

Bioclimatic Implications and Distribution Patterns of the Modern Ground Beetle Fauna (Insecta: Coleoptera: Carabidae) of the Arctic Slope of Alaska, U.S.A.

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(Received 3 September 1998; accepted in revised form 16 March 2001)

ABSTRACT. Some 56 species of Carabidae have been previously reported on the Arctic Slope of Alaska; of these, only nine have been found at coastal sites in the region. Though for some taxa (e.g., most species of *Bembidion*) this may reflect a lack of suitable habitat in the coastal environment, for most others it probably reflects the summer temperature differences between the relatively cool coastal areas (mean July temp [mJt] of ca. 4°C) and warmer interior sites (mJt of ca. 9–10°C). The boundary between the relatively species-rich interior fauna and the more depauperate coastal fauna is probably also approximated by the inland limit of incursions of cool summer coastal fogs, which coincides with a sharp vegetational boundary. Additional systematic collecting of specimens and a coordinated effort to gather climate data will be needed to delimit distributional limits more closely and to provide background data for both modern environmental monitoring and paleoenvironmental reconstructions.

Key words: Alaska, Carabidae, climate, Coleoptera, distribution, environments, paleoenvironment, vegetation

RÉSUMÉ. On a déjà rapporté la présence d'environ 56 espèces de carabidés sur la pente arctique de l'Alaska; de ces espèces, seulement neuf se trouvaient dans des zones côtières de la région. Bien que pour certains taxons (p. ex., la plupart des espèces *Bembidion*), ce fait pourrait témoigner du manque d'un habitat propice dans l'environnement côtier, pour la plupart des taxons, il est un reflet des différences de température estivale entre les zones littorales relativement fraîches (moyenne de la température en juillet [mtj] d'environ 4°C) et des sites plus chauds de l'intérieur des terres (mtj d'environ 9 à 10°C). La délimitation entre la faune de l'intérieur relativement riche en espèces et la faune côtière plus pauvre est probablement aussi définie par la limite, à l'intérieur des terres, des intrusions estivales du brouillard côtier frais, qui coïncident avec une démarcation très nette de la végétation. D'autres collectes systématiques de spécimens et un effort coordonné en vue de recueillir des données climatiques seront nécessaires pour établir des limites de distribution plus précises et pour fournir des données de base en vue du contrôle de l'environnement contemporain comme de la reconstitution paléoenvironnementale.

Mots clés: Alaska, carabidés, climat, coléoptères, distribution, environnements, paléoenvironnement, végétation

Traduit pour la revue *Arctic* par Nésida Loyer.

Реферат: Около 56 особей Carabidae было обнаружено ранее на Арктическом Склоне Аляски; только 9 из них были обнаружены в прибрежной зоне региона. Хотя для некоторых видов (например, несколько разновидностей *Bembidion*), это, возможно, вызвано отсутствием условий выживания в прибрежной зоне, для других причина кроется в разнице летних температур между относительно холодной прибрежной зоной, где средняя температура июля равна +4С, и более теплой внутренней зоной с температурой +9, +10С. Граница между регионом с относительно пазнообразным животным миром и более бедным прибрежным регионом проходит примерно по черте прохладных летних прибрежных туманов, совпадающей с резким разграничением растительности. Необходимо произвести дополнительный и координированный сбор климатических данных для более точной делимитизации распространительных пределов и для обеспечения основной базы данных, необходимой как для современного мониторинга окружающей среды, так и для реконструкций палео окружающей среды.

Ключевые слова: Аляска, Carabidae, климат, распространение, окружающая среда, палео окружающая среда, растительность

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INTRODUCTION

Lindroth (1961–69) produced the benchmark synthesis of Alaskan and Canadian Carabidae. More recently, Bousquet (1987) contributed significantly to our understanding of this fauna, though most of his range extensions were in eastern Canada. Local Alaskan site records (Watson et al., 1966; Morgan et al., 1986) have helped refine our knowledge of modern ranges, but still the fauna of this vast area is well known from only a handful of sites.

Knowledge of the modern distribution of Coleoptera is of more than passing interest to the non-entomological community. As our concern over potential impacts of global warming rises, attention is necessarily focused on the Arctic, where impacts from any warming will be most severe. Beetles respond extremely rapidly to environmental change (Elias, 1994), and carabids are relatively abundant, easily monitored, and extremely sensitive to such change. Thus, precise knowledge of their present range limits (and changes therein) can provide a benchmark against which the global warming scenario can be tested in this sensitive region. These same limits, and the climatic parameters associated with them, can also be used for paleoenvironmental reconstructions based on the coleopteran remains preserved in organic-bearing sediments (Elias, 1994, 1996). This paper synthesizes what is currently known of the modern geographical distribution of the Arctic Alaskan carabid fauna, in the hope that it might be useful in both those areas of investigation and serve as a basis for more refined future studies.

MODERN ENVIRONMENTS OF THE ARCTIC SLOPE

The area of concern for this study consists of the Arctic Coastal Plain and northern Arctic Foothills of Alaska (the region north of the dashed east-west line in the Arctic Foothills in Fig. 1; Wahrhaftig, 1965), collectively referred to in this work as the Arctic Slope of Alaska (Fig. 1). The Arctic Slope as thus defined is a broad region of approximately 135 800 km² in total area, about the size of Tajikistan or the U.S. state of Wisconsin.

The northern Arctic Foothills consist of broad, gently rolling foothills, generally immediately underlain by a layer of windblown dust, or loess, up to 30 m thick, which was deposited principally during times of major glaciation in the Brooks Range to the south. Portions of the foothills also are underlain by broad glacial moraines of early and middle Pleistocene age, although late Pleistocene moraines (those less than about 135 000 years old) are situated far upvalley in the Brooks Range proper.

The Arctic Coastal Plain is a broad, low-lying and poorly drained plain that ranges up to about 125 km in width from the coast to its boundary with the Arctic Foothills. For the most part, it is less than 30 m above sea level, and slopes in much of the region are imperceptible. Most of the surface is also water-saturated; in some areas,

more than 50% of the terrain lies beneath shallow thermokarst lakes, created by thawing and collapse of the ice-rich permafrost that exists as little as 15 cm below the ground surface, even at the height of summer.

The vegetation in the region is broadly defined as “tundra,” though the absence of coniferous trees as a uniquely defining characteristic obscures a myriad of vegetational subtleties, variations on scales of decimeters to tens of meters, that can in turn be highly significant to surface-dwelling insect faunas. The principal woody taxa are shrub alder (*Alnus crispa* [Ait.] Pursh) and dwarf birch (*Betula nana* L.), with numerous species of willow (*Salix* spp.), rare poplar (*Populus balsamifera* L.), and an assortment of low ericaceous shrubs and prostrate heaths (*Vaccinium* spp., *Ledum palustre decumbens* [Ait.] Hult., *Empetrum nigrum* L., and others). Alders and poplars are for the most part restricted to sheltered valleys in the Arctic Foothills, whereas the others extend well into the coastal plain, for some taxa considerably beyond mapped limits (e.g., Hultén, 1968; Welsh, 1974). Young (1971) recognized three broad tundra plant assemblages (zones) in the region: a shrub tundra of the foothills (Zone IV), a low-arctic, herb-dominated tundra of the coastal plain (Zone III), and a floristically depauperate tundra at Point Barrow (Zone II).

An excellent introduction to the vegetational complexity of the Coastal Plain was provided in the outstanding vegetational atlas of the Prudhoe Bay area (Walker et al., 1980). More recently, Walker (1997) has also described additional significant vegetational differences in the coastal plain, which reflect differences between organic-rich acidic substrates and more mineralic non-acidic soils along the immediate coastline.

In general, the climate of the region is dominated by long, cold, dark winters and summers that are cool and overcast much of the time, despite 24-hour daylight in the weeks before and after the summer solstice. The long-term climatic norms of the region are known from only three sites—Barrow, Kaktovik (= Barter Island), and Umiat—and the records from this last, inland site are discontinuous (Fig. 2). However, on the basis of the available data, it can be said that summers along the coast are cool to cold; mean July (warmest month) temperatures (mJt) are only 3.8°C at Barrow, and 3.6°C at Barter Island. At Umiat, in contrast, mean July temperatures are closer to 10°C. Mean annual precipitation ranges from 150 to 250 mm/yr, but extremely low evaporation results in abundant surface water on the coastal plain in all but the driest summers.

The significant difference between coastal and inland summer temperatures is probably determined by the innermost extent of the frequent summer fogs. This fog belt most likely controls the vegetational zonation noted by Young (1971) and the carabid faunal distributions documented here as well, though at present data from intervening sites are insufficient to demonstrate either case conclusively. This fog-belt boundary is at most a few tens of kilometers inland from the modern coast; changes in the

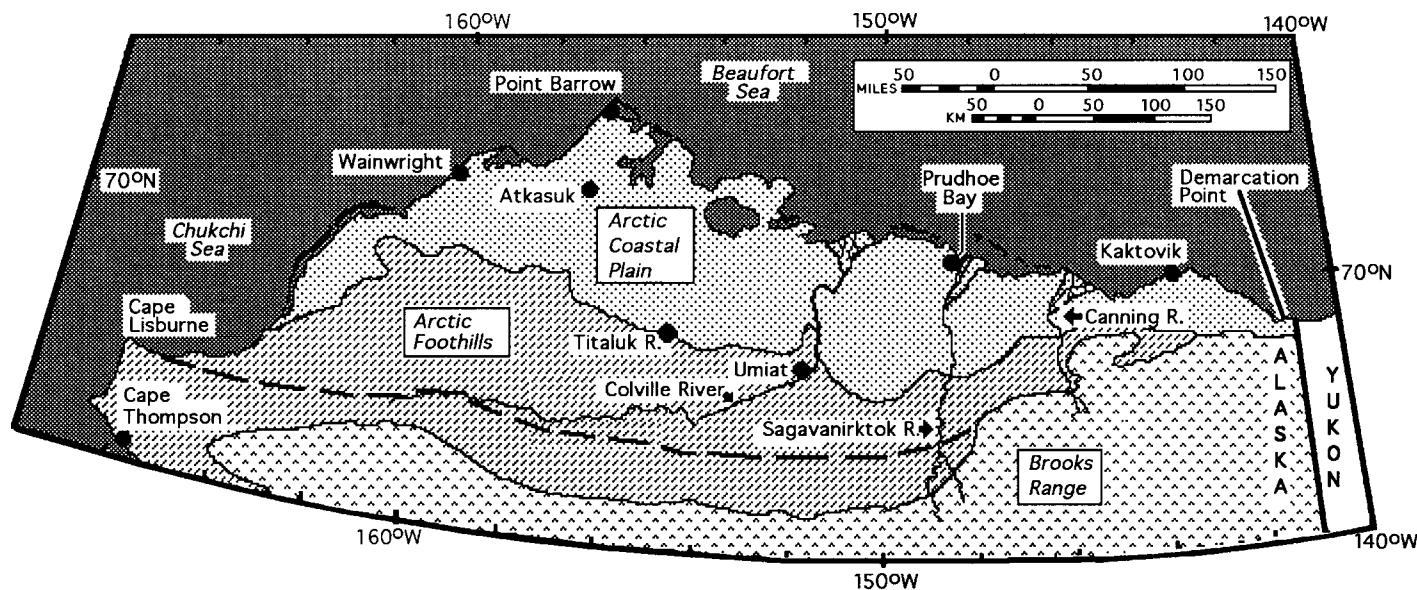


FIG. 1. Index map of northern Alaska, showing locations of sites mentioned in text. Physiographic divisions after Wahrhaftig (1965). Dashed line represents approximate boundary between northern and southern sections of the Arctic Foothills Province. Kaktovik is a village on Barter Island on the eastern coast.

position of its inner margin may be expected to have significant impacts on biotic distributions.

METHODS

The carabid records in this study are based on published data and on the personal collection of the author, which includes numerous specimens collected during geologic surveys along the entire Arctic coastal region between Barrow and Camden Bay, east of Barter Island. Undoubtedly, numerous additional northern Alaskan specimens remain to be documented, particularly in the Canadian National Collection (CNC) of Insects in Ottawa, the Canadian Museum of Nature collections, those at the University of Alberta and the California Academy of Sciences, and probably other major museum collections. The faunal list from Cape Thompson (Watson et al., 1966) was included in this study for comparative purposes, even though this site is slightly outside the restricted area of interest, because it is one of the most intensely studied and thus best-known single sites in the general region. A computer literature search via BIOSIS was performed searching under "Carabidae and Alaska" to ensure that possible published records unknown to the author were not overlooked. Data were tabulated by locality (Table 1), with literature reference(s) noted for each species.

RESULTS

Only five publications were found that document the modern Arctic Slope Carabidae, if one considers Lindroth's (1961–69) multivolume set as a single major work. In these, a total of 56 species have thus far been recorded

from this area, and of these, only about 16% (9 spp.) are known to occur at the modern coastline (Table 1). In contrast, 22 species are known from Cape Thompson, a coastal site to the southwest of the Arctic Slope (Fig. 1). The remaining species in the Arctic Slope fauna are restricted to areas farther inland, though some are known from only one or two of the most inland sites.

DISCUSSION

Though the differences between the coastal and inland faunas have been recognized for some time by people working in the area, it is helpful to be able to document which species actually occur on the coast and which are restricted to more inland sites. The taxonomically difficult subgenus *Cryobius* (genus *Pterostichus*) is one of the most common and abundantly represented ground-beetle taxa both in the modern fauna and in subfossil assemblages (cf. Nelson, 1982; Morgan et al., 1986; Nelson and Carter, 1987). But of this large subgenus, represented in the Arctic Slope fauna by some 12 species (Lindroth, 1961–69; Table 1), only four species are found in the coastal environments: *P. (C.) brevicornis*, *P. (C.) nivalis*, *P. (C.) pinguedineus*, and *P. (C.) tareumiut*. These last three have all been found at Barrow (arguably the most thoroughly studied site in the study area, but also the most marginal climatically; cf. Young, 1971), and they also occur at Cape Thompson and at inland sites (Table 1). The absence of *P. (C.) nivalis* and *P. (C.) pinguedineus* in published records from other coastal locales may be an artifact of insufficient collecting.

Amara alpina, the most northerly ranging of carabid beetle species, has been found at virtually every site where collecting has been undertaken. Its northern limit is in the

TABLE 1. The known modern Carabid beetle fauna of the Arctic Slope of Alaska and its distribution, based on published reports. See Fig. 1 for locations of sites. (Atqasuk = Meade River of earlier records.)

Species	Barrow	Barter Island	Demarcation Point	Other Coastal	Cape Thompson	Atqasuk	Umiat	Titaluk River	References ¹
<i>Agonum exaratum</i> (Mannerheim)							×	×	1,4
<i>Amara alpina</i> (Paykull)	×	×		×	×	×	×	×	1,2,4,5
<i>Amara bokori</i> Csiki							×	×	1,4
<i>Amara colvillensis</i> Lindroth							×		1
<i>Amara glacialis</i> (Mannerheim)						×	×	×	1,5
<i>Amara patruelis</i> Dejean							×		1
<i>Amara quenseli</i> (Schönherr)								×	4
<i>Asaphidion alaskanum</i> Wickham								×	4
<i>Bembidion alaskense</i> Lindroth							×	×	1,5
<i>Bembidion arcticum</i> Lindroth					×	×	×		1, 2
<i>Bembidion bimaculatum</i> (Kirby)							×		1
<i>Bembidion compressum</i> Lindroth						×	×	×	1,5
<i>Bembidion dauricum</i> (Motschulsky)							×		1
<i>Bembidion foveum</i> Motschulsky							×		1
<i>Bembidion hastii</i> Sahlberg				×	×		×		1,2,5
<i>Bembidion hyperboreaorum</i> Munster							×		1
<i>Bembidion lapponicum</i> Zetterstedt							-	×	1,5
<i>Bembidion lenae</i> Csiki							×		1
<i>Bembidion sulcipenne hyperboroides</i> Lindroth							×		1
<i>Bembidion poppii schalleri</i> Lindroth							×	×	1,5
<i>Bembidion rusticum lenensoides</i> Lindroth							×		1
<i>Bembidion semipunctatum</i> (Donovan)							×		1
<i>Bembidion sordidum</i> (Kirby)								×	4
<i>Bembidion umiatense</i> Lindroth							×		1
<i>Bembidion yukonum</i> Fall							×		1
<i>Blethisa catenaria</i> Brown								×	6
<i>Carabus chamissonis</i> Fischer von Waldheim							×	×	1,4
<i>Carabus truncaticollis</i> Eschscholtz					×	×	×	×	1,2,4,5
<i>Diacheila polita</i> (Falderman)					×		×		1,2
<i>Dyschirius melancholicus</i> Putzeys								×	3,5
<i>Elaphrus angusticollis angusticollis</i> Sahlberg							×	×	1,4
<i>Nebria nivalis nivalis</i> (Paykull)					×	×	×	×	1,2,5
<i>Notiophilus aquaticus</i> (Linnaeus)						×	×		1,5
<i>Notiophilus borealis</i> Harris					×		×	×	1,2,5
<i>Pelophila borealis</i> (Paykull)							×		1
<i>Pterostichus agonus</i> Horn		×	×	×	×	×		×	1,2,4,5
<i>P. circulosus</i> Lindroth							×		1
<i>P. costatus</i> (Menetries)				×	×	×		×	1,4
<i>P. sublaevis</i> (Sahlberg)			×	×	×		×	×	1,2,4,5
<i>P. vermiculosus</i> (Menetries)				×	×		×	×	1,2,4
<i>P. (Cryobius) auriga</i> Ball					×				1,2
<i>P. (C.) bryanti biocryus</i> Ball					×				1
<i>P. (C.) brevicornis</i> (Kirby)				×	×	×	×		1,2,5
<i>P. (C.) caribou</i> Ball						×	×	×	1,4,5
<i>P. (C.) kotzebuei</i> Ball					×	×	×	×	1,2,5
<i>P. (C.) mandibularoides</i> Ball							×	×	1,5
<i>P. (C.) nivalis</i> (Sahlberg)	×				×			×	1,2,5
<i>P. (C.) parasimilis</i> Ball					×	×	×		1,2
<i>P. (C.) pinguedineus</i> (Eschscholtz)	×				×				1,2
<i>P. (C.) similis</i> Mannerheim					×	×	×		1,2
<i>P. (C.) tareumiut</i> Ball	×			×	×				1,2
<i>P. (C.) ventricosus ventricosus</i> (Eschscholtz)					×	×	×	×	1,2,4
<i>Stereocerus haematopus</i> (Dejean)					×	×	×	×	1,2,4
<i>Stereocerus rubripes</i> (Motschulsky)						×		×	1,4
<i>Trichocellus cognatus</i> (Gyllenhal)								×	4
<i>T. mannerheimi</i> (Sahlberg)							×	×	1,4

¹ References: 1 = Lindroth, 1961–69; 2 = Watson et al., 1966; 3 = Bousquet, 1987; 4 = Morgan et al., 1986; 5 = Nelson, unpubl. record; 6 = Nelson, 1983.

Canadian Arctic Islands at Devon Island, north of Hudson's Bay (Lindroth, 1961–69). *Pterostichus agonus*, on the other hand, has been found at numerous coastal sites but not at Barrow, suggesting that its natural limit occurs at the modern coast and that the seemingly trivial climatic

differences between Barrow and Kaktovik (Barter Island; Fig. 2), for example, may be significant as far as this species is concerned. Both *Pterostichus sublaevis* and *P. costatus* are also absent from Barrow but have been collected at other coastal sites.

The genus *Carabus*, represented at inland sites by two species, is not found at the coast; its large size makes it unlikely it has been missed. Only one species (*C. truncaticollis* Esch.) is present at Atkasuk (= Atkasuk or Meade River) or at Cape Thompson (Table 1). The cryptic genus *Dyschirius*, on the other hand, could easily be missed by collectors because of its subterranean habit and small size. It is known from but one species (*D. melancholicus*) at a single site (Table 1). A number of other species are also known from the two most thoroughly collected inland sites, the Titaluk River and Umiat (Lindroth, 1961–69; Morgan et al., 1986; Nelson, unpubl.), but not from Atkasuk. If Atkasuk is indeed representative of an inland habitat intermediate between the coast and Umiat and the Titaluk River, climatic records from this site might well be useful to define the factors that help limit the distribution of these species, as well as *Agonum exaratum*, *Amara bokori*, and *Trichocellus mannerheimi*, among others.

The wealth of species of *Bembidion* represented in Lindroth's collections from Umiat may well represent a collecting artifact, reflecting the vast expanses and diversity of riparian habitats along the Colville River and tributaries at and near this site. Apparently, almost no collecting has been done along the upper reaches of similar large rivers in the region, such as the Anaktuvuk, the Sagavanirktok, or the Canning. Other species, like the relatively rare species *Blethisa catenaria*, *Pelophila borealis*, and *Trichocellus cognatus*, might also prove to be more widespread given better mapping of their distribution from additional intense collecting at inland sites. Such collecting might also produce records of other taxa not yet known from the Arctic Slope of Alaska, but known from the Brooks Range and its southern flanks (e.g., *Blethisa inexpectata* Goulet & Smetana).

POSSIBLE CLIMATIC AND VEGETATIONAL CONTROLS ON DISTRIBUTIONS

Young (1971), who documented fine-scale floristic zonation in northern Alaska, attributed the reduced Barrow

flora (even more depauperate than that of other coastal sites) to its location on a peninsula that is fog-shrouded or overcast through most of the summer. The carabid fauna seems in full agreement with his assessment of the vegetational diversity at Barrow, in that the four-species Barrow fauna is even less diverse than the known fauna from other coastal sites, where much less intense collecting has yielded as many as seven different Carabid taxa (Table 1). *Pterostichus agonus*, *P. costatus* and *P. sublaevis*, in particular, are each at least 10 mm long and would have been found had they occurred at Barrow; all have been collected from at least one other coastal site to the east.

Mean July temperatures could be used as proxies for total and maximum summer warmth for the region. These are difficult to know, however, since only Barrow, Barter Island, and Umiat have long-term instrumented records (Fig. 2), and the records at Umiat are discontinuous. What does show in the record is that Umiat, with a mean July temperature of approximately 10°C, is considerably warmer than the more coastal sites (3.6–3.8°C). This is likely a critical factor in the greater species diversities present at inland sites.

Ultimately, one long-term goal should be to document the climatic “envelopes” in which different species are currently living, as was done for *Blethisa catenaria* (Nelson, 1983). Such records can help both with interpreting past environments and in monitoring future environmental change in the absence of instrumented records. Such work has recently been completed for many species, resulting in development of a Mutual Climatic Range (MCR) method for interpreting past environments (Elias, 2001). Further refinement, however, will require a much more thorough knowledge of the distributional limits of the numerous abundant taxa that occur within the region, as well as a greater knowledge of local climatic variation near the coast.

Knowledge of these climatic “envelopes” will allow more refined use of the abundant coleopteran remains from sediments as paleoclimate indicators. Detailed knowledge of past climatic variation is critical to understanding the natural component of climate change as we attempt to

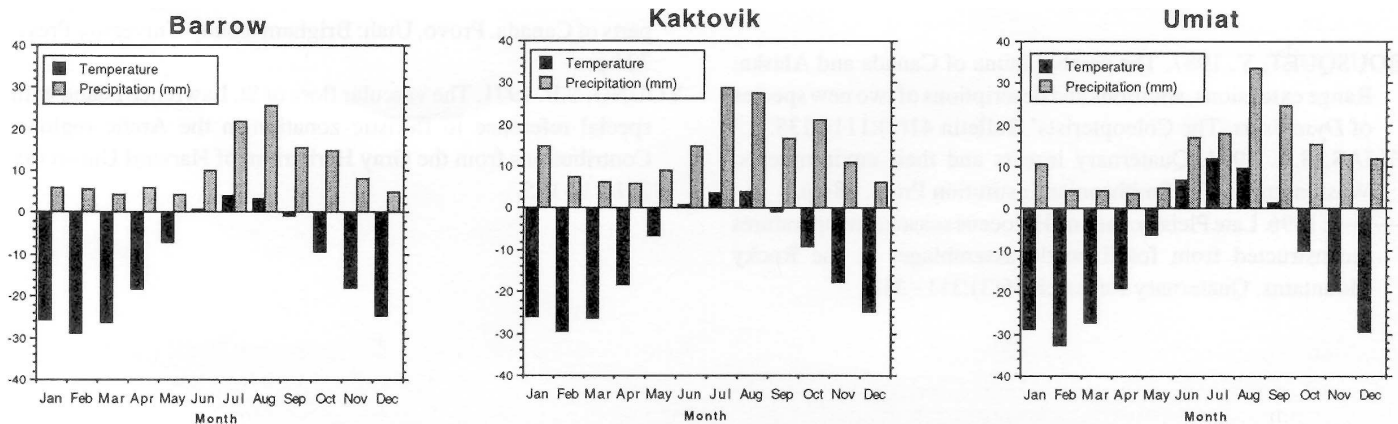


FIG. 2. Climatographs for Barrow, Kaktovik (= Barter Island), and Umiat, Alaska. Mean monthly temperatures are in degrees Celsius (°C). Mean monthly precipitation values are in mm of water equivalent. Based on U.S. Government data (National Weather Service, 1949–78).

determine the impact of human activities on the global climate system.

SUMMARY

At this stage, our knowledge of the size of the carabid fauna of the Arctic Slope is inadequate for detailed analysis, though it does appear clear that numerous species found at inland sites are not present in the coastal fauna. This apparent decrease in carabid diversity most likely reflects the significant differences between summer temperatures (particularly mean July temperatures) on the coast and those at more inland sites. The inland sites most different in temperature from coastal sites are those in proximity to the Brooks Range in the Arctic Foothills, though some collecting bias seems likely. This preliminary synthesis of published records is intended to serve as a basis for future work. It should provide at least some modest benefit to those working to understand past environmental change and to monitor the changes anticipated for this century.

ACKNOWLEDGEMENTS

My sincere thanks go to Mrs. Susan Cole for her assistance with the computer literature search of BIOSIS. Many thanks to George Ball for identifying specimens of *Pterostichus*, subgenus *Cryobius*, from the Titaluk River, and to Yves Bousquet for identification of *Dyschirius melancholicus* from the same site. Three anonymous reviewers provided gracious critical reviews of an earlier draft of this paper, and their suggestions were most helpful. Andrei Strukov provided the Russian translation of the abstract, and Sheila McCarthy assisted in printing it. Financial support for this study was provided in part by grants from the Natural Science Division Grants Fund of Colby College. Many of the specimens in my personal collection were obtained while I was working with the U.S. Geological Survey in northern Alaska from 1975 to 1980.

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