drites, enstatite chondrites, and R chondrites). There are basically four different populations of chondrules, each associated with a particular type of chondrite (*5*). If the solar system was well mixed, as the ^{26}Al (*2*) and ^{60}Fe (*7*) evidence indicates, how is it that different types of chondrules ended up in different parent bodies when chondrule formation occurred over more than a million years? Data for both ordinary and carbonaceous chondrites indicate clustering in ^{26}Al-^{26}Mg ages, but in separate sets of events (*2*). It will be interesting to extend this record to enstatite and R chondrites. The high-precision techniques introduced by Villeneuve *et al*. should be extended to low Al/Mg phases in CAIs to further establish the solar system magnesium isotopic evolution curve.

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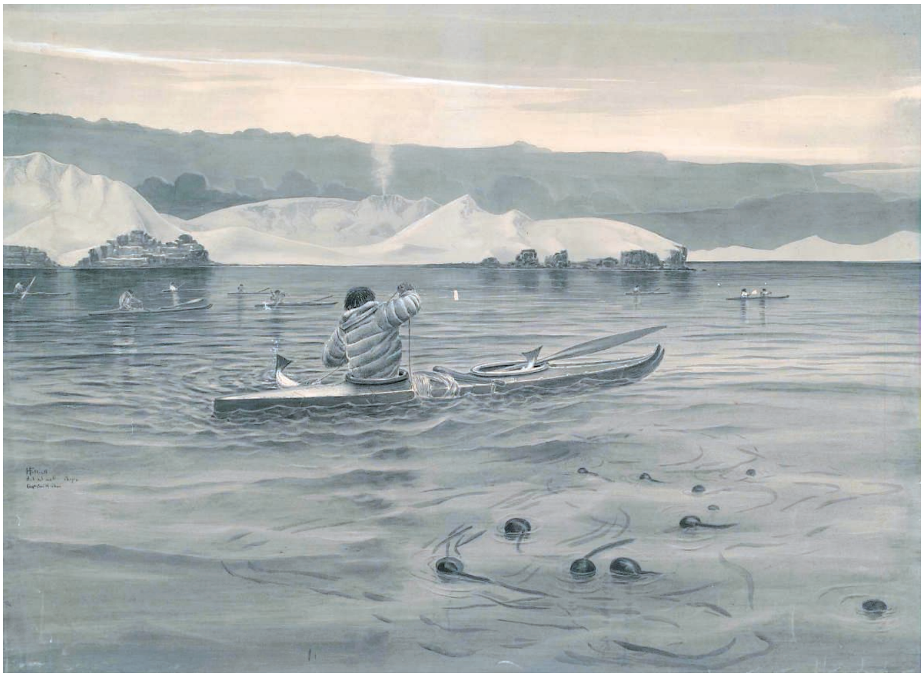
ANTHROPOLOGY

Coastal Exploitation

Torben C. Rick[1] and Jon M. Erlandson[2]

How did ancient hunter-gatherers influence coastal environments?

The development and spread of agriculture and pastoralism during the past 10,000 years is often seen as the tipping point when humans fundamentally changed our relationship with the natural world. Ancient hunter-gatherers also altered their environments, although the extent to which they did so remains hotly debated (*1*–*3*). Hunter-gatherers may have caused major alterations of terrestrial ecosystems, including the use of fire to enhance resource productivity and the translocation of various animals to new regions (*3*, *4*). They are implicated in massive megafaunal extinctions in the Americas and Australia (*2*, *3*). Recent archaeological research from coastal areas shows that they also substantially altered and enhanced marine ecosystems in other ways, some of which obscure the definition of the term "hunter-gatherer."



Ancient fisheries. In this painting by Henry Wood Elliott from 1872, traditional Aleuts fish in kelp forests of the Aleutian Islands. For centuries or millennia, hunter-gatherers around the world used comparable technologies and techniques to exploit near-shore fisheries.

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Shellfish, fish, and other coastal resources have been harvested by hunter-gatherers for more than 150,000 years, with the earliest evidence found in South Africa (*5*). Some early hunter-gatherers influenced the size and structure of near-shore shellfish populations by ~23,000 years ago—the earliest evidence for human impacts on marine populations to date (*6*, *7*). Shellfish size reductions intensified during the past 10,000 years as human populations grew and moved into new areas, but the declines documented by 23,000 years ago demonstrate human influence on the structure of near-shore organisms and ecosystems at a very early date—often millennia before the earliest historical accounts.

Ancient exploitation of keystone species by hunter-gatherers also affected the structure and function of near-shore coastal ecosystems. Native American predation of sea otters in California after ~9000 years ago and in the Aleutians ~3000 years ago allowed abalone and sea urchin populations to expand greatly, changing the entire structure of the kelp forest ecosystem. Such "trophic cascades" may have resulted in localized urchin barrens (areas where sea urchin populations are so large that entire kelp forests are depleted) (*8*, *9*). Compared with those seen in contemporary or historical kelp forests, these ancient urchin barrens may have been short-lived or localized, however, with human harvest of urchins replacing the predatory controls once provided by sea otters.

Cod, a keystone species that is depleted in the North Atlantic today, may have been locally overfished by hunter-gatherers in the Gulf of Maine beginning some 3500 years ago, with archaeological data indicating the greatest reduction in larger, older individuals (*10*). This may have reduced predation pressures on lower trophic level animals, especially medium-sized predators such as floun-

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ders, sculpins, and dogfish, a pattern that mirrors changes seen after the recent collapse of cod in the North Atlantic (*10*). Reductions in top-level predators and increases in medium-sized predators were noted in Gulf of Maine archaeological sites, but unlike the urchin expansions following commercial fisheries, no increase in urchins was identified in the archaeological data, suggesting that these effects were more localized than those of historical commercial fisheries.

Human hunting and fishing in ancient coastal ecosystems thus caused declines in key species, triggered trophic cascades, or reduced the size of prey. However, hunter-gatherers also appear to have improved the productivity of certain resources in some marine ecosystems. For instance, the depletion of sea otters in California waters may have greatly increased the productivity of nearshore shellfish (*9*). On North America's Northwest Coast, clam gardens—human-made rock walls and terraces—have been reported from the San Juan Islands to Alaska (*11*). Hunter-gatherers constructed these clam gardens in the low intertidal, expanding and maintaining the area for clams to live and be harvested. The antiquity of clam gardens is poorly documented, but their widespread occurrence suggests that they may span centuries or possibly millennia and likely greatly increased clam yields. This example of mariculture transcends traditional definitions of hunter-gatherers and provides evidence of intentional environmental management similar to anthropogenic burning in terrestrial landscapes.

Through daily consumption of shellfish and other resources in productive estuaries and marshes, hunter-gatherers also altered coastal ecosystems by depositing vast quantities of shells and other refuse, creating "shell islands" that were often the highest and best drained landforms in the region. Chantuto hunter-gatherers in Mexico created shell mounds 3 to 11 m high that formed islands in the wetlands and were used to process and collect shellfish (*12*). Similar anthropogenic shell islands have been found along the Gulf of Mexico, the San Francisco Bay, and elsewhere. Constructed above rising postglacial seas, they often form microhabitats of plant and animal communities distinct from much of the surrounding landscape.

These cases of predation pressure, trophic cascades, and landscape modification and management show that hunter-gatherers were important components of coastal ecosystems for millennia. Hunter-gatherer environmental interactions in coastal areas and beyond represent a complex and dynamic continuum—from degradation to active management and enhancement—that blurs the division between the natural and anthropogenic worlds deep into human prehistory.

By the end of the 20th century, humans had "domesticated nature," leaving few if any truly wild places on Earth (*13*). However, emerging evidence suggests that hunter-gatherers altered many coastal and island ecosystems long before historical accounts of early European explorers provide evidence for phenomenal abundance compared with modern marine ecosystems (*14*). This increasing antiquity of human alteration of marine and terrestrial environments provides important baselines or benchmarks for the long-term management, restoration, and sustainability of Earth's ecosystems.

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IMMUNOLOGY

The Yin and Yang of Follicular Helper T Cells

The balanced expression of two transcription factors controls the development of a subset of T cells that support B cell maturation.

Amit Awasthi and Vijay K. Kuchroo

The human immune system can harness an arsenal of lymphocytes called CD4$^+$ T cells, in an adaptive response to infection by a variety of pathogens, including parasites, bacteria, and fungi. Once activated, CD4$^+$ T cells can differentiate into subsets of helper T cells [T_H1, T_H2, T_H17, regulatory T (T_{reg}), and follicular T (T_{FH})], whose effector functions include secreting the cytokines necessary for clearing pathogens and inducing inflammatory responses. Each helper T cell subtype is also critical for helping B lymphocytes produce pathogen-specific antibodies (*1*). Until now, master transcription factors have been identified that regulate the generation of helper T cell lineages except for T_{FH} cells. On pages 1006 and 1001 of this issue, Johnston *et al.* (*2*) and Nurieva *et al.* (*3*), and a study by Yu *et al.* (*4*), report that the transcription factor Bcl6 is a master transcription factor that controls the generation of T_{FH} cells. However, Bcl6 must work against another transcription factor, Blimp-1, to promote this differentiation process.

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Although distinct from other helper T cells, similarities between T_{FH} and other helper T cell lineages have been suggested (*5*, *6*). For instance, like T_H17 cells, T_{FH} cells produce high amounts of the cytokine interleukin-21 (IL-21). This cytokine drives a feed-forward amplification loop for T_H17 generation (*7*, *8*). Mice lacking IL-21 or the IL-21 receptor not only fail to produce T_H17 cells (*7*, *8*), but are also defective in T_{FH} cell development and antibody isotype switching, and lack germinal centers, the regions in lymph nodes where final B cell maturation takes place (*9*, *10*).

Despite similarities with other helper T cells, T_{FH} cells appear to be a distinct lineage of T cell. Each helper T cell subset expresses a lineage-specific master transcription factor: T_H1 cells express T-bet, T_H2 cells express

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