haddock	*Melanogrammus aeglefinus*	3.6	0.00	0.40	0.00	0.05	0.11
Atlantic halibut	*Hippoglossus hippoglossus*	4.6	0.00	0.00	0.00	0.29	0.21

TABLE 8.1 (*continued*)

COMMON NAME	SCIENTIFIC NAME	FRACTIONAL TROPHIC LEVEL	OCC. 1 4350 BP	OCC. 2 4100 BP	OCC. 3 3550 BP	OCC. 4 1600 BP	PLOW ZONE 400 BP
Pollock	*Pollachius virens*	4.5	0.00	0.40	0.00	0.02	0.00
Atlantic wolffish	*Anarhichas lupus*	3.2	0.00	0.00	0.00	0.00	0.32
Flounder, windowpane	*Scophthalmus aquosus*	3.2	0.00	0.00	0.15	0.02	0.11
Atlantic salmon	*Salmo salar*	4.5	0.00	0.26	0.00	0.00	0.00
American eel	*Angulla rostrata*	3.7	0.00	0.00	0.15	0.02	0.00
Sea urchin	*Strongylocentrotus droebachiensis*	2.0	0.00	0.13	0.00	0.02	0.00
Seal, harp	*Phoca groenlandica*	4.0	0.00	0.13	0.00	0.00	0.00
Alewife	*Alosa pseudoharengus*	3.5	0.00	0.13	0.00	0.00	0.00
Gastropod, waved whelk	*Buccinum undatum*	2.6	0.00	0.13	0.00	0.00	0.00
Bivalve, ocean quahog	*Arctica islandica*	2.1	0.00	0.13	0.00	0.00	0.00
White shark	*Carcharodon carcharias*	4.6	0.00	0.00	0.00	0.00	0.11
Harbor porpoise	*Phocoena phocoena*	4.2	0.00	0.00	0.00	0.06	0.00
Cusk	*Brosme brosme*	4.0	0.00	0.00	0.00	0.05	0.00
Right whale	*Eubalaena glacialis*	4.2	0.00	0.00	0.00	0.03	0.00
Atlantic mackerel	*Scomber scombrus*	3.5	0.00	0.00	0.00	0.03	0.00
Bluefish	*Pomatomus saltatrix*	4.5	0.00	0.00	0.00	0.02	0.00

NOTE: From Spiess and Lewis (2001).Species ordered from highest to lowest average percent bone fragments pooled across the four distinct occupations ("Occ.") with median ages of occupation (from Bourque 1995). Fractional trophic levels for each species are from Froese and Pauly (2002) and Steneck et al. (2004).

The earliest clear evidence of human occupation in the Penobscot Bay area comprises a scattering of Early and Middle Archaic projectile points in styles found over large portions of northeastern North America that date between about 8500 and 6000 BP (Bourque 2001). The earliest intact archaeological components, however, are manifestations of the Small Stemmed point tradition, found primarily from southern New York to the mid-Maine Coast and dating between about 5000 and 4500 BP (Bourque 1995). The Turner Farm site produced the only significant faunal sample from this period.

The next clear cultural manifestation in the region, known as the Moorehead Phase, seems to be a regional descendant of the Small Stemmed point tradition and dates between about 4500 and 3800 BP (Bourque 1995). This was a population located between the Kennebec and St. John's rivers and devoted to a maritime lifestyle that included extensive fishing for cod and swordfish, as well as terrestrial hunting (Figures 8.3 and 8.4). Also characteristic of the Moorehead Phase is a complex pattern of mortuary behavior that included multiple, large cemeteries with ocher-filled graves furnished with beautifully crafted locally made artifacts and exotics from other regions. Some of the exotic artifacts come from sources (e.g., Ramah Bay, Labrador) as far as 1,000 miles away (Bourque 1995).

All traces of the Moorehead Phase disappeared around 3800 BP. Immediately thereafter a very different cultural manifestation appeared on the scene. Known as the Susquehanna Tradition, it took over territory not only of Moorehead Phase people but also apparently of all contemporaneous Northeastern cultures as far north as the St. Lawrence River (Bourque 1995:244–254). The earliest reliable dates for the Susquehanna Tradition in Maine do not exceed 3700 BP. There is now an archaeological consensus that the Susquehanna Tradition represents a complete break with the Moorehead Phase, making the arrival of a new population the likely explanation for its appearance. In southern New England, where the Susquehanna Tradition also looks like a population replacement, the pattern remained in place and changed over time for nearly 1,000 years. In Maine, however, its tenure was apparently brief, with the latest reliable radiocarbon dates falling no later than 3500 BP, and the artifact styles that typify the later phases of the Susquehanna Tradition to the south are rare or absent there.

The archaeological record becomes weak and ambiguous after the disappearance of the Susquehanna Tradition and does not revive until around 2800 BP when the earliest ceramic pottery appears and midden accumulation resumes. Thereafter, the rate of midden accumulation at the Turner Farm site and elsewhere in Penobscot Bay appears to increase throughout the remainder of the prehistoric period (Bourque 1995:169–222).

Beginning in the mid-sixteenth century, the presence of Europeans in the Gulf of St. Lawrence began to impact populations in the Gulf of Maine and, by AD 1600 (~400 BP), Europeans began to appear there on a regular basis. By that time, European demand for beaver pelts had caused indigenous economies to shift toward terrestrial beaver hunting at the expense of pursuing marine foods (Bourque 1995; Bourque and Whitehead 1994). Thereafter, native occupation of the coastal zone decreased as epidemics drastically reduced populations, and as new population amalgamations established villages in the interior.

FAUNAL TRENDS AT THE TURNER FARM SITE

To search for trends in faunal assemblages and fishing activity over time, we quantified the abundance and trophic level of all dominant species found in the Turner Farm midden (Table 8.1). Specifically, we assigned each species a fractional trophic level (TL) value (Froese and Pauly 2002) based on the trophic level of prey it consumed. Thus, primary producers, herbi-

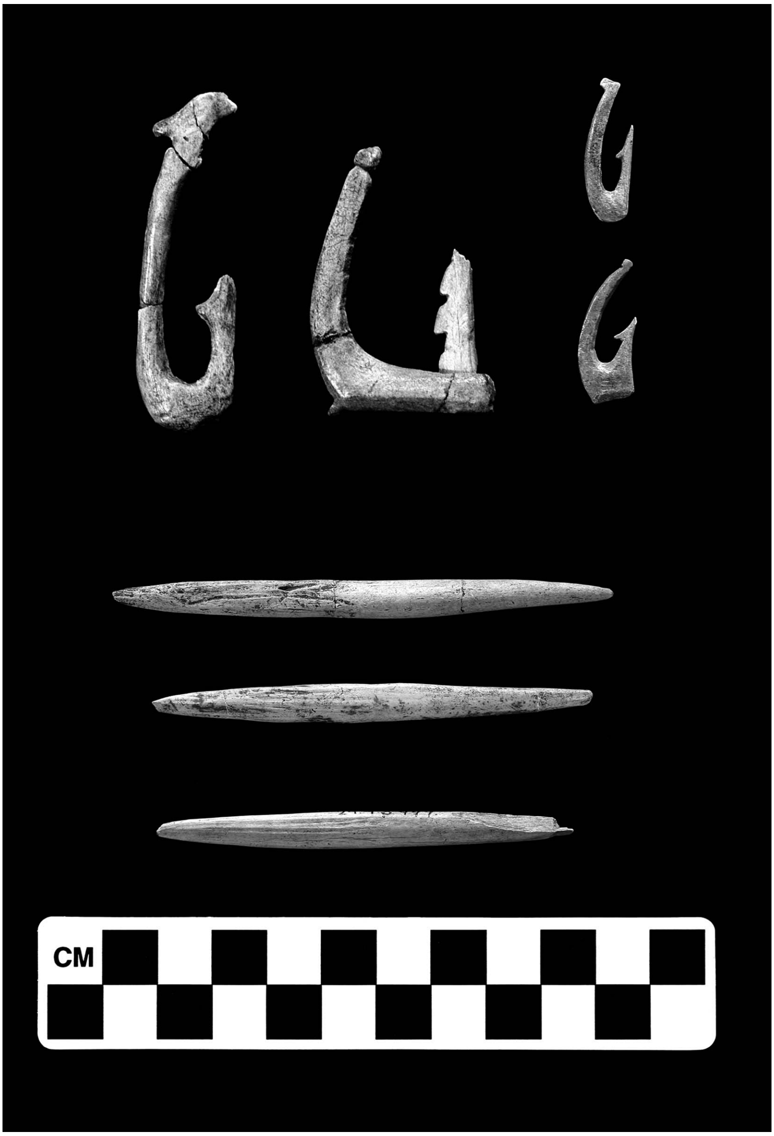

FIGURE 8.3. Bone artifacts from the Turner Farm site. The large hooks in the upper row are from Occupation 2 (~4350 BP) and probably were used to catch cod. The small hooks are from late prehistoric strata and are appropriately sized to catch flounder, the bones of which were extremely abundant in these strata. The bone points below the hooks represent an artifact type commonly found in late prehistoric contexts where flounder bone is abundant, and may have served as the central piercing element in leisters, such as the example shown in Figure 8.4.

vores, mesopredators, and apex predators were assigned TL numbers ranging from 1 to 4.6 (Table 8.1). All taxa were compiled at the level of species or at the TL possible (some bones could only be identified as seal or flounder, for example). Operationally we defined apex predators as species with a fractional trophic level of four or more. Mesopredators were assigned TLs between 3.0 and 4.0. We assigned lower fractional TLs to invertebrate mesopredators such as crabs (Figure 8.1), although they were absent from the midden (Table 8.1). Species with

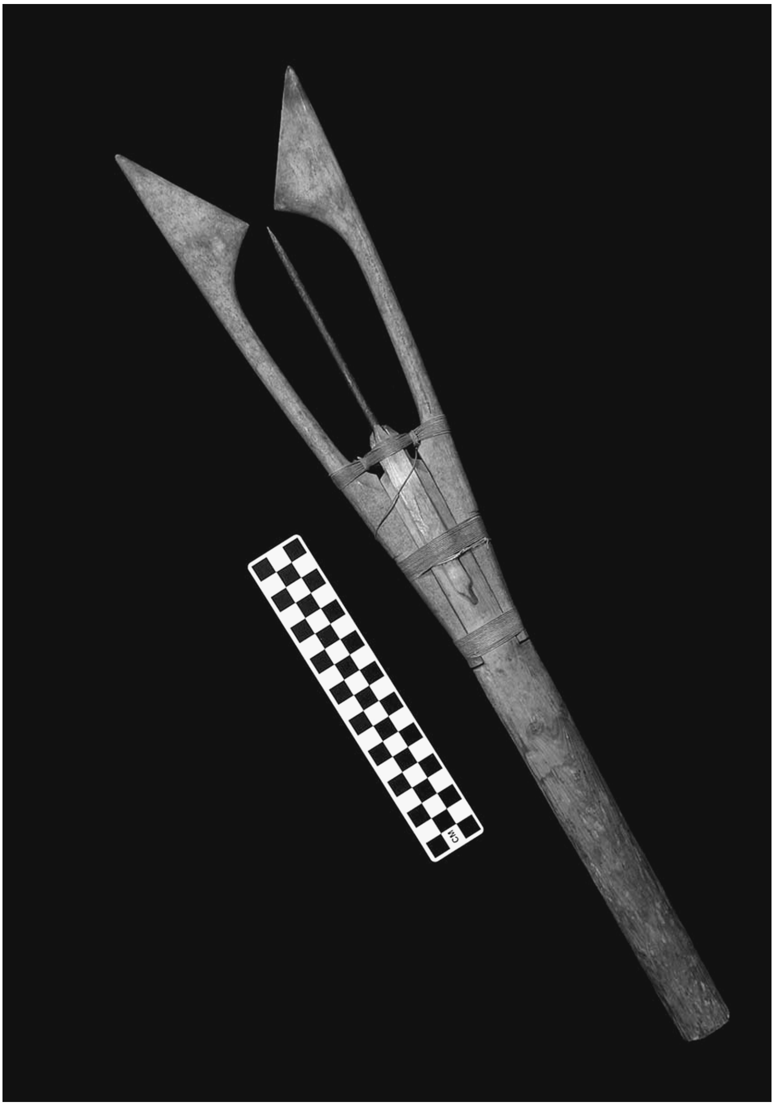

FIGURE 8.4. Leisters were used historically throughout the Maine–Maritime Provinces region to spear fish, including flounder. The central piercing element of this nineteenth-century Penobscot specimen is of steel and may represent a modern modification of the bone point used prehistorically. The shaft of this example has been sawed off.

TLs < 3.0, including suspension feeders and herbivores, were relatively rare and thus were pooled for this analysis.

Apex predators declined and mesopredators increased proportionally over the five-occupation sequence (Figure 8.5). The most important trends were the decline in Atlantic cod and increase in flatfish (four species of flounder including American dab). Another group of mesopredators, the sculpins (probably several species), also increased. Today, sculpins are the most abundant fish in Maine's cod-depleted nearshore benthic communities (Figure 8.1b and c; Steneck 1997). There was no clear trend among the suspension feeders or herbivores.

Two groups of apex predators, seals and dogfish, increased slightly in abundance during the prehistoric period (Figure 8.5, Table 8.1), possi-

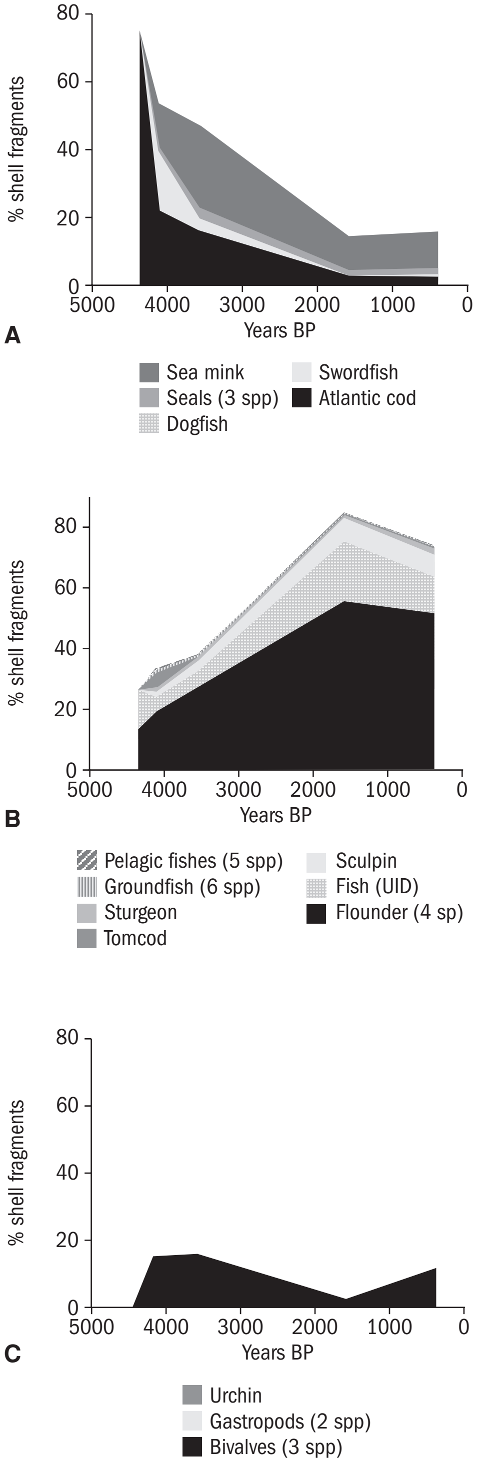

FIGURE 8.5. The proportion of bone and shell fragments in middens with median dates ranging from 4350 to 400 BP separated by trophic level groups of (A) apex predators, TL ≥ 40; (B) mesopredators TL ≥ 3.0, <4.0; and (C) suspension feeders and herbivores TL < 3.0 (data in Table 8.1).

bly because their populations were being released from competitive suppression as cod decreased in abundance and size over time. Recent declines in cod stocks in the 1980s to 1990s were followed by such an increase in dogfish (Fogarty and Murawski 1998) and seals (Trzcinski et al. 2006). The upward trend in seals is particularly interesting because they swallow their prey (predominantly fish) whole and would have been at a competitive disadvantage against large cod, which eat a wider size range of fish, including all species consumed by seals. The large cod found in the Turner Farm middens (i.e., averaging 1 m long) may well have reduced the prey available for seals, thereby putting them at a competitive advantage over the seals.

We suspect that the changes we have observed at the Turner Farm site were caused by a human-induced reduction of apex predators brought about by fishing practices (e.g., via enhanced fishing pressures, altered fishing methods, technology, or traditions, such as the abrupt culture change evident during the brief occupation by people of the Susquehanna Tradition). We regard climate change as an unlikely cause because climate conditions for cod in coastal zones should have improved during the cooling of the Little Ice Age of the thirteenth to nineteenth centuries AD (Grove 2001; Planque and Fredou 1999), when their abundance at Turner Farm reached a low point. Further, by the 1600s AD, large and abundant cod were reported at numerous other nearby coastal areas, such as in Rosier's AD 1605 account of fishing at nearby Pemaquid (Quinn and Quinn 1983:25–311).

STABLE ISOTOPES AND MARINE FOOD WEB MODELS

Faunal remains from the Turner Farm site described briefly above and elsewhere (Spiess and Lewis 2001) indicate that prehistoric people consumed many species of marine fishes for at least 5,000 years before European colonization (Table 8.1). However, as Spiess and

Lewis (2001:86) pointed out, "it is difficult to estimate the relative contribution of fish versus mammals [primarily deer] to the diet of the site's inhabitants" based only on faunal identification. Nor can faunal identification alone reveal where an organism was captured. To shed light on these issues, we turn to stable isotope analyses. We then consider if the several millennia of prehistoric harvesting could have affected relative abundances and even altered marine food webs.

Where isotopically distinct primary producers occur at the base of the food web, it is possible to use stable carbon and nitrogen isotopes of animal tissue (e.g., bone collagen, muscle, lipids) to reconstruct animal diets and energy flow within the ecosystem, as well as animal foraging behavior (Michener and Schell 1994; Michener and Kaufman 2007). In most temperate marine settings, for example, kelp and sea grasses incorporate more ^{13}C-enriched dissolved inorganic carbon during photosynthesis than most species of phytoplankton (Fry and Sherr 1984). Consequently, kelp and sea grasses have more enriched, or more positive, carbon isotope values (expressed as δ^{13}C) than phytoplankton. The δ^{13}C value of the food sources is passed on, with some modification (~1–2‰ enrichment with each trophic level [Fry and Sherr 1984]), to the tissues of the consumer (Figure 8.6). Similarly, the δ^{15}N value of the food sources is passed on, with some modification (~3‰ enrichment for each trophic level [Ambrose and DeNiro 1986; Fry 1988; Minagawa and Wada 1984]) to the consumer such that nitrogen isotopes can be used to discern the relative trophic positions of organisms living within an ecosystem (Wada et al. 1991; Figure 8.6).

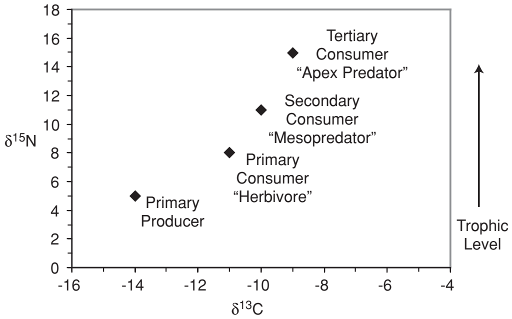

FIGURE 8.6. Simplified models of carbon and nitrogen isotope fractionation in a marine food web where kelp is the only primary producer, and each consumer is subsisting solely on organisms from the next lower trophic level. The largest carbon fractionation occurs at the lowest trophic level energy transfer, when the carbohydrate-bound carbon (i.e., primary producers) is converted to protein-bound carbon (i.e., muscle tissue of consumers). Names used for consumers in food web interactions are included in quotes (see text).

In Penobscot Bay, the dominant marine primary producers are benthic macroalgae (e.g., kelp), sea grass, and phytoplankton. For various species of macroalgae, carbon and nitrogen isotope values range between −12 and −27‰, and between 5 and 8‰, respectively (Fry 1988; McMahon et al. 2005). Sea grass isotope values range between −3 and −15‰ for carbon (McMillan et al. 1980) and 4 and 6‰ for nitrogen (B. Johnson, unpublished data). For Gulf of Maine phytoplankton, carbon isotope values range between −18 and −27‰, with nitrogen isotope values between 5 and 9‰ (Fry 1988; McMahon et al. 2005). Detritus and dissolved organic matter derived from these photosynthesizing organisms is consumed by passive suspension feeders and deposit feeders such as polychaetes, amphipods, isopods, mollusks, and sea urchin (Josefson et al. 2002; Duggins and Eckman 1994), then passed up the food web, with the appropriate isotope fractionations occurring at each trophic level (e.g., Lesage et al. 2001). In certain settings, it is possible to use isotopes to determine the degree to which marine species depend on various primary producers (Bustamante and Branch 1996; Stephensen et al. 1986; Duggins et al. 1989).

The dominant primary producers in Penobscot Bay generally occupy different ecological settings. Kelp and other benthic macroalgae grow on rocks in relatively shallow nearshore environments, whereas sea grasses (primarily *Zostera marina*) are the dominant producers in more protected, shallow, sediment-dominated environments. Rocky shores dominate most outer exposed habitats near the islands of North Haven and nearby Vinalhaven, as well as the corresponding outer coastal region (Figure 8.2), so the nearshore setting would have been kelp and benthic algal dominated. Sea grass was probably locally abundant primarily in the Fox Island Thoroughfare adjacent to the Turner Farm site.

The food web contribution of kelp and other algae relative to pelagic phytoplankton declines with distance from the shore (Mann 1973; Steneck and Dethier 1994), and phytoplankton become the dominant primary producer in pelagic, offshore systems. Within the nearshore kelp forest ecosystem, sea urchins are dominant herbivores, but they appear in low abundance in the middens at Turner Farm (Spiess and Lewis 2001), implying that they probably would have had little impact on the standing kelp biomass. Sea grass is slower than kelp to break down and is consumed by fewer organisms (Harrison 1989). Epiphitic algae in grass beds, however, is taken up by primary consumers and has isotopic values similar to that of the sea grass (Hoshiko et al. 2006). These trophic pathways presented in Figure 8.1 are localized to these areas of production.

The isotopic composition of marine animal tissues can be used to determine the degree to which these animals forage in nearshore versus offshore settings (Aurioles et al. 2006; Burton et al. 2001; Kaehler et al. 2000; Lesage et al. 2001). Tissue from animals that forage on kelp or sea grass in nearshore waters are enriched in ^{13}C, whereas those that forage in more pelagic, offshore waters are depleted of ^{13}C. When more than two sources of primary carbon are present (e.g., kelp, sea grass, phytoplankton, epiphytic algae), the use of multiple chemical tracers (e.g., nitrogen, carbon, and sulfur isotope compositions and C/N values) and isotope mixing models can elucidate more specific information on energy transfer and food web structure (e.g., Phillips and Koch 2002).

For this study, we analyzed the isotopic composition of well-preserved Middle and Late Holocene deer, bear, cod, sculpin and flounder bone collagen from the Turner Farm site to determine if the major species found in middens are trophically linked to the prehistoric people. We evaluated the degree to which members of the marine community show isotope signatures indicative of nearshore kelp and sea grass communities. We also analyzed modern muscle tissue from cod, flounder, and sculpin collected from the Gulf of Maine to compare to the Holocene record of fish diets and evaluate the degree to which fish diets may have changed over the last 4,000 years.

Cod are trophic generalists that feed on small and large crustaceans and, as they grow and mature, on other fishes (discussed further below). We predict that if cod and other coastal fish were abundant in coastal zones near the Turner Farm site, they would be enriched in ^{13}C, reflecting the presence of kelp and/or sea grass beds. Isotopically depleted cod would reflect a shift to a more phytoplankton-based, offshore food web. Flounder and to a lesser extent, sculpins commonly live in shallow sediment-dominated habitats colonized by the eelgrass *Zostera marina*. Thus, we predict that the isotopic composition of flounder and sculpin will be more enriched in ^{13}C than the cod, reflecting coastal kelp and perhaps some sea grass-derived organics at the base of the food web.

ISOTOPIC TRENDS IN PENOBSCOT BAY

Our study includes stable isotope analysis of one to four samples of deer, bear, cod, sculpin, and flounder bones picked from four different strata in the Turner Farm midden. Two samples of modern cod were analyzed, one caught by a local lobsterman in July 2005 not far from the Turner Farm site, and the other collected by the state of Maine's Department of Marine Resources (DMR) inshore trawl surveys in May 2006. Three modern flounder and sculpin were also collected by the DMR inshore surveys in May 2006. The archaeological bone collagen was extracted and prepared after Harrison and Katzenberg (2003). White muscle tissue was lipid-extracted from the modern fish.

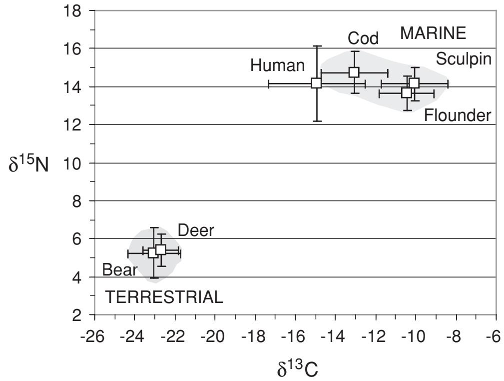

FIGURE 8.7. The average stable isotope composition (±1 SD) of Holocene (4000–400 BP) bone collagen from the dominant species in the Turner Farm midden. This figure illustrates the vastly different isotopic fields occupied by marine verses terrestrial animals (shaded regions). The human isotope data (from a 3500 BP cemetery at the Turner Farm site; Bourque and Krueger 1994) plot very close to the marine field, implying that human diets were heavily influenced by marine fish.

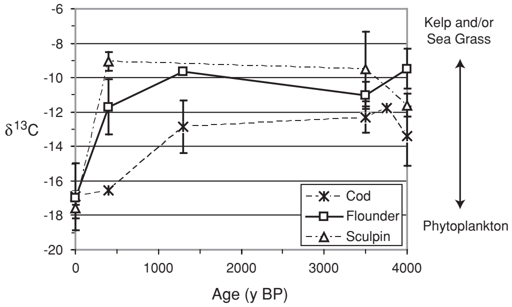

FIGURE 8.8. The average carbon isotope composition (±1 SD) of archaeological cod, flounder, and sculpin bone collagen and modern muscle tissue, where age is plotted in thousands of years (ka) BP. Dramatic shifts in cod diets occurred sometime between 1300 and 400 BP.

All samples were run in the Environmental Geochemistry Laboratory at Bates College using a ThermoFinnigan Delta Plus Advantage stable isotope ratio mass spectrometer interfaced to a Costech elemental analyzer via the combustion interface. Atomic C/N ratios between 2.9 and 4 and the presence of collagen "ghosts" were used to verify the presence of intact collagen in the archaeological samples (after Tuross et al. 1988).

The isotope data for the Holocene deer and bear bones were not statistically different from each other (Figure 8.7), suggesting that they ate similar diets comprised almost exclusively of C_3 vegetation (e.g., leaves, shoots, berries, etc.). In contrast, the Holocene cod, flounder, and sculpin samples were significantly more enriched in ^{15}N and ^{13}C relative to the bear and deer samples (Figure 8.7). The marine fish incorporated more isotopically enriched and variable carbon at the base of the food web (e.g., phytoplankton, kelp, sea grasses) and occupied a higher trophic level relative to the terrestrial animals analyzed.

The human isotope data were also enriched relative to the bear and deer data, implying that marine resources were an important component to the human diet (in agreement with Bourque and Krueger [1994]). Thus, it appears that the Turner Farm humans were eating a diet dominated by marine fish, as well as some terrestrial animals. At this stage, it is impossible to be more precise about the degree to which these different animals were consumed, and the importance of shellfish to the diet.

Temporal changes in the carbon isotope composition of the flounder, sculpin, and cod provide insight into the types of primary consumers at the base of the food web through the Middle to Late Holocene (Figure 8.8). Between 4000 and 1300 BP, the isotope data for cod, flounder, and sculpin were relatively consistent. In general, more ^{13}C-depleted values were measured in cod and more enriched values were measured in sculpin and flounder through the time series. This suggests that flounder and sculpin fed on nearshore kelp and/or sea grass–associated organisms compared to cod that had a much larger foraging range often taking them far from kelp-associated organisms in the coastal zone (Figure 8.8).

The most significant prehistoric decline in carbon isotope values appears to have occurred in cod at 400 BP (Figure 8.6). This may indicate that large cod were extirpated from nearshore environments, while sculpin and flounder persisted and were hunted there. It is possible that cod's high food value (especially its preservability) stimulated offshore and distant fishing following coastal extirpation. While cod may have been overfished at some point before 400 BP, there is no evidence that sea urchin populations expanded as a result. The carbon isotope signature of nearshore sculpins and flounders remained enriched indicating that kelp and/or sea grass dominated throughout the prehistoric period. Importantly, sea urchin remains did not increase during the later occupations (Figure 8.5). In contrast, other researchers have reported an increase in sea urchin fragments and other herbivore remains in archaeological sites where predators were extirpated, including Simenstad et al. (1978) in the Aleutians and Erlandson et al. (2005) in California.

In general, the biomass of benthic macroalgae is currently high in coastal Maine (post-1995) due to overfishing of sea urchins in the early 1990s (Steneck and Sala 2005). As fishery trawl surveys generally avoid shallow rocky areas where kelp is most abundant, the relatively depleted ^{13}C signal of modern fish samples may reflect the more offshore, phytoplankton-based nature of the sampling locations.

The convergence of isotopic values in the modern fish may represent evidence for a loss of biodiversity accompanied by overfishing of the marine food web (e.g., Steneck et al. 2004). Alternatively, the isotope data may merely reflect homogeneity in the food sources available at the collection sites. Sampling at finer spatial scale resolution will be necessary to determine the extent and significance of the recent carbon isotope depletion and the loss of biodiversity.

DISCUSSION

Cod were ecologically important as the largest abundant apex predator in Gulf of Maine coastal ecosystems (Steneck and Carlton 2001). Individuals more than 180 cm long and weighing over 95 kg were recorded as recently as the 1800s (Collette and Klein-MacPhee 2002). Significantly, Turner Farm site faunal remains indicate average body lengths of about a meter (Jackson et al. 2001; Steneck and Carlton 2001).

Atlantic cod were targeted by the earliest inhabitants of the Turner Farm site and dominated midden deposits until around 3500 BP. The carbon and nitrogen isotope signatures from both cod and human bone indicate that the marine coastal ecosystem supported populations of people and cod for at least several thousand years. The prominence of cod in this and other middens throughout the region from Maine's Boothbay Harbor (Carlson 1986) to Canada's Bay of Fundy (Lotze and Milewski 2004) is easy to understand. Cod have high food value, are easy to catch because they do not resist capture, and can be preserved with simple techniques available to prehistoric people (Kurlansky 1997).

Because of its large size and high food value, the decline of Atlantic cod through time at the Turner Farm site probably reflects a real decline in cod stocks/populations rather than a change in climate or fishing preference. Further, while most of the fish bone isotope signatures were consistent with those associated with kelp forest (or benthic algal-dominated) ecosystems, the carbon isotope values from 400 BP suggest a more pelagic, phytoplankton-based food web (Figure 8.6). If cod had become locally rare in the nearshore kelp forests surrounding North Haven and Vinalhaven, prehistoric cod fishers may have been forced to travel offshore.

We suspect that large and old cod living close to shore were locally overfished. Large cod may live for 30 to 50 years, but their rate of growth slows with age (Collette and Klein-MacPhee 2002; Scott and Scott 1988). The archaeological record suggests that the prehistoric human population of North Haven grew over time, and fishing pressure could have eventually extirpated stocks locally. The decline of this large apex predator is important because it could have relaxed population controls at lower trophic levels, resulting in a mesopredator release. In a recent case study from the Canadian Maritimes, a similar release occurred when collapsed cod stocks seem to have resulted in increases in shrimp and crab populations (Worm and Myers 2003).

The increase of flounders, sculpins, and dogfish over time in the Turner Farm samples is also in accord with declining cod stocks. Importantly, cod diets change as they grow. When they first reach the benthos, they feed on small crustaceans; later in their juvenile life they feed on decapods such as shrimp, crabs, and lobsters (Langton and Bowman 1980). As they grow to larger sizes, adult cod become increasingly piscivorous, feeding on larger fish. Since cod longer than a meter are known to feed on several species of flounder (Langton and Bowman 1980), it is possible that the increase of flounders in the Turner Farm middens reflects a mesopredator release from the loss of large cod in the areas. Similarly, flounder, sculpins, and dogfish all increased in abundance following the recent collapse of Atlantic cod in the southern Gulf of St. Lawrence (Hanson and Lanteigne 2000) and in the Bay of Fundy (Lotze and Milewski 2004). It is important to note that such a mesopredator release could have occurred if only the largest cod in the population were extirpated, since smaller cod function differently as predators only of invertebrates. Thus, an absence of large cod does not necessarily indicate that the species was absent from the region—the situation in modern times that Steneck et al. (2004) identified as trophic level dysfunction in the Gulf of Maine.

At the Turner Farm site, seal abundance varies inversely with cod, increasing dramatically with time. Given their high value for food and pelts, seals would likely have been hunted by early coastal peoples as they were in the North Pacific (Hildebrandt and Jones 2002). The relative scarcity of seal bone in prehistoric Gulf of Maine middens reported by Lotze and Milewski (2004) and Spiess and Lewis (2001; Table 8.1) suggests that they may have been less abundant in the region's prehistoric coastal ecosystems where cod were limiting their prey. According to Frank et al. (2005), recent increases in seal abundances may likewise reflect the collapse of cod populations because of a mesopredator release in small forage fish that seals can swallow, although marine mammal protection legislation has also likely had a strong influence on the dramatic increase in seal populations in the United States and Canada (Baraff and Loughlin 2000; Trzcinski et al. 2006).

Lobsters and crabs are strikingly absent from the Turner Farm site faunal samples (Table 8.1; Steneck et al. 2004). In fact, none have been found at archaeological sites anywhere in the Gulf of Maine (Lotze and Milewski 2004). This is surprising given their current hyperabundance in Maine's coastal zone, where lobster population densities can exceed two per meter square in boulder habitats (Butler et al. 2006; Steneck 2006; Steneck and Wilson 2001). Their abundance in early historic times is suggested by reports that Europeans captured very large ones with boat hooks (Quinn and Quinn 1983:283, 307). One possible explanation for this absence is a prehistoric scarcity of lobsters and crabs resulting from cod predation that allowed them to survive only in low numbers and/or hidden in sheltered refugia were they would have been particularly difficult to catch. A prehistoric depletion of cod in nearshore coastal zones could have had significant demographic consequences for lobsters. Lobsters begin life on the benthos, in shallow-water nearshore coastal zones (i.e., <20 m; Butler et al. 2006). Thus, a loss of predators could have contributed to local increases of lobsters by the time of early European colonial fisheries. Supporting such an inference is the fact that lobsters and crabs were commonly eaten by cod in Maine's coastal zone during the 1800s (Herrick 1911; Smith 1879), suggesting that these predators did indeed suppress lobster and crab population densities in coastal zones during early prehistoric times (Butler et al. 2006). Another possibility, however, is that lobster and crab shells may not preserve well in shell middens. Their exoskeletons are well calcified and so, like sea urchins, might be expected to preserve well in the alkaline environment of shell middens. Indeed, both decapods can preserve well in the fossil record (Bishop 1986). However their shells are made of chitin, a polysaccharide embedded in a hardened proteinaceous matrix that may succumb to biological degradation in the well-oxygenated context of a shell midden. Furthermore, if they were at all abundant prehistorically, their shells would, as today, likely be commonly found along the shore. If so, an occasional specimen would likely have been collected along with small gastropods that are often found in the lenses of beach gravel used to cover prehistoric house floors. In any case, the high abundances of today may well be another manifestation of mesopredator release (Steneck and Carlton 2001).

Despite our evidence for declines in apex predators and increases in mesopredators, we found no evidence of change in sea urchin abundance and, by inference, kelp forests (Steneck et al. 2002). In other coastal zones, predator declines were followed by increases of sea urchins in middens (e.g., Erlandson et al. 2004, 2005; Simenstad et al. 1978). Thus, the possible changes to coastal food webs by prehistoric cultures in Maine were relatively subtle by being confined to apex and mesopredators, compared to the larger changes that affected herbivory recently (Steneck et al. 2002, 2004).

That prehistoric peoples negatively affected ecosystems is no longer novel, but there have been few reported marine examples, and we suspect the effects we describe here were very localized. Many past studies have focused on agricultural or large-scale societies affecting terrestrial ecosystems (Redman 1999). We suggest that prehistoric hunter-gatherers in Penobscot Bay negatively affected a highly productive marine coastal ecosystem but did so very locally. As an example of how a simple fishing technology might have fished down a coastal Maine marine food web, we offer two examples of local cod stock depletion from the seventeenth century.

In AD 1614, Captain John Smith described Monhegan Island (about 20 km from the Turner Farm site) as a marvelous fishpond. He reported 15 to 18 fishermen using small boats to catch cod at a rate of 60,000 fish per month. This developed into a fishing station where as many as 80 fishing boats were based in the island's harbor between AD 1616 and 1622. Yet the station closed a few years later in AD 1626 (McLane 1992). About a decade later, a very small English fishing station was established at a very rich fishing location on Richmond Island near Casco Bay in Maine (about 100 km southwest of the Turner Farm site). This station, initially operating just three small vessels, produced 2,000 quintals (100 tons) of salt cod in AD 1639. Thereafter, however, catches rapidly declined to only 257 quintals by AD 1641 despite a threefold increase in fishing effort (Baxter 1884:155, 163–169, 215, 283, 312, 335).

Importantly, these very early fishing stations operating close to shore at a spatial scale comparable to prehistoric fishing efforts in Penobscot Bay appear to have rapidly depleted local cod stocks. The history of the early English fishing stations suggests that localized nearshore fisheries suffered nonsynchronous booms and busts. This asynchrony is important because it argues against cod stock declines having been climate driven.

The evolution toward larger boats with greater range continued following local coastal extirpations. By AD 1840, a "Report of the Joint Select Committee on the Fisheries, Maine legislature, 1841" (reported in O'Leary 1996) stated: "The coast of Maine, is in some parts sterile." From that period forward a greater proportion of Maine's landings came from more distant locations. By the mid 1800s, the fishing fleet from Massachusetts was fishing primarily on Canada's Scotian Shelf (Rosenberg et al. 2006). Although coastal cod of that era may not have been economical to harvest using the hook and line methods of the day, they were not absent. For example, scientists studying crabs collected them from the stomachs of cod in Casco Bay (Smith 1879). However, as discussed earlier, decapods are food for juvenile cod, so it is unlikely that abundant and large inshore cod such as the meter-long cod in Maine's prehistoric middens survived in Maine's coastal zones into the mid-nineteenth century.

Both the Turner Farm site faunal sample and early historic records of fishing in Maine suggest that depletions can occur at small spatial and temporal scales. Recent research on cod population structure has revealed why this is true. Rather than vast schools of interbreeding fish, as cod stocks have traditionally been characterized, they are actually composed of mosaics of loosely connected metapopulations in which some substocks are very localized (Bentzen et al. 1996). For example, a small stock was identified in the mouth of the Sheepscot River in Maine, and tagging studies showed a high proportion were recaptured in the same area over a six-year period (Perkins et al. 1997). The local nature of cod stocks helps explain why the chronology of extirpation can be so asynchronous. Even at larger scales, evidence suggests that coastal stocks in Maine collapsed in the 1930s (Steneck 1997), whereas offshore Canada and U.S. stocks declined decades later (Myers et al. 1997). Thus, localized depletions of cod due to low-tech fishing may have happened repeatedly beginning in prehistoric times.

CONCLUSIONS

The Gulf of Maine is one of the world's most productive and species-depauperate marine ecosystems, leaving it relatively susceptible to changes in trophic structure and function. A prime driver of ecosystem change is overfishing that first depletes key predators in upper trophic levels, causing former prey species to increase and become the new targets for fishing effort. Such cases of fishing down food webs have significantly affected other nearshore ecosystems on historical (and archaeological) timescales. While it is tempting to assume Maine's coastal ecosystem was pristine at the time of European contact, we have presented archaeological and isotope evidence from the Turner Farm site in Penobscot Bay suggesting that localized fishing down of nearshore coastal food webs may have begun thousands to hundreds of years before European fishers first arrived. Apex predators in this ecosystem were the first targeted and dominate the midden bone mass in the earliest strata (~4350 BP). However, cod were also among the first to decline in relative abundance. Thus by ~3550 BP, cod no longer were the dominant species represented in the middens. By ~1600 and 400 BP cod were a minor midden constituent. Coincident with this cod decline, mesopredators such as flounder and sculpins increased over the next 3,500 years. Although the nearshore fauna appears to have changed locally due to prehistoric fishing pressures, we found minimal indication in the stable carbon isotope composition of cod, sculpin, or flounder bone collagen between 4350 and 1200 BP that sea urchin populations expanded enough to induce kelp deforestation. Cod did show an isotope change before European contact, however, suggesting that fished individuals were no longer coming from a kelp forest ecosystem. By about 400 BP, it is possible that cod had been extirpated from the nearshore kelp-dominated coastal zone, forcing the site's occupants to travel farther to catch them. The ease in capture and preservation of cod may have made them sufficiently valuable to prehistoric people that they expended extra effort to pursue this species. In sum, prehistoric changes to food web structure and functioning at the Turner Farm site suggest that significant human impacts in Gulf of Maine coastal ecosystems—although probably localized in nature—may have started earlier and been of greater magnitude than previously thought. As a result, the fragility of this coastal ecosystem may be underestimated.

ACKNOWLEDGMENTS

This research was an outgrowth of the Long-Term Ecological Records of Marine Environments, Populations, and Communities Working Group supported by the National Center for Ecological Analysis and Synthesis (funded by NSF grant DEB-0072909, the University of California, and the University of California, Santa Barbara). Additional support for RSS came from the National Undersea Research Program (Avery Point, Connecticut) and the University of Maine's Sea Grant Program. We thank Charlotte Lehmann, Kim Rodgers, and Carl Noblitt for sample preparation and analysis. Bob Lewis assisted in figure preparation. This research was funded in part by Bates College and the Maine Marine Research Fund, established by the 120th Session of the Maine Legislature, administered by the Maine Technology Institute, and funded through a bond issue approved by Maine voters.

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