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Dynamics of sea mammal and bird populations of the Bering Sea region over the last several millennia $\stackrel{\text{\tiny{\%}}}{\sim}$

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Abstract

The secular dynamics of sea mammal and bird populations of the Bering Sea region over the last several millennia are reconstructed. We identify osteological material from the cultural layers of ancient sea-mammal hunter settlements as well as natural deposits in Chukotka, Kamchatka, and the Aleutian and Commandor Islands. Changes in species composition of mammals and birds of this region are identified. Climatic changes are reconstructed from complex investigations of peat and coastal deposits in Chukotka and the Aleutian Islands. All material was radiocarbon dated (about 400 dates). It was found that the main factors affecting the dynamics of sea mammal and bird populations in the northern part of the region over the last several thousand years were summer precipitation and sea ice conditions, whereas in the southern part, precipitation and summer temperature dominated. © 2004 Elsevier B.V. All rights reserved.

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1. Introduction

The increase in anthropogenic factors over the last several millennia due to the transition from huntergatherer to producer economies is well known. "Western" civilizations only began to settle the Bering Sea region in XVIII–XIX centuries and as such, local people were able to preserve their traditional way of life until comparatively recent times. People in this coastal strip lived in permanent settlements for hundreds and thousands of years. This fact, combined with the existence of permafrost and cold conditions—

* Corresponding author. *E-mail address:* histecol@orc.ru (A.B. Savinetsky). providing good preservation of animal and plant remains-facilitates the reconstruction of the history of the regions' ecosystems, in particular the influence of anthropogenic and climatic factors on the dynamics of the animal populations. Our aim is to collect and investigate data on the secular dynamics of harvested populations of mammals and birds and to estimate the influence of different factors on this process. To this end, we have the following specific goals: (1) to estimate the composition and dynamics of mammal and bird populations according to original data and the literature, (2) to determine the influence of climatic and geomorphologic factors such as air temperature, precipitation, summer sea ice conditions and sea level on mammal and bird populations, and (3) to establish the period of occupation by people and the influence of anthropogenic factors on animal populations over the last several millennia.

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2. Study area

Our investigations in the region are limited to coastal ecosystems, including shoreline tundra that is permanently exposed to local marine influences. This zone includes a narrow strip of land running immediately along the shoreline that is periodically flooded by seawater and constantly exposed to the surf, as well as water above the slope of the shore that is continuously exposed to the surf (Leont'ev, 1961). The Bering Sea is situated between the Eurasian and North American continents. Water circulation is induced by the permanent inflow of water from the Pacific Ocean through numerous Aleutian straits. The Bering Strait, whose cross-sectional area is 210 times less, connects the Bering Sea to the Arctic Ocean. The main direction of flow in the Bering Strait is northward (Coachman et al., 1975). The difference in sea level between the Bering and Chukchi Seas is about 0.5 m.

An important characteristic feature of the Bering Sea is its division into two very different zones—deep water (southwest) and shelf (northeast). The boundary between them stretches from the Alaska Peninsula to Cape Navarin. The shelf, which is wide and shallow (less than 200 m deep), represents about 45% of the Sea's total area. Distribution of sea ice in the Bering Sea is unique, stretching south for 1700 km each year (Walsh and Johnson, 1979). In winter, almost the entire shelf zone is covered by ice, whereas its distribution over the deep-sea zone is limited by warm water from the central basin. The formation of ice begins at the end of September and lasts until June. However, ice can often be found all year round in the Bering Strait, especially when northerly winds occur.

Polynyas are of great importance in the northern part of the region as numerous mammals and birds spend the winter there, e.g. bowhead (*Balaena mysticetus*), walrus (*Odobenus rosmarus*), bearded seal (*Erignathus barbatus*), ringed seal (*Pusa hispida*), largha (*Phoca largha*), oldsquaw (*Clangula hyemalis*) and eiders (Bogoslovskaya and Votrogov, 1981). The formation of polynyas depends on several factors mainly wind direction but also currents and temperature regime (Stirling, 1980; Stringer and Groves, 1991). The climate of the Bering Sea region is determined in general by atmospheric circulation (Leonov, 1960), with a strong influence from sea currents. The Alaskan warm stream results in milder climate in the eastern part of the sea than in the western part. Mean annual temperature ranges from +4.4 °C on Unalaska Island to -8.4 °C on Cape Dezhnev; mean January temperature from 0.0 to -21.4 °C, and mean July temperature from +10.8 to +5.4 °C. Mean annual precipitation is 280 mm in the Bering Strait and 1500 mm in the eastern part of the Aleutian Islands.

Marine and coastal mammals and birds of the Bering Sea region can be divided into three groups. The first group includes species that are mainly pagophilic (ice-loving) and inhabit the northern part of the region-bowhead, white whale (*Delphinapterus leucas*), walrus, ringed seal, ribbon seal (*Phoca fasciata*), spectacled eider (*Somateria fischeri*), king eider (*Somateria spectabilis*), Steller's eider (*Polyysticta stelleri*), emperor goose (*Philacte canagica*), red phalarope (*Phalaropus fulicarius*), pomarine jaeger (*Stercorarius pomarinus*), herring gull (*Larus argentatus vegae*), glaucous gull (*Larus hyperboreus*), Sabine's gull (*Xema sabini*), ivory gull (*Pagophila eburnea*) and Ross' gull (*Rhodostethia rosea*).

The second group avoids ice (pagophobic) and lives in the southern part of the sea-right whale (*Balaena* glacialis), blue whale (*Balaenoptera musculus*), sei whale (*Balaenoptera borealis*), sperm whale (*Physeter* catodon), some dolphins, sea lion (*Eumetopias juba*tus), fur seal (*Callorhinus ursinus*), sea otter (*Enhydra lutris*), extinct Steller's sea cow (*Hydrodamalis gigas*), all albatrosses, storm-petrels and cormorants (except the pelagic cormorant, *Phalacrocorax pelagicus*), glaucous-winged gull (*Larus glaucescens*), slatybacked gull (*Larus schistisagus*), red-legged kittiwake (*Rissa brevirostris*), ancient murrelet (*Synthliborammphus antiquus*), Cassin's auklet (*Ptychoramphus aleuticus*), whiskered auklet (*Aethia pygmaea*) and rhinoceros auklet (*Cerorhinca monocerata*).

The third group inhabits both areas with ice and without and includes some species with circumpolar distribution-gray whale (*Eschrichtius gibbosus*), fin whale (*Balaenoptera physalus*), Minke's whale (*Balaenoptera acutorostrata*), humpback whale (*Meggaptera novaeangliae*), killer whale (*Orcinus orca*), largha (*Phoea largha*), harlequin (*Histrionicus histrionicus*), oldsquaw (*Clangula hyemalis*), common eider (*Somateria mollissima*), fulmar (*Fulmarus glacialis*), black-legged kittiwake (*Rissa tridactyla*), murres (*Uria* sp.), crested and least auklets (*Aethia* cristatella, Aethia pusilla), parakeet auk (*Cyclorrhynnchus psittacula*), tufted puffin (*Lunda cirrhata*), horned puffin (*Fratercula corniculata*) and pelagic cormorant.

3. Materials and methods

Coastal, archeological, peat bog, and buried soil deposits, among others are used to study the Holocene history of coastal zone ecosystems. Our original material comes from deposits of different origin collected from several points on the north coast of Chukotka, in the northern and central parts of the Bering Strait, on the east and west coast of Kamchatka, and on several islands—Adak, Amchitka, Buldir, and Shemya (Aleutian Islands) and Bering Island (Commandor Islands) (Fig. 1). The objects are examined using paleozoological (bones of mammals, birds and fish, and the remains of sea invertebrates), paleobotanical (plant remains, charcoal, spore-pollen, phytolith and diatom analyses) paleopedological, and geomorphological methods, as well as radiocarbon dating. To overcome the limitations inherent in each method, each of the sites has been examined using several methods.

Our peat samples come from the northern part of the region—Uelen peat bog on Chukotka Peninsula (Fig. 1), Naskak peat bog (St. Lawrence Island), two peat deposits from Shemya Island (Near Islands, Aleutians), and one from Adak Island (Andreanoff Islands, Aleutians). In addition to macro plant remains, which allow us to reconstruct the history of vegetation of a specific peat bog, pollen and spores



Fig. 1. Site location map: 1—Zhupanovo, 2—Galgan, 3—Masik, 4—Yandogai, Pinakul, Nunyamo, 5—Leimin, Tunytlin, Eilekei, Ekven, Nynluvak, 6—Dezhnevo, Naukan, 7—Uelen peat deposit, 8—Chigetun, 9—St. Lawrence archeological sites, Naskak peat deposit, 10—Cape Krusenstern, 11—Cape Espenberg, 12—Cape Prince of Wales, 13—Cape Denbigh, 14—Nunivak Is., 15—Akun Is., 16—Unalaska Is., 17—Amaknak Is., 18—Umnak Is. (Chaluka, Sheep-Creek, Oglodax'), 19—Anangula Is., 20—Adak Is., 21—Amchitka Is., 22—L. Kiska Is., 23—Buldir Is., 24—Shemya Is., 25—Attu Is., 26—Bering Is.

also demonstrate the history of vegetation of the region, while diatoms and microinvertebrates show changes in climate and hydrology, etc. Additional information was gained from the study of the physical structure of peat samples.

Radiocarbon analysis is, in many cases, the only method that permits synchronization of material obtained from deposits of different genesis. The majority of conventional radiocarbon dates used were determined by the Group of Historical Ecology at the A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences.

To estimate the change in climatic conditions of the region, we used layer-by-layer changes in ash content of the peat and the degree of its decomposition, in addition to published data on the movement of glaciers, and other findings. In cases of good drainage, these conditions are determined by the secular dynamics of warming and the saturation of the deposits (Dinesman et al., 1989, 1996, 1999).

To determine the degree of change in precipitation over the time of formation of the whole layer, we used the allogenic ash content of the layers. The ash content of pure peat cannot exceed 15% (P'yavchenko, 1963). All proportions that exceed this figure are caused by the introduction of mineral particles into the accumulating peat through the surface drainage of atmospheric precipitation from the adjoining slopes, or during periods of flooding.

To estimate the change in the summer temperature regime, we used indicators of layer-by-layer changes in the degree of peat decomposition. The degree of decomposition is determined by the percentage content of unstructured matrix, containing small particles of non-humified remains along with humic matter. Aerobic microorganisms, which actively function only in the upper, peat-forming layer, play the primary role in the decomposition of organic remains. After being covered with a developing layer of peat, the degree of decomposition attained remains practically unchanged (Tyuremnov, 1976). Microorganism activity in the peat layer is only possible with suitable warmth and sufficient moisture, and is suppressed by low temperature, drying, or waterlogging. If the humidity of the peat does not exceed its moisture capacity, the deciding factor influencing decomposition is temperature (Prozorova, 1988). Protracted waterlogging of a well-drained peat bog is unlikely, so that changes in the degree of peat decomposition reflect changes in the temperature regime during the warm half of the year.

In addition, we investigated coastal deposits to provide information on changes in sea level and other climatic factors such as summer sea ice conditions, as well as the dynamics of the vegetation of the region. Coastal deposits were from the Chukotka coast, Shemya Island (Near Islands, Aleutians), Buldir Island (Rat Islands, Aleutians) and Adak Island (Andreanoff Islands, Aleutians).

The study of animal population dynamics was based almost entirely on osteological material from the cultural layers of archeological sites, since other kinds of bone deposits are extremely rare. We collected bones from several sites on the north coast of Chukotka, in the northern and central parts of the Bering Strait, on the east and west coast of Kamchatka, and from several islands—Adak, Amchitka, Buldir, and Shemya (Aleutian Islands) and Bering Island (Commandor Islands) (Fig. 1). In addition, we used data from the scientific literature, making a total of 75,000 bones from roughly 50 sites.

The ancient coastal inhabitants of the region, users of the area of modern Itelmens, Korvaks, Kereks, Eskimos, Chukchi and Aleuts, lived in semi-underground dwellings, built from driftwood and/or whale bones. The remains of food-bones of mammals, birds and fish, and the remains of invertebrates (mollusks, sea urchins)-and other domestic waste, as well as artifacts, formed "kitchen middens" near the dwellings. Lengthy residence led to the trampling and discontinuous development of plant cover and soil, and the gradual accumulation of sand, sandy loam, or loam deposits. Periodic soaking of the developing layer by atmospheric precipitation led to its gradual transformation into a "cultural layer"-a stratum of genetically connected azonal horizons of soil, enriched with bones, artifacts, and humus (Avdusin, 1959). Radiocarbon dating shows that cultural layers can be formed over hundreds and thousands of years.

To study animal remains from the cultural layers, we laid out pits several square meters in area, from which material was removed from recognizable stratigraphic horizons at no more than 5-10 cm at a time. Material was screened or sorted by hand. Bones buried in the cultural layer were distributed differentially. For example, skulls, mandibles, scapulae, and ribs of whales used by ancient Eskimos in the construction of drying racks, dwellings and pits for meat were mainly preserved in the ruins of dwellings and were scarce in the midden layers.

The investigation of some middens showed that the rate of bone accumulation was very low (Dinesman et al., 1999; Savinetsky, 2002). We therefore used the number of identified specimens (NISP) for the quantification of bones (see Dinesman et al., 1999 for detailed description). In order to ascertain the changes in taxonomic composition, we used the percentage portion of each species. However, in order to estimate the dynamics of catch of each species it is necessary to calculate the rate of deposition of bones. To do this, it is necessary to correlate the number of bones of each species in the sample (NISP), with the duration of the time interval of its accumulation (t). The rates of accumulation of bones obtained for different species (NISP/t) are useful for direct comparison and serve as a relative index of the number of individuals procured by hunters. The chronological boundaries of the accumulation periods can be determined by a graph of the growth of the cultural layer, constructed through field descriptions of the profiles, and by radiocarbon dating of samples selected from them. It should be kept in mind that the total numbers of remains, and any transformed indices through time, attest to the dynamics of procurement, which depends on many factors, including the number of hunters, methods of harvest, and so on. In order to proceed from indicators of procurement to faunal population numbers it is necessary to use special methods.

For many years, various modifications of DeLury's method have been used to determine the population sizes of hunted vertebrate animals (DeLury, 1947). These have been widely used in the analysis of the state of recent populations of cetaceans and pinnipeds and the determination of their harvest quotas (Allen, 1966; Bockstoce and Botkin, 1983; Allen and Kirkwood, 1988). In the modification of the method that is proposed by Chapman (1974), the average number of animals (*N*) during period *t*, the quantity of the hunted prey (*C*), and the hunting effort (*f*) expended on obtaining it are linked together in the equation $N_t = C_t/qf_t$, where *q* is the hunting coefficient (the efficiency), the magnitude of which is determined by the methods of hunting. The ratio C_t/f_t included

in this equation estimates the number of prey per unit of hunting effort, or, in other words, the effectiveness of the hunt-in English-language literature, the CPUE (catch per unit effort). With stability of the hunting coefficient q, the quantity CPUE changes in proportion to the abundance of the population being hunted, independent of the replenishment of the latter and its overall death rate (Ricker, 1975), and in this case it can serve as a relative index of the number of animals.

It is evident that the reconstruction of secular changes in the relative number of animals by osteological materials from archeological sites results in an estimate of the procured prey, the hunting effort, and the hunting coefficient of the hunting groups of the past centuries. As a relative index of the number of animals procured by early hunters during period of time t, the number of animal bones (NISP) accumulated for this period at the site can be used, and it is not difficult to obtain with a sufficiently representative selection of radiocarbon-dated bones. The dynamics of hunting effort may be estimated by the changes in human paleopopulations. With consideration of the very general assumptions of paleodemography, the average numbers of paleopopulations in the period t is directly proportional to the quantity of burials (Acsadi and Nemeskeri, 1970; Ubelaker, 1978) and, in some cases, to the accumulation rate of the cultural layer (see Dinesman et al., 1999; Dinesman and Savinetsky, 2003b; Savinetsky, 2002; for detailed description).

On the basis of available data on the composition of hunting catch (primarily birds) from different localities, we attempted to estimate the dynamics of biodiversity of species in the region using two indices. The first, the Shannon Index of diversity, taken from information theory, is the most widely employed (Magurran, 1983). The second, the Brillouin Index, which we prefer, is used when it is impossible to guarantee chance in selection, as in our case.

4. Results and discussion

Long-term archeological investigations show that people have occupied this territory, with the exception of several islands, for several thousand years. These people were not only living in the region but also using sea products as food and in domestic life (Dikov, 1977, 1979; McGhee, 1996).

4.1. Taxonomic composition of bones

4.1.1. Sites on the coasts of Kamchatka and Koryak upland

The central part of the west and east coasts is dominated by the ancient Itelmen culture. Osteological material was identified from the Zhupanovo site (Kronotski Bay, southeastern Kamchatka) (Vereschagin and Nikolaev, 1979; Burchak-Abramovich et al., 1987; Savinetsky and Ptashinsky, 1999), which existed from 1500 to 500-300 ¹⁴C years BP. In total, 1003 bones were identified. The largest number of mammal remains belonged to sea mammals (fur seal, sea otter, bearded seal and largha) all of which still inhabit this region. Among terrestrial mammals, polar fox and moose bones were found (Vereschagin and Nikolaev, 1979). The latter have not been found in Kamchatka before. The largest number of bird bones belonged to sea birds (Alcidae, Anatinae and Lari), all of which are common now, with the exception of the short-tailed albatross (Diomedea albatrus) and Bewick's swan (Cvgnus bewickii).

The north coast of Kamchatka is dominated by the ancient Koryak culture. The Galgan site, situated on the northwest coast of Kamchatka, is the only site with identified bones belonging to this culture (Savinetsky and Ptashinsky, 1999). This site existed during the first millennium AD. 636 bones were identified. The largest number belonged to sea mammals and birds that are now common in this region, with the exception of the swan goose (*Cygnopsis cygnoides*), which is no longer found there.

From the northwestern coast of the Bering Sea to the Anadyr lowland is a territory dominated by Kereks. Unfortunately, there is no archeozoological material from this region.

4.1.2. Sites on the coasts of Chukotka

This territory is inhabited by Eskimos and coastal Chukchi. Ancient Eskimo settlements are located from Krest Bay in the Anadyr Bay to Baranov Cape on the Arctic coast of Chukotka. We investigated several sites from Mechigmen Bay to the mouth of the Chigetun River.

In 10 sites, we identified the bones of whales hunted by ancient sea-mammal hunters (Table 1, supplementary material). The largest number of bones belonged to the gray whale (87.3%). The individual age of the animals was measured according to McCartney (1978) and Knyazev and Savinetsky (1995), revealing that about 90% of harvested animals were yearlings. Some of the bones from three sites were radiocarbon dated: Masik (17 bowheads, 25 gray whales), Ekven (30 bowheads, 34 gray whales), Chigetun (27 bowheads and 27 gray whales) (Dinesman and Savinetsky, 2003a). The bones were deposited from about 2700 ¹⁴C years BP until the present. The pattern of radiocarbon dates suggests that whaling was not evenly distributed through history (Fig. 2). It is very likely that harvesting depended on the abundance of whales as well as the number of hunters. Twenty-seven walrus mandibles from Ekven were also radiocarbon dated.



Fig. 2. Reconstructed history of catch of bowhead (solid line), gray whale (dotted line) and walrus (dot and dash line) according to radiocarbon dates of bones from ancient sites in Chukotka.

Bones of smaller species were identified from four sites (Table 2, supplementary material). At Masik, Ekven and Nynluvak, mammals dominated in the hunting catch. At Dezhnevo, they were equal to birds. Fish remains were very rare at all sites.

The taxonomic composition of harvested mammals is similar at different sites (Table 3, supplementary material). Bones of sea mammals dominated (85.4-98.0%), with the largest number belonging to the ringed seal (68.8-89.5%). Remains of walrus and bearded seal ranged from 0.5-8.2% and 2.8-15.1%, respectively, depending on the site. A small number of polar bear bones were seen almost everywhere. Remains of largha, ribbon seal, white whale and harbor porpoise were scarce. Since these species are mainly piscivorous (fish-eating), this tallies with the almost complete absence of fish remains.

Birds were actively harvested by ancient hunters of Chukotka. The catch was dominated by real sea birds and coastal birds like waterfowl and shorebirds (Table 4, supplementary material). Terrestrial birds comprised only 2-3%. Colony-nesting birds-crested auklet, murres, and pelagic cormorant-dominated among the real sea birds. Among the coastal birds, the dominant species-spectacled and king eiders, and oldsquaw-form large flocks during migration. The difference between sites may be explained by local peculiarities such as the location of colonies and migratory paths.

The excavation of a well-stratified midden in Dezhnevo permitted reconstruction of the harvesting dynamics of the main species in this region over six radiocarbon-dated periods (Dinesman et al., 1999; Savinetsky, 2000) (Table 5, supplementary material).

4.1.3. Sites on the American coast and islands of the Bering strait

Archeozoological studies were conducted on St. Lawrence Island (Geist and Rainey, 1936; Collins, 1937). Cultural layers of these sites formed 2300–100¹⁴C years BP (Dumond, 1998). The largest number of bones belonged to walrus, seal and dog. There were a few bones of reindeer, bighorn sheep and hare, all of which are no longer found on the island. Friedmann (1934a) identified 800 bird bones from 45 species. Remains of thick-billed murre, crested auklet, common and king eiders, and pelagic cormorant dominated in the layers. Bones of old-

squaw, long-tailed jaeger, black-legged kittiwake, guillemot, red-faced cormorant and short-tailed albatross were numerous. The latter two species are no longer present on the island.

Only mammal bones were identified from the cultural layer in Cape Krusenstern (Anderson, 1986), which formed $2000-1000^{-14}$ C years BP. Among 3574 bones, 96% belonged to sea mammals, mainly ringed seal (72.4%) and bearded seal (22.5%). In contrast to Chukotka, there were few walrus remains (0.1%). Only bird bones were identified from the Cape Prince of Wales excavations (Friedmann, 1941). The taxonomic composition of bones is very similar to those from the Ekven and Dezhnevo sites in Chukotka. Bones of bearded and small seals dominated at the Iyatayet and Nukleet sites in the region of Cape Denbigh in Norton Sound (Henderson, 1952; Giddings, 1964). Walrus, white whale and reindeer bones were numerous. Only a species list for bird bones is given (Friedmann, 1934b). It is interesting to note the presence of red-faced cormorant bones since this species is no longer found in this region.

4.1.4. Sites on the south-west Alaskan coast

No archeozoological investigations were carried out on the sea coast of Yukon-Kuskokwim Delta, though ancient Eskimo sites are known there (Shaw, 1982). The suspicion that this territory was occupied around 2500 ¹⁴C years BP was confirmed by the finding of ancient sites (2100¹⁴C years BP) on the Nunivak Island (Nowak, 1982). Of the bones excavated from three sites (Chatters, 1972; Souders, 1997), largha, walrus and sea lion dominated. In the horizons formed about 1460 ¹⁴C years BP, sea lion bones were twice as abundant as walrus bones. During the period 350-200 years ago, the number of sea lion bones decreased abruptly (2.1%) and were four times less prevalent than walrus bones. Now there are no sea lion rookeries on the island and local people do not hunt them (Nowak, 1988).

4.1.5. Sites of the Aleut-Commandor Island range

The Aleutian Islands and part of Alaska Peninsula are inhabited by Aleuts. This territory was occupied about 8700 ¹⁴C years BP according to radiocarbon dating (Laughlin, 1975). Akun Island (Fox Islands) is the easternmost Aleutian Island with archeozoological results. Bones of mammals (n = 104; 7 species) and

birds (n = 426; 27 species) were excavated from layers formed during the last 1200 years (Turner and Turner, 1974; Yesner, 1977). The largest number of mammal bones belonged to fur seal and sea lion. A few bones belonged to wolf, brown bear and reindeer, which are gone from the island now. The most abundant bird bones were thick-billed murre (31.1%), short-tailed albatross (25.2%) and shearwater (16.1%). Bird bones were identified from Unalaska Island (n=363; 31)species) and nearby Amaknak Island (n = 107; 21 species) (Friedmann, 1934b, 1937). The largest number of bones belonged to murres, king eider and pelagic cormorant. Of the identified species, all are common on the islands now, except for short-tailed albatross. About 20,000 bones were identified from four sites on Umnak Island (Ashishik-Point, Chaluka, Sheep-Creek, Oglodax') and nearby Anangula Island (Lippold, 1966; Denniston, 1972; Yesner, 1976, 1977; Yesner and Aigner, 1976). The age of the most ancient lavers with bones is about 3700 ¹⁴C years BP (Aigner, 1966; Denniston, 1966). Bones of fur seal are most abundant and in some layers largha and sea lion. The presence of fox bones only in the upper layer can be connected to the arrival of Russian hunters. Shearwater, albatross, fulmar, cormorant and murre bones dominated among the birds.

In 1999, we took part in an expedition to Adak Island (Dr. Dixie L. West, P.I.) and dug test pits on two sites—on the coast of Sweeper Cove (ADK-009) and Clam Lagoon (ADK-171). Remains of marine invertebrates (mollusks, sea urchins, chitons) dominated in both. Fish bones comprised about 90% of all bones. On site ADK-009, we found a piece of Steller's sea cow bone, among the rare bones of sea lion, largha and sea otter, with a radiocarbon age of 1710 ± 70^{-14} C years BP (Beta-135537). The cultural layer of this site began to be formed 1888 ± 50 ¹⁴C years BP (IEMAE-1265). Three radiocarbon dates of animal bones from the cultural layer of the Clam Lagoon site (ADK-171) demonstrated that this island was occupied by people at least around $6000-6141 \pm 123$ ¹⁴C years BP (IEMAE-1281), 6172 ± 192 (IEMAE-1248), 6525 ± 94 (IEMAE-1296).

In the Rat Islands group, we have archeozoological results for Amchitka, Little Kiska and Buldir. Five sites on Amchitka were studied by archeozoological method (Desautels et al., 1971). Mammal bones (n=1263) were identified on only one site (N 31).

Sea otter and largha bones dominated. Bird bones (n = 11,444) were identified on all five sites (Harrington, 1987; Siegel-Causey et al., 1991). They belonged to at least 59 species, the most abundant being cormorants (25.9%)-primarily pelagic cormorant (14.5%)-common eider (11.0%) and auklets (9.6%). It is interesting to note the presence of bones of double-crested (Phalacrocorax auritus), Japanese (P. filamentosus) and Palass's (P. perspicillatus) cormorant (Siegel-Causey et al., 1991). The doublecrested cormorant does not nest to the west of Unalaska Is. (Kessel and Gibson, 1978), though it was earlier known there (Gabrielson and Lincoln, 1959; Murie, 1959). In contrast to other species of cormorants, it prefers to nest on the ground and its nests are easily accessible to terrestrial beasts of prey. Perhaps the introduction of polar foxes caused the disappearance of this cormorant from some of the Aleutian Islands. The Japanese cormorant, which nests in the western Pacific, has not been sighted in the Aleutians before. The finding of the carpometacarpus of Palass's cormorant in the Amchitka is unique. It is the first time this endemic, now extinct, species has been discovered outside the Commandor Islands. Distribution of this species was probably wider earlier. The investigated sites are about 2550 ¹⁴C years BP (Desautels et al., 1971) but there are sites on this island of 4780 ± 280 ¹⁴C years BP (Beta-29407) (U.S. BIA n.d.).

Bird bones (n = 546; 34 species) from Little Kiska Island were identified by Friedmann (1937). The largest number belonged to pelagic cormorant (24.2%), short-tailed albatross (12.5%) and common eider (12.5%). In 1997 we took part in an expedition to Buldir Island. Radiocarbon dating of the bottom level of the cultural layer demonstrated that this island was occupied at least 2347 ± 84 ¹⁴C years BP (IEMAE-1224). Bones of sea lion and largha were most abundant. The worked piece of the rib of Steller's sea cow was found there. Its radiocarbon age is 1611 ± 67 ¹⁴C years BP (IEMAE-1228). Bird bones (n = 306; 22 species) belonged mostly to auklets and ancient murrelet (Lefevre and Siegel-Causey, 1993).

The Near Islands are the westernmost group of the Aleutian Islands. Radiocarbon dating demonstrated that people occupied this island at least 3500 ¹⁴C years BP (Corbett et al., 1997; West et al., 1999). Bones identified by Lefevre (in press) from one of the

sites (ATU-061) on Shemya Island demonstrated the predominance of fur seal bones among mammals, and puffin, murre and shearwater bones among birds. The large number of fur seal bones suggests the presence of rookeries or a migratory path. Bird bones (n=211; 17 species) from Attu Island were identified by Friedmann (1937). The largest number belonged to pelagic cormorant (46.9%), glaucous-winged gull (14.2%) and short-tailed albatross (8.5%).

The Commandor Islands were uninhabited until the time of their discovery in 1741 by Bering's expedition. G. Steller, the naturalist of the expedition, described two new endemics, now extinct species-Steller's sea cow and Pallas's cormorant. The numerous sea cow bones found on the coast of Bering Island are considered to be from the extermination of this species in the XVIII century (Domning, 1978). We made a series of 25 radiocarbon dates of redeposited sea cow bones found in the coastal deposits (Savinetsky, 1992) (Fig. 3).

4.2. Changes in fauna and distribution of mammals and birds

According to osteological analysis, most of the species have retained their geographic distribution during the last 2000–3000 years. The area inhabited by some sea mammals, e.g. sea lion and fur seal, has not decreased, though the distribution pattern has changed. Thus, apparently there were rather large sea lion rookeries on Nunivak Island, where they are



Fig. 3. Steller's sea cow population according to radiocarbon dates of bones from Bering Island (Commandor Islands).

now rare. Changes in the area of Steller's sea cow are evident. It is now clear that it also inhabited the Aleutian Islands.

Some changes were noticed for terrestrial mammals, though their portion in the hunting catch was low. Bighorn disappeared in north–east Chukotka about 2500 years ago. Red fox also inhabited this area. Reindeer, bighorn sheep and hare most probably disappeared from St. Lawrence Island, wolf, brown bear and reindeer from Akun Island, and moose from Kamchatka.

In total, bones of 109 bird species were found in this region. The largest number of bones belonged to Alcidae, Anatinae, Procellariiformes, and Phalacrocoracidae. There is not always a correlation between population and quantity of catch, since the catch depends on the availability of prey and the advisability of hunting it. Often this is dependent on the location of the site. For instance, short-tailed shearwater migrates in enormous flocks through the Bering Strait but it rarely appeared in the catch because its route is far from the coast. On the other hand, in the Aleutian Islands it passes through for feeding and is actively harvested by hunters.

For 20 sites, the Shannon and Brillouin Indices of biodiversity were calculated based on the total number of bird remains (Figs. 4 and 5). The indices ranged from 1.426–3.110 and 1.349–2.952, respectively. The largest significance is noted for the Dezhnevo and Amchitka sites. The interpretation of the differences between sites is rather difficult because often we do not know the duration of the existence of the deposition. As an example, the results of calculations show that the significance of the indices in different well-dated layers of Dezhnevo ranges from 2.390 to 2.825 according to the Brillouin Index (Savinetsky, 2002).

4.3. Population dynamics of mammals and birds

As stated above, the dynamics of rate of bone deposition is an index of the catch dynamics. The index of the catch dynamics depends not only on the animals' population but also on the number of hunters, hunting gear, etc. We use the effectiveness of the hunt (CPUE) as an index of animal population, determined as a proportion of hunting catch and



Fig. 4. Shannon Index of Species Diversity of bird remains from ancient sites in the Bering Sea region: 1—Number of identified specimens (NISP); 2—Minimal number of individuals (MNI).

number of hunters (or number of all residents of ancient settlements, in our case). The dynamics of catches of bowhead, gray whale and walrus by 200year intervals for the period 2500-500 ¹⁴C years BP was considered above (Fig. 2). The dynamics of relative number of residents of the Ekven settlement was reconstructed by radiocarbon dating the burials in the Ekven cemetery (Dinesman et al., 1999). Data received permitted the reconstruction of the population dynamics of bowhead, gray whale and walrus (Fig. 6). Three periods of high numbers of gray whale were observed-2100-1700 ¹⁴C years BP, 1300-900 years ago, and 700-500 years ago. During the entire period from 2300-1300 ¹⁴C years BP, the bowhead whale population was low. Walrus was also relatively low. About 1300 years ago, the relative abundance of these two species abruptly increased.

To reconstruct the population dynamics of hunted species in the hunting area of Dezhnevo, we used the thickness of the well-dated horizons of the cultural

layer as an index of hunting effort (Dinesman et al., 1999; Savinetsky, 2002). This permitted the estimation of the CPUE, which is directly proportional to the abundance of populations of hunted animals. Based on the trends of changes in size of this index, hunted animals from the catchment area of the Dezhnevo Eskimos were divided into three groups (Dinesman et al., 1999). In the first group are walrus, horned puffin, and willow ptarmigan, the abundances of which fell steadily from 2480-1270 ¹⁴C years BP. The second group includes 15 species-seal and Arctic fox, sea birds (the northern fulmar, pelagic cormorant, murres, crested auklet, least auklet, parakeet auklet, and glaucous gull), and coastal-tundra birds (oldsquaw, king eider, red phalarope, pomarine and parasitic jaegers.) They all reached maximum numbers 2280-1940 ¹⁴C years BP. The third group includes sea birds (guillemot and black-legged kittiwake) and shore-tundra birds (long-tailed jaeger and the common, spectacled and Steller's eiders). They reached their maximum



Fig. 5. Brillouin Index of Species Diversity of bird remains from ancient sites in the Bering Sea region: 1—Number of identified specimens (NISP); 2—Minimal number of individuals (MNI).

numbers 1940–1730 ¹⁴C years BP. As is clearly seen, in 1730 ¹⁴C yr BP a multi-century depression appeared in the numbers of all hunted animals in the Dezhnevo area, reaching its culmination in 1450– 1270 ¹⁴C years BP. Such a large-scale, unidirectional change in the abundance of animals strikingly different in their ecology could have been brought about by dramatic changes in the region.

Using the same method, we reconstructed the dynamics of the relative abundance of some harvested species—sea lion, sea otter, largha, Steller's sea cow, Canada goose, cormorants, auklets and other true sea birds—in some Aleutian sites (Savinetsky, 2000). Data for Ashishik-Point (Denniston, 1972) and Chaluka (Aigner, 1966; Lippold, 1966; Vasil'evskii, 1973) on Umnak Island, and for Amchitka sites (Desautels et al., 1971) consisted of good descriptions and radiocarbon dates of the cultural layer. The results are not very detailed because of the low quantity of

data but in general we can say that the abundance of sea lion has decreased from 3700 ¹⁴C years BP to the present. Sea otter and largha populations were high during the period 3700–2000 ¹⁴C years BP and then decreased 2000–1200 ¹⁴C years BP. They then increased again but numbers were far from the previous maximum. The changes in fulmar and gull populations were similar to those of sea lion, and the changes in the abundance of short-tailed albatross, short-tailed shearwater, common eider, harlequin, and auklets approximated those of sea otter and largha. The population dynamics of Canada goose are quite different from those of other species.

4.4. Influence of changes in abiotic factors on the dynamics of animal populations

In order to determine the causes of the discovered changes in the number of mammals and birds in the



Fig. 6. Relative abundance of populations of bowhead (solid line), gray whale (dotted line) and walrus (dot and dash line) in the hunting area of the ancient settlement Ekven (Chukotka). CPUE is an index of relative abundance of animals.

region, it is necessary to examine the regularities of the dynamics of the coastline, sea level, and climate of the Bering Sea coast. The formation of the shore relief in the Holocene was mainly due to the rise in sea level that began about 18,000 years BP due to waning of the Late Pleistocene ice cover in the Northern hemisphere. This caused a eustatic rise in sea level, modification of the shoreline and its migration inland (Hopkins, 1967; Kaplin, 1982; Kaplin et al., 1991; etc.).

Our investigations in Chukotka allowed us to reconstruct the dynamics of the north-eastern Chukchi coasts over the last 7000 years (Dinesman et al., 1996, 1999). Formation of the present-day outlines of the coast began 6000-4000 ¹⁴C years BP, after sea level stabilized at a level similar to that which exists now (Svitoch, 1977; Badyukov and Kaplin, 1979; Kaplin, 1982; Kaplin et al., 1991). The sea level about 2500 14 C years BP was probably lower than present by 1.5-2.0 m. An increase took place about 2500-2300 and 1450-1300 ¹⁴C years BP. 2300-1450 ¹⁴C years BP was a stable period. On the other side of the Bering Strait, investigations on the changes in sea level were carried out in the region of Cape Krusenstern (Giddings and Anderson, 1986) and Capes Prince of Wales and Espenberg (Mason and Jordan, 2001). Giddings and Anderson (1986) found eight beach ridges located up to 8 km inland from the present shoreline, which were formed from 4500 to 500 ¹⁴C years BP. Mason and Jordan (2001) suggested that regional sea level was about 1.5 m below present 6000 ¹⁴C years BP and there was a slight rise in sea level of 0.27 mm year⁻¹. on average. For the Bering Sea overall, Hopkins (1967) distinguished the Krusenstern transgression in the period until 6000-5000 ¹⁴C years BP. Sea level was 1 m above present 2700-1700 ¹⁴C years BP, 2 m below present 1500-1100 ¹⁴C yeasrs BP, 1 m above present 1200-900 ¹⁴C years BP and 1 m below present 600-500 ¹⁴C years BP.

The history of relative sea level in the Aleutian Islands was summarized by Black (1980, 1982). Based on radiocarbon dating of tephra sequences, he suggested that relative Holocene sea level rose to its present level about 5000^{14} C years BP on Attu Island, 6500^{-14} C years BP on Amchitka Island, 7500^{-14} C years BP on Adak Island, 8600^{-14} C years BP on Atka Island, 8400^{-14} C years BP on Umnak Island, and $11,000^{-14}$ C years BP in Cold Bay (Alaska Peninsula). Our data on the sea level at Shemya Island (Kiseleva et al., 2002) demonstrate that it became stable about 5000^{-14} C years BP.

There were several periods of high and low sea level at the Commandor Islands (Razzhigaeva et al., 1999). Low sea level was up until 4300, from 3400–2880, 2250–1200 and 750–0 ¹⁴C years BP, high sea level was from 4300–3400, 2880–2250 and 1200–750 ¹⁴C years BP.

Data on changes in sea level in different areas of the Bering Sea region are not uniform, perhaps because of different tectonic and isostatic movements. It is therefore difficult to apply data from one area to other areas in the region.

We have explained the dynamics of the number of some species of animals living in the vicinity of the Dezhnevo site and especially the discovery of regularities in the dynamics in the number of sea mollusks that were collected on the beaches by the early Eskimos, on the basis of secular changes in sea level (Dinesman et al., 1996, 1999). The number of mollusks was low until 2300 ¹⁴C years BP (Fig. 7). Evidently, the rebuilding of the seabed that occurred at that time, connected with the change in depth, was unfavorable for them. It is significant that cockle (Serripes groenlandicus) and soft-shell clam (Mya truncata) that settled the loose substrates, very unstable in the wave zone, were lowest in number. During the period 2300-1500 ¹⁴C years BP when sea level was stable, the number of mollusks increased. By 1940–1730¹⁴C years BP, mussels (*Mytilus trossulus*) that lived on the compact substrates reached their maximum. Cockles and soft-shell clams were highest in number later (1730-1450¹⁴C years BP). Such delay can be explained by the slow accumulation of loose deposits, the formation of which was caused not just by reworking of the sea bed but also by sedimentation of the fine mineral fractions. Finally, from 1450 to 1270 ¹⁴C years BP, during a new rise in sea level which brought a new cycle of reworking of the sea bed, the number of all three species again dropped sharply. The relationship between sea level and the number of mollusks is also confirmed by the Spearman rank-order correlation, which for the three species of mollusks is -0.84 (P < 0.05). Among vertebrate animals, a significant correlation between changes in number of animals and changes in sea level can be seen in only four species-common and Steller's eiders, glaucous gull, and long-tailed jaeger. Mollusks are an essential food for the first two species, while in the case of the other two the correlation is indirect.

The influence of changes in sea level on the dynamics of animals is not well understood. Nevertheless, we drew attention to an interesting regularity that would suggest that this phenomenon is perhaps an important factor for this region. Comparison of times when Holocene sea level first reached its present position and times of the first known settlements show a lag of about 1500 years (Table 6, supplementary material). It is hard to explain such a similarity between regions. We can surmise that this period is



Fig. 7. Composition and accumulation rate of seashells in the cultural layer of the ancient Eskimo settlement Ekven.

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necessary for the formation of high-productivity benthic biocenoses.

The dynamics of summer sea ice conditions were estimated in the Bering Strait region from buried peaty layers in coastal deposits (Dinesman et al., 1996, 1999). Investigation of these layers demonstrated that about 1300–1200 ¹⁴C years BP, a period characterized by an increase in the amount of summer sea ice began. This period coincides with the increase in number of bowhead and walrus (Fig. 6), two species for which sea ice distribution plays an important role.

Reconstruction of temperature and precipitation changes was mainly based on changes in the rate of decomposition and allogenic ash content of peat samples. In the northern part of the region, it was carried out on two peat deposits: Uelen, in the northeastern part of Chukotka (Fig. 8), and Naskak, on the north coast of St. Lawrence Island (Fig. 9). The correlation (+0.71; P < 0.01) between the rate of decomposition of these two depositions is high. There is no correlation between the ash content of the peat deposits. The difference may be explained by local site characteristics. The Naskak peat deposit is situated not far from the coast and sand impurities may have Aeolian origin from the expanded gentle beach (Lozhkin et al., 1998).

Data on the south-western part of the Bering Sea region were taken from Shemya Island, in the Western



Fig. 8. Reconstruction of temperature and precipitation according to changes in rate of decomposition (solid line) and allogenic ash content (dotted line) of peat samples in the north-eastern part of Chukotka (Uelen peat deposit).



Fig. 9. Reconstruction of temperature and precipitation according to changes in rate of decomposition (solid line) and allogenic ash content (dotted line) of peat samples in the northern part of the Bering Sea (St. Lawrence Island, Naskak peat deposit).

Aleutian Islands (Fig. 10). The sequence of changes in temperature and precipitation in the northern and southern parts of the Bering Sea region do not coincide. The allogenic ash content of peat samples showed that during Early and most of Middle Holocene, near-coast ecosystems in the northern and southern parts developed under conditions of increased precipitation, compared to today. In Chukotka, this period finished about 5600 ¹⁴C years BP and in the Western Aleutian Islands about 1500 years later. There was a short period of increased precipita-



Fig. 10. Reconstruction of temperature and precipitation according to changes in rate of decomposition (solid line) and allogenic ash content (dotted line) of peat samples in the south-western part of the Bering Sea (Aleutian Islands, Shemya Island peat deposit).

tion around 2000 ¹⁴C years BP in Chukotka, in the Aleutians the changes were within today's limits.

In Chukotka, for 15 of 30 species for which we have data, calculations showed that there is a negative correlation (Spearman rank-order correlation) with a high degree of reliability (-0.81; P < 0.05) between atmospheric moisture and number of animals. These species include mammals (ringed seal, bearded seal, polar bear, and Arctic fox) and birds (all four species of eiders, oldsquaw, pomarine jaeger, crested auklet, parakeet auklet, murres, glaucous gull, and northern fulmar). Also, a high negative correlation of number with precipitation, though not statistically significant, was also noted for ten species. For only two speciespelagic cormorant and black-legged kittiwake-is there a non-significant positive correlation with precipitation. We are far from suggesting that an increase in precipitation leads to a general reduction in the number of species; there is no real basis for this assumption. In this case, we can speak only of a decrease in the number of animals in the hunting area of the early Eskimo site being studied. Thus, with southerly winds, when the greatest precipitation is experienced, some birds (e.g. Anatidae) shift to the northern, Arctic Ocean coast.

For only four species-long-tailed jaeger, blacklegged kittiwake, common eider, and Steller's eiderwas there a positive correlation (with a high degree of significance) with temperature during the warm period of the year. Among almost all other species there was also a positive correlation with temperature but its significance was not high.

In the southern part of the Bering Sea region the situation is different; most sea mammal and bird populations demonstrate a negative correlation with temperature and a positive correlation with precipitation. However, a shortage of data makes it difficult to make reliable statistical estimates. The correlation can be explained by the increase in productivity of the sea in this region during the decrease in temperature and the corresponding increase in upwelling. Only two species show a positive correlation with temperature-Canada goose and Steller's sea cow. It should be noted that Canada goose is the only terrestrial species for which we have data and its feeding is not directly connected with the sea. The correlation between number of sea cow and temperature is high (+0.69; P < 0.05). Steller's sea cow is the only

mammal in this region that feeds on seaweed. The distribution of this species was more widespread during the late Holocene. Findings of remains demonstrate that this species inhabited the Aleutian Islands at least 1000 years ago and was not immediately exterminated after ancient sea mammal hunters occupied the islands. Most likely, hunting pressure, low migratory activity, and low birthrate, against a background of unfavorable conditions, resulted in isolation of separate groups of animals on different islands and then extermination. The discovery of the Steller's sea cow in the Commandor Islands in the middle of the XIX century supports the idea of a decline in population because of unfavorable conditions ("Little Ice Age"). That is why it took only 27 years for their complete extermination. That is why it took only 27 years for their complete extermination.

5. Conclusions

- When using zooarcheological material in order to infer population dynamics of mammals and birds, it is necessary to go from the composition of hunting harvests to an estimate of the animal catch in the hunting areas and then to estimates of the relative abundance of various populations. Changes in the rate of accumulation of bones of each species over time can be used as an indicator of hunting catch. The dynamics of effectiveness of the hunt can be used as an index of secular changes of population numbers.
- 2. In the last thousands of years, century-long cyclical changes in number, similar to the secular changes in the numbers of animals in other natural zones, have occurred among the hunted mammals and birds of the coastal ecosystems of the Bering Sea region.
- 3. The secular cyclical changes in numbers of mammals and birds of the region are determined primarily by exogenic factors—temperature, amount of precipitation, summer sea ice cover, and changes in sea level.
- 4. In the northern part of the region, one of the most important factors influencing the number of animals was the amount of summer precipitation. The temperature regime had a lesser effect. In the southern part of the region, the most important factors were the temperature regime and precipitation.

- 5. The rise in sea level could have had a negative effect on the productivity of benthic fauna and the number of some species of mammals and birds.
- 6. The overall species composition of the mammalian and avian fauna of the region has not changed significantly over the last 3000 years. However, the relative abundance and location of certain species has varied in relation to environmental conditions.
- 7. During the last several millennia, the northern extent of mammal and bird distribution in the southern part of the region has tended to shift southward. By comparison, northern species are tending towards a wider distribution.
- 8. Traditional activities of hunter-gatherers did not usually significantly affect the state of animal populations. However, in some cases—for example, with isolated populations—hunting, together with negative climatic forcing, could have led to the disappearance of populations.

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