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The Kelp Highway Hypothesis: Marine Ecology, the Coastal Migration Theory, and the Peopling of the Americas

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ABSTRACT

In this article, a collaborative effort between archaeologists and marine ecologists, we discuss the role kelp forest ecosystems may have played in facilitating the movement of maritime peoples from Asia to the Americas near the end of the Pleistocene. Growing in cool nearshore waters along rocky coastlines, kelp forests offer some of the most productive habitats on earth, with high primary productivity, magnified secondary productivity, and three-dimensional habitat supporting a diverse array of marine organisms. Today, extensive kelp forests are found...
I can only compare these great aquatic forests . . . with the terrestrial ones in the intertropical forests. Yet if in any country, a forest was destroyed, I do not believe nearly so many species of animals would perish as would here, from the destruction of the kelp. Amidst the leaves of this plant, numerous species of fish live, which nowhere else could find food or shelter; with their destruction the numerous cormorants and fishing birds, the otters, seals, and porpoise, would soon perish also; and lastly, the Fuegian[s] . . . would . . . decrease in numbers and perhaps cease to exist. (Charles Darwin [1909:256–257]; 1 June 1834, Tierra del Fuego, Chile)

INTRODUCTION

Despite some important discussions about the feasibility of a coastal migration route (e.g., Fladmark 1979; Mason 1894), theories about the human colonization of the Americas were dominated by terrestrial models for most of the twentieth century. These terrestrial models generally involved hunting peoples walking from northeast Asia across Beringia near the end of the Pleistocene, passing through the fabled “ice-free corridor” and into the heartland of North America. Only considerably later, according to these models, did the descendants of land-based Paleoindians settle in coastal habitats and gradually adapt to life by the sea. Some scholars warned that the dearth of early coastal sites might be due to rising post-glacial sea levels, but numerous ~13,000 year
old (cal BP; all dates in this article are expressed in calibrated calendar years before present) sites in interior regions and a lack of coastal shell middens older than about 10,000 years left the Pacific Coast relatively peripheral to debate about how people got to the New World.

During the last decade or so, despite the effects of rising seas and marine erosion on the archaeological record, the coastal migration theory has emerged as an increasingly viable alternative for the peopling of the Americas (see Dixon 1999, 2001; Erlandson 1994, 2002; Fedje et al. 2004; Gruhn 1994; Jones et al. 2002; Mandryk et al. 2001). The transformation of the coastal migration theory from marginal to mainstream is the result of the gradual accumulation of geological and archaeological evidence from both coastal and interior regions around the Pacific Rim. Fluted Clovis-like points have now been found from coast to coast in North America, for instance, and terminal Pleistocene sites have been identified in several areas along the Pacific Coast of North and South America (see Erlandson et al. 1996; Keefer et al. 1998; Richardson 1998; Sandweiss et al. 1998). These include shell middens or human skeletal remains found on islands in Alta and Baja California, sites that demonstrate that coastal Paleoindians had seaworthy boats and other maritime capabilities between about 13,000 and 11,500 cal BP (Des Lauriers 2006; Erlandson 2007; Johnson et al. 2002; Rick et al. 2005).

Evidence for even earlier maritime voyaging by anatomically modern humans (*Homo sapiens sapiens*) has emerged from islands of the western Pacific Rim, including the colonization of Australia roughly 50,000 years ago and additional ocean voyaging to the islands of western Melanesia, the Ryukyu Archipelago, and Japan between 40,000 and 30,000 years ago (see Erlandson 2002; Fedje et al. 2004; with references). By the Last Glacial Maximum (LGM) these colonizing voyages placed maritime peoples near the base of the Kurile Islands, which could have provided a series of staging points for a maritime migration to the Kamchatka Peninsula and the south coast of Beringia (Erlandson 1994:269).

While the feasibility of a coastal migration route into the New World has grown, recent geological and archaeological evidence has clouded the potential of an interior route to account for the earliest human colonization of the Americas. Recent geological studies suggest that the ice-free corridor between the Laurentide and Cordilleran ice sheets only became passable about 13,000 years ago (Burns 1996; Dixon 1999:30; Jackson and Duk-Rodkin 1996; Mandryk et al. 2001), for instance, and there is increasing interest in the hypothesis that humans colonized the Americas before that time (Madsen 2004; Mandryk et al. 2001; Meltzer 2004). Although the site remains controversial (see Fiedel 1999), widespread scholarly acceptance of debate about a 14,500 year old occupation of the Monte Verde site near the coast of Chile (Dillehay 1997; Meltzer et al. 1997) has also contributed to a broader interest in the coastal migration theory by American archaeologists.

If a variety of evidence now suggests that a coastal migration around the North Pacific may have contributed significantly to the peopling of the Americas, relatively little is known about the paleogeography and paleoecology of North Pacific coastlines or their feasibility as a late Pleistocene migration route. Our primary goal in this article is to help fill that gap by discussing the nature and productivity of nearshore habitats around those portions of the Pacific Rim that may have served as a migration
route for early maritime peoples moving from East Asia into the Americas. Our focus is on the ecology and history of kelp forests, which are present today around much of the Pacific Rim from Japan to Baja California.

ECOLOGICAL CONTEXTS FOR THE COASTAL MIGRATION THEORY

In this section we examine some issues related to coastal productivity, kelp forest ecology, and the paleoecology of North Pacific coastlines since the Last Glacial Maximum (LGM). These discussions provide a broader ecological context for understanding the habitats and resources early coastal peoples may have encountered during a gradual migration from Northeast Asia into the Americas.

Latitudinal Variation in Coastal Productivity

Anthropological characterizations of marine or aquatic productivity have often been relatively negative (e.g., Osborn 1977; Washburn and Lancaster 1968; Wilson 1981), but many coastal ecosystems offer a diverse array of both marine and terrestrial resources for human foragers, especially those with efficient boats (Ames 2002; Bailey and Milner 2003; Erlandson 2001; Yesner 1980). Not all coastal ecosystems are equally productive or accessible for maritime peoples, of course, and latitudinal variations in coastal productivity around the Pacific Rim are significant, especially in considering the potential for human migrations around the North Pacific. If such migrations occurred, they took place primarily in higher latitudes (35–70°N), where the coastal oceans are relatively productive and large-bodied prey species tend to be concentrated. Freshwater ecosystems, in contrast, are generally more productive in lower latitudes, with numerous biological consequences. Anadromous fish are found primarily in high latitudes, for instance, but catadromous species dominate at low latitudes, reflecting the selective advantage of adult life in food-rich environments (Gross et al. 1988). Similar patterns are seen in evolutionary radiations among many aquatic mammals. Despite their nearly ubiquitous distribution in freshwater habitats, for instance, otters radiated into the sea only at higher latitudes, while small cetaceans radiated into freshwater habitats (river dolphins) only at lower latitudes. Other biological manifestations of high-latitude marine productivity are seen in rainbow trout (Oncorhynchus mykiss) that grow slowly in fresh water while anadromous conspecifics (steelhead) grow rapidly in the sea. Coastal grizzly bears (Ursus arctos) also achieve a maximum adult body mass two to three times greater than those in inland regions. These patterns suggest that the high productivity of northern coastal ecosystems—where resources of both land and sea were accessible—would have been powerful magnets for early coastal or maritime peoples migrating around the North Pacific.

Marine Ecology of the Coastal Migration Route

During the Last Glacial Maximum, between about 25,000 and 20,000 years ago, global sea levels were more than 100 meters lower than today, exposing large expanses of the now submerged continental shelves around the Pacific Rim, including the broad and low-lying plains of Beringia that once connected Northeast Asia and Northwest North America. Since the 1980s, several authors (e.g., Colinvaux and West 1984; Elias et al. 1997; Guthrie 1989; Hopkins et al. 1982) have published extensively on the nature and productivity
of Beringia’s terrestrial environments, but descriptions of the potential productivity of coastal resources and their possible role in facilitating or inhibiting coastal migrations around the North Pacific have been comparatively vague (e.g., Hopkins et al. 1982; Mason 1894) and little was known about the specific nature of nearshore ecosystems.

Recent reconstructions of the post-glacial flooding of Beringia, however, suggest that its south coast was geomorphically complex (Figure 1; Manley 2002) with numerous bays, inlets, and islands that may have provided rich habitat for a variety of seals and cetaceans, walrus (*Odobenus rosmarus*), the massive (and now extinct) Steller’s sea cow (*Hydrodamalis gigas*), and other relatively large-bodied marine animals (Brigham-Grette et al. 2004:59). During the summer months, such convoluted coastlines—especially when combined with the low gradient of the Beringian platform—may have offered broad expanses of productive intertidal and nearshore habitats for early maritime peoples to hunt, forage, and gather in. As Ames (2002:38) illustrated, along such convoluted coastlines people in seaworthy boats can access much larger areas of nearshore habitat—and transport much larger loads back to residential bases—than those traveling on foot.

Much of the northern Pacific Rim is also characterized by marine upwelling or other forms of oceanic mixing that fuel high plankton production in coastal zones, primary productivity that is passed to higher trophic levels where it is more available to humans. Another major source of coastal productivity around the North Pacific is found in extensive kelp forests that concentrate biomass, magnify secondary productivity, subsidize terrestrial productivity, and support relatively complex food webs in coastal ecosystems (see Dayton 1985; Duggins et al. 1989; Graham 2004; Maron et al. 2006; Polis et al. 1997; Steneck et al. 2002).

### Modern Kelp Forest Ecology

Around the Pacific Rim today, kelp forests dominate shallow rocky coasts in cool and cold-water marine habitats. The distribution of kelp forests is physiologically constrained by water temperature (generally <20°C) and the availability of light, firm substrates, and nutrients (Mann 1973; North 1994; Steneck et al. 2002). Fast-growing and structurally complex, kelps are generally limited to nearshore waters less than about 30 m deep (Dayton 1985; Graham et al. 2003). Kelp forests are common from Japan to the Aleutians and down the Pacific Coast of North America into Baja California (Figure 2). After a break in the tropics—where productive coral reefs, mangrove swamps, estuaries, and other coastal habitats support similar suites of marine fish, shellfish, and other aquatic animals—kelp forests continue along the Andean Coast, from Peru to Tierra del Fuego.

The North Pacific has an especially diverse array of kelps, with at least 21 species in the northeastern Pacific alone (Dayton 1985:235; Druehl 1970; Estes and Steinberg 1988). Large canopy-forming kelps dominate many Pacific Rim kelp forests, including the giant kelps (*Macrocystis* spp.) which grow to heights of 45 m along the west coasts of North and South America (Graham et al. 2007). Smaller canopy kelps (e.g., *Nereocystis luetkeana, Alaria fistulosa*) reach heights up to 10 m and are common from central California to Alaska and from the Aleutians to northeast Asia, respectively (Druehl 1970). Stipitate kelps are smaller (<5–10 m long), but *Laminaria* dominates many
North Pacific kelp forests from Japan and northeast Asia to coastal Alaska and the Pacific Northwest (Druehl 1970).

Most Pacific kelps thrive along rocky shorelines in conditions of ample light, high nutrients, and moderate water temperatures, but some varieties have adapted to subarctic conditions with strong seasonal fluctuations in light levels, nutrient availability, and water temperatures—even surviving beneath winter sea ice and blooming during a limited growing season (Dunton and Dayton 1995). In the Sea of Okhotsk, for instance, kelp forests form an almost continuous belt along the coastline, photosynthesizing during ice-free summers and growing from carbohydrate stores during ice-packed winters. As Dayton (1985:235) noted, some North Pacific kelps also exhibit considerable morphological and ecological diversity depending on local conditions, ranging from perennial to annual and from floating canopies to short prostrate turfs. Under the right conditions, however, kelps tend to grow relatively rapidly, enriching coastal ecosystems with organic production derived from their spores and plant detritus (Graham et al. 2007).

Around the North Pacific, kelp forests historically supported or sheltered a similar suite of animal and plant resources heavily exploited by
coastal and maritime peoples with relatively high population densities. These include sea mammals (sea otters, pinnipeds, etc.), a variety of marine shellfish (abalones, sea urchins, mussels, chitons, etc.) and fish, sea birds, and edible seaweeds. Many of these resources—including numerous members of the same genus or species (e.g., the sea otter, *Enhydra lutris*) found in nearshore habitats around much of the northern Pacific Rim—were harvested historically with relatively simple technologies. Some species were available in aggregations of highly vulnerable or behaviorally naive fauna (pinniped rookeries, seabird colonies, and salmon runs, etc.) that could be captured in large numbers. For maritime peoples, along with providing a diverse array of food resources, kelp forests also reduce nearshore wave energy and provide holdfasts for boats.

**Figure 2.** General distribution of kelp forest ecosystems (hatched areas in white) of the Pacific Rim region today. Inset: shell midden on San Miguel Island, California, with high concentration of abalone shells, sea urchin tests, and the remains of other kelp forest organisms (figure drafted by M. Graham; inset photo by M. Moss).

**Reconstructing Late Pleistocene Kelp Distributions**

For the broader Pacific Rim, the geographic distribution and ecological productivity of kelp forests near the end of the LGM are not well understood. Due to the clear parameters that govern their growth today, the distribution of kelp forests in the past can be roughly approximated (see Kinlan et al. 2005), but direct evidence for their geographic distribution or productivity is limited (Graham et al. 2003). Based on the diversity of North Pacific kelp species, as well as the organisms strongly
associated with kelp communities, Estes and Steinberg (1988; see also Estes et al. 1989) argued for a deep antiquity of kelp forests in the area. During the Pleistocene, for instance, the massive sea cow ranged from Japan around the North Pacific to central California, where it almost certainly fed primarily on kelp (Clementz 2002). Kelp itself does not preserve well in the fossil record (Estes et al. 2005:591; Graham et al. 2003) and virtually all late Pleistocene shorelines where such fossils might be found have been submerged by rising postglacial seas or lost to coastal erosion. The same can be said for most coastal archaeological sites (see below) dating to the late Pleistocene, where we might hope to find the remains of organisms such as large abalones (Haliotis spp.) and sea urchins (Strongylocentrotus spp.) strongly associated with kelp forests (see Graham 2004). In the future, indirect evidence for the presence and productivity of kelp may come from isotopic or trace element studies of the organic fractions of fossil organisms or even seafloor sediments, but the baseline research to determine the feasibility of such methods has not yet been done. For now, we are left with estimating the distribution of ancient kelp forests through the use of bathymetric maps, sea level curves, and sea-surface temperature data.

Kinlan et al. (2005) modeled the changing distribution of kelp forests along the California Coast during the past 20,000 years, for instance, concluding that kelp forests were significantly more extensive and productive during the terminal Pleistocene than they are today. If this holds true for the broader Pacific Rim, rocky coastlines along much of the North Pacific may have been even more attractive for early maritime peoples than they were for the dense Native American populations that occupied much of the Pacific Coast at the time of European contact. Moreover, the generally cooler sea-surface temperatures that characterized the LGM in the North Pacific may have shifted the boundaries of kelp forest ecosystems into somewhat lower latitudes than they are found in today, possibly narrowing the tropical gap in kelp forests in the eastern Pacific.

Today, the survival of productive kelp forests in the Sea of Okhotsk also suggests that kelp forests existed along much of the North Pacific Coast through the LGM (Steneck et al. 2002). Kelps also survive under the coastal sea ice of the arctic Beaufort Sea, where they have probably persisted since the beginning of the Pleistocene (Vermeij 1991). Given the apparent abundance of complex rocky shorelines, sea surface temperatures consistent with kelp growth, seasonal sea ice cover, and the dearth of sediment-producing glaciers along most of Beringia’s south coast, there is no reason to think productive kelp forests were not present. For much of the period between about 18,200 and 14,700 years ago, moreover, late-spring to early-fall sea surface temperatures appear to have warmed to 8–11°C in the far northwestern Pacific, when sea ice cover may have been limited to about six months per year (Sarnthein et al. 2006:142–43) and kelp forests may have been even more productive.

Clearly, the south coast of Beringia would have been highly dynamic during the early post-glacial period. With the possible exception of the Younger Dryas cold spell (∼13,000–12,000 cal BP), this was a time of rapid sea level rise and flooding of the Beringian platform. Coastal ecosystems are inherently dynamic, however, and rocky intertidal and nearshore kelp forest communities are full of organisms capable of rapid recruitment and growth, suggesting that nearshore productivity would
have continued to support the larger and more mobile organisms at higher trophic levels. Fueled by high primary productivity driven by a combination of summer plankton blooms and nearshore kelp growth, estuaries with freshwater and terrigenous input, Beringia’s south coast probably attracted a wealth of larger animals (marine and terrestrial) that could have helped early coastal peoples expand their range from Northeast Asia into the Americas. Shortly after the LGM, populations of cetaceans and other sea mammals of the North Pacific may also have been relatively large, making coastal scavenging a highly productive activity.

KELP FORESTS AND NORTH PACIFIC COASTAL ARCHAEOLOGICAL SITES

From the indirect evidence of maritime activity in the Ryukyu Islands and Japan dating to the late Pleistocene, a vast geographic gap exists in coastal archaeological records from Northeast Asia and the now submerged south coast of Beringia. Only future archaeological investigations in the Kurile Islands and the Kamchatka Peninsula will determine if evidence for Pleistocene maritime activity or coastal settlement is present in these areas. Archaeological investigations on the submerged southern shore of Beringia itself would be extremely challenging given the combination of late glacial shorelines located far from current coastal ports, Holocene sedimentation, the expense of ship time, and the logistics of cold water, deep diving, and high wave energy in the Bering Sea.

Reconstructing the late Pleistocene coastlines and human history of the Pacific Coast of North America is also fraught with difficulties, but much of the area has been more intensively investigated by archaeologists and geologists. This research has provided baseline data that has helped scientists find increasingly early archaeological sites along the coastlines of the Pacific Northwest, southern California, and Baja California. From Alaska to Baja California some of the earliest coastal archaeological sites in North America are situated in island or mainland locales adjacent to highly productive kelp forest habitats. These include terminal Pleistocene sites (>11,500 cal BP) at Arlington Springs, Daisy Cave, and Cardwell Bluffs on California’s Northern Channel Islands, as well as on Cedros Island off Baja California. The Arlington Springs site (CA-SRI-173), dated to about 13,000 cal BP (Johnson et al. 2002; Rick et al. 2005) contains only scattered human remains and no faunal remains or diagnostic artifacts. At Daisy Cave (CA-SMI-261) and Cardwell Bluffs (CA-SMI-678), however, components dated between about 12,000 and 11,500 cal BP contain the remains of large red abalones (*Haliotis rufescens*), black turban snails (*Tegula funebralis*), and other marine shellfish strongly associated with kelp forest habitats. At Daisy Cave and other Channel Island sites dated between about 10,200 and 9000 cal BP, the remains of black abalones (*H. cracherodii*), black turban, sea urchin (*Strongylocentrotus* spp.), pinnipeds, sea otter, California sheephead (*Semicossyphus pulcher*), and other fish commonly found in nearshore kelp forests have all been recovered (see Erlandson, Braje, et al. 2005; Erlandson, Rick, et al. 2005; Rick et al. 2001, 2005). At two sites on Cedros Island dated between about 11,500 and 12,000 cal BP, Des Lauriers (2006) has also documented evidence for the exploitation of a variety of marine resources (black abalones, sea otters, etc.) common in kelp forest communities.
Early coastal sites are rare from San Francisco Bay to Vancouver Island, probably because of a history of subsidence earthquakes and tsunamis associated with the Cascadia Subduction Zone (see Atwater 1987; Darienzo and Peterson 1990; Erlandson et al. 1998), but numerous sites dated between about 10,700 and 9000 cal BP have been identified along the coastlines of British Columbia and Southeast Alaska (see Fedje et al. 2004). Most of these components lack well-preserved faunal remains, but the 10,600 year old Kilgi Gwaay site produced the remains of sea otters and other animals common in kelp forest habitats (Fedje et al. 2005).

DISCUSSION AND CONCLUSIONS

In reviewing the evidence for associations between early maritime peoples and kelp forest communities, we are not suggesting that all early Pacific Coast sites will be found adjacent to kelp forests or contain evidence for their exploitation. Indeed, in many cases, estuaries, large salmon streams, pinniped rookeries, and seabird colonies may have been equally attractive to early maritime peoples. In other cases, following productive rivers inland from the coast—or hunting mammoths or elk in peri-coastal upland areas—may have been as tempting as following the coast.

Clearly, there is much to be learned about the antiquity of human settlement and subsistence in various coastal areas from Japan to the Kurile Islands and Kamchatka, and from the south coast of Beringia to the southern tip of Tierra del Fuego. There is also much to be learned about the distribution and productivity of kelp forests, estuaries, mangrove forests, and coral reefs around the Pacific Rim in the past, as well as the degree to which their productivity may have influenced the antiquity, demography, and migrations of maritime peoples near the end of the Pleistocene.

Current evidence suggests, however, that anatomically modern humans had colonized or explored several archipelagos in the eastern Pacific by 50,000 to 30,000 years ago, islands that could only be reached with seaworthy boats. During the LGM, maritime peoples living in the islands of Japan would have been adapting to relatively cool waters, potentially comparable to those in parts of the Gulf of Alaska today. Between about 18,200 and 14,700 years ago, three extended warming episodes in the northwestern Pacific may have reduced seasonal sea ice cover significantly, increased human access to intertidal and nearshore habitats, and facilitated the migration of maritime peoples from northeast Asia to Beringia (Sarnthein et al. 2006). By about 16,000 to 15,000 years ago, a migration route following the outer coast of northwestern North America appears to have been open and productive, providing an opportunity for maritime peoples to migrate down the Pacific Coast into more temperate climates.

Along with the relatively high productivity of kelp forests and other coastal habitats, such a coastal migration route had a number of advantages over interior routes. Climatically, coastlines are generally more equable than adjacent interior regions, which can be brutally cold or hot. Fresh water sources tend to be concentrated and easily accessible in coastal zones (Faure et al. 2002) and coastlines also provide access to a diverse array of plant and animal foods from both marine and terrestrial ecosystems—resources that tend to be tightly packed in the relatively mountainous and steep coastlines that characterize most of the Pacific Rim.
By definition, a coastal route could also have been traversed by maritime peoples entirely at or near sea level, with no major geographic barriers after about 15,000 years ago. The linear distribution of similar coastal habitats and resources could have provided expanding human populations with an ecologically similar and easily followed migration corridor from northeast Asia to northwest North America and beyond.

In contrast, terrestrial peoples migrating through the interior from Beringia to southern South America at the end of the Pleistocene would have encountered numerous physical barriers (massive glaciers, large rivers, mountain ranges and alpine passes, deserts, etc.) and a wide variety of terrestrial ecosystems: from Arctic tundra, to relatively sterile periglacial landscapes, boreal and rain forests, grasslands, deserts, and more. As Madsen (2004:20–21) noted, foragers traversing these environmental “megapatches” would have encountered a wide variety of habitats, plants, and animals, some with very different properties or behaviors that required new technologies and knowledge to successfully exploit.

A variety of archaeological, anthropological, genetic, and geological evidence provides growing support that one or more coastal migrations contributed to the peopling of the Americas (Erlandson 2002; Fedje et al. 2004; Gruhn 1994; Kemp et al. 2007). Ecological data suggest that North Pacific coastlines would have provided early maritime peoples numerous opportunities to hunt, fish, and gather in juxtaposed marine and terrestrial habitats. Some of the most productive of these coastal ecosystems were kelp forests that are nearly ubiquitous along cool or cold-water rocky coastlines of the Pacific Rim. Characterized by relatively high primary productivity and supporting predictable aggregations of marine organisms harvested and eaten by coastal peoples for millennia, Pacific Rim kelp forests may have provided a linear and relatively homogenous ecological setting through which early maritime peoples could have migrated to the New World.

Along the Pacific Coast of North America, some of the earliest archaeological sites are found in island or mainland coast settings adjacent to productive kelp forests. Where faunal remains are preserved, many of these sites contain evidence for the harvest of shellfish, fish, and sea mammals common in kelp forests. Between about 18,000 and 13,000 years ago, as glaciers and sea ice retreated from North Pacific coastlines, a linear band of productive kelp forests may have extended discontinuously from Japan to Baja California, providing a “kelp highway” that could have facilitated the migration of maritime peoples into the New World (Steneck et al. 2002:453).

Showing that a coastal migration around the North Pacific was possible or even highly plausible is obviously not the same as demonstrating that such a migration took place. Given the rising seas, coastal erosion, and dramatic coastal landscape changes that have occurred since the end of the LGM, proving that such a coastal migration took place will be extremely challenging. More archaeological research is urgently needed on land and beneath the sea to help search for late Pleistocene sites along the coastlines of Japan, the Kurile Islands, Kamchatka, Beringia, and the Pacific Coasts of North and South America. Additional research on the paleoecology of North Pacific coastal ecosystems is also needed to provide a better understanding of the problems and potentials posed by a coastal migration route from Asia to the Americas.
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