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# Forty Years of Northern Natural Science

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ABSTRACT. In a review of some of the research activities in the North over the past 40 years, with special reference to the arctic areas of Canada and Alaska, we find that most of the objectives outlined in the early 1950s have been achieved. We now know much more about the plants, terrestrial arthropods, freshwater ecology, marine ecology and terrestrial vertebrates. We have at least a conceptual view of how the different organisms fit together in the natural arctic ecosystem. The ecosystems appear to be rather simple and relatively stable, but do not have unlimited resilience.

Key words: Arctic, northern, biology, review, 40 years

RÉSUMÉ. Une recension des activités de recherche qui a eu lieu dans le Nord au cours des 40 dernières années, tout particulièrement dans les régions arctiques du Canada et de l'Alaska, montre que la plupart des objectifs définis au début des années 50 ont été atteints. Nous en savons maintenant beaucoup plus sur les plantes, les arthropodes terrestres et l'écologie de l'eau douce et de l'eau de mer ainsi que sur les vertébrés terrestres. Nous saisissons, au moins au niveau des concepts, la façon dont les divers organismes s'imbriquent dans l'écosystème naturel de l'Arctique. Les écosystèmes paraissent plutôt simples et relativement stables, bien que n'ayant pas une résistance à toute épreuve.

Mots clés: Arctique, Nord, biologie, recension, 40 années

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## INTRODUCTION

Over the past 40 years, there have been some major advances in northern natural science. Forty years ago there was a resurgence in basic research in the Arctic and the North, following the end of World War II. This research, aided originally by the developments in transportation, aerial photography, radar, etc., during the war, has in recent years benefited through the various technological advances based on these early postwar developments. In particular, LANDSAT imaging has had far-reaching applications (Thie *et al.*, 1974; Hibler *et al.*, 1975; Ahlnas and Wendler, 1979; Dey *et al.*, 1979; Thie, 1979; Pala, 1982; Sims, 1983; Borstad, 1985). This will soon be followed by RADARSAT.

During World War II, the Fisheries Research Board of Canada launched a survey of the fishery potential in northern freshwater for strategic reasons. An Arctic Station of the Fisheries Research Board of Canada was established in Montreal, and in 1959 it carried out a large-scale airborne survey of the Barren Grounds covering major parts of the Mackenzie and Keewatin districts of the Northwest Territories. Parts of the Arctic Archipelago were surveyed in 1962 (McPhail and Lindsey, 1970).

In the late 1940s a number of other surveys and expeditions were launched to further our basic knowledge of natural science in the North. In this context can be mentioned the Calanus expeditions of 1947-55 (Dunbar, 1956) and the Jacobsen-McGill University Arctic Research Expedition to Axel Heiburg Island (Muller, 1962).

Organized entomological research in northern Canada began in 1947 as a joint project of the Defense Research Board, Department of National Defence, and the Entomology and the Botany and Plant Pathology divisions of the Department of Agriculture (Freeman and Twinn, 1955; Riegert, 1985). This research was aided by the establishment of the Lake Hazen field laboratory on Ellesmere Island (Oliver, 1963).

Stations like the Arctic Research Laboratory (which became the Naval Arctic Research Laboratory in 1967) at Barrow, Alaska, started in 1947 (Reed, 1969), and the Arctic Institute station established on Devon Island in 1960 (Apollonio, 1960) were to play a major role in future research advances in the North.

While these early initiatives expanded our knowledge and made significant advances in our understanding of northern natural science, it was the major economically driven projects starting in the 1950s that have really established modern northern research and understanding. Important here were the environmental studies started in 1959 for Project Chariot in the Plowshare Program (Wilimovsky and Wolfe, 1966), the International Biological Program (IBP) projects in 1964-74 (Cameron and Billingsley, 1975; Brown, 1975; Bliss, 1977; Tieszen, 1978; Brown *et al.*, 1980; Hobbie, 1980), the Environmental Studies on James Bay (Canada, Department of the Environment, 1976), the Beaufort Environmental Monitoring Project (LGL Ltd., 1985), and others. The Mackenzie Valley Pipeline Inquiry (1974-77) and the Alaska Highway Pipeline Inquiry (1978) prompted further studies (LeBlond, 1979), as did oil and gas exploration, the Trans Alaskan Gas and Oil Pipeline projects and the Arctic Islands Pipeline proposal. For example, the Eastern Arctic Marine Environment Studies Program (Sutterlin and Snow, 1982) was initiated in response to proposed oil and gas exploration in the Canadian Eastern Arctic. Studies prepared for the Polar Gas Project have resulted in the accumulation of masses of new information, some of which is summarized in Davis *et al.* (1980), McLaughlin (1982) and LGL Ltd. (1983). The Outer Continental Shelf Environmental Assessment Program has funded research on the Alaskan marine environment (Science Applications, Inc., 1980), and the Arctic National Wildlife Refuge Coastal Plain Resource Assessment program has assembled information on the fish, wildlife and their habitats on the north Alaskan coastal tundra (U.S. Department of the Interior, 1982, 1985; Garner and Reynolds, 1983, 1984). Titles and abstracts of scientific papers supported by the Polar Continental Shelf Project have been assembled by Hobson and Voyce (1974, 1977, 1980, 1983).

It is not possible, and indeed not worthwhile, to repeat all of the findings from these many studies. Instead, I have decided to consider the last 40 years of endeavour against the needs identified by experts in the early 1950s. Fortunately, in 1955 the

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Arctic Institute of North America felt it timely to review the current state of northern research in the various fields of science. In a series of papers gathered together and edited by Rowley (1955) various authors indicated what they thought should be the objectives of future studies in each area of specialization.

I have chosen, for the most part, to use these objectives as a framework to introduce the achievements over the past 40 years. I have decided to be selective rather than comprehensive. I will consider the natural sciences as synonymous with biological sciences for the present purpose, as the physical and social sciences are too far from my normal areas of pursuit. I will place most emphasis on the area in Canada north of the polar limit of tree-like conifers as defined by Hustich (1953).

## PLANTS

### *Objectives*

Raup (1953:74) conveniently outlined some of the botanical problems that should be studied in the arctic and subarctic regions. Although I will not deal with each individual entry, his listing is worth repeating.

a. Botanical exploration.
   1. Floristic exploration: the western arctic islands, interior of arctic islands, interior of Labrador-Ungava Peninsula, interior of Keewatin, northern Manitoba and Saskatchewan, western Mackenzie, eastern and northern Yukon, northern British Columbia, mountains and plateaus in interior Alaska.
   2. Description and analysis of plant communities.

b. Flora of boreal America.
   3. Preparation of a comprehensive "Flora," with keys and descriptions, preferably illustrated.

c. Origin and distribution of the flora.
   4. Preparation of range maps of species.
   5. Investigation of genetic variability in species as related to their geographic behaviour in Pleistocene and post-Pleistocene time.
   6. Relation of species distribution to development of landscapes.

d. Origin and distribution of plant communities.
   7. Relation of development of plant communities of arctic and subarctic land forms, particularly with respect to cryoplanation.
   8. Reconstruction of post-Pleistocene landscapes, both as to morphology and biota.
   9. Investigation of the concepts of "succession" and "climax" as applied to boreal vegetation.
   10. Relation of climate, both local and general, to the nature and distribution of vegetation.
   11. Effects of man and other animals upon the vegetation.
   12. Effects of fire upon native vegetation.
   13. Studies of peat deposits and other fossil remains.

e. Problems in applied botany.
   14. Sustained yield utilization of native forests and grasslands.
   15. Investigation of agricultural expansion.
   16. Interpretation of vegetation as an indication of "kind of ground."
   17. Interpretation of air photographs for the mapping of natural resources and "kind of ground."

After the basic work on the geography of plant life had been done, Raup (1953) thought there were many physiological problems that could be tackled. He observed that

> Arctic vegetation bristles with problems relating to the physiological relations between the plants and their environments. Water relations in arctic vegetation are very poorly understood, as are those involving the availability and use of mineral salts. The nitrogen cycle in arctic and subarctic regions is particularly worthy of investigation. [Raup, 1953:73.]

### *Achievements*

Floristic exploration has continued apace (e.g., Hale, 1954; Schofield and Cody, 1955; Savile, 1959, 1961, 1963; Beschel, 1961; Bursa, 1961, 1963; Booth and Barrett, 1971; Brassard, 1972; Mason *et al.*, 1972; Barrett and Teeri, 1973; Kuc, 1974; Schulten, 1975; Barrett and Thomson, 1975; Brassard *et al.*, 1979; Ritchie, 1984; Kojima and Brooke, 1985; Brooke and Kojima, 1985; Soper and Powell, 1985). There are now many descriptions and analyses of plant communities (e.g., Savile, 1959; Johnson, 1969; Larsen, 1972, 1973; Forest Management Institute, 1974; Muc and Bliss, 1977; Hsiao, 1980; Thompson, 1980; Bliss and Svoboda, 1984; Bliss *et al.*, 1984; Soper and Powell, 1985). It is now evident that climate, drainage, nutrients, soil type, snow cover and short growing season all govern the composition of arctic plant communities. The combination of limited soil moisture in mid-summer and very low nutrient levels is the primary reason for low plant cover and low plant productivity in the polar deserts (Bliss *et al.*, 1984).

A number of comprehensive "Floras" with keys, descriptions, illustrations and sometimes maps have been produced (e.g., Anderson, 1959; Wiggins and Thomas, 1962; Porsild, 1964; Hulten, 1968; Welsh, 1974; Porsild and Cody, 1980). Range maps of species have been provided for many taxa (Hulten, 1958, 1962, 1963a,b, 1971; Polunin, 1959; Porsild, 1964; Cody, 1971; Young, 1971). Hulten (1937), having established the phytogeographical importance of Beringia as a centre for survival and dispersal, set the scene for most of the succeeding biogeographic studies in the North (Thomson, 1972; Murray, 1978; Steere, 1978).

It is now well established that much of central Alaska and the Yukon remained an ice-free Pleistocene refugium, and most biogeographers now accept the concept that Beringia has served as an important centre of origin of the modern biota: the role of Beringia as an area of survival is central to the interpretation of floristic diversity and relatively high frequence of endemism in the area (Ritchie, 1984).

Satellite and airborne remote sensing have now been used to not only indicate vegetation and ground conditions (Schreier *et al.*, 1982), but also for ecological mapping (Oswald and Senyk, 1977; Cowell *et al.*, 1979; Ducruc, 1980; Bradley *et al.*, 1982), ecological land classification and the establishment of ecozones (Zoltai, 1979, 1980; Wiken and Bird, 1984). Microrelief emerges as the principal control of the plant environments within the flat tundra of the North (Webber, 1978). In the sea, Ellis and Wilce (1961) have shown that regular intertidal zonation comparable with areas farther south is rare in the Arctic and exists only in sub-arctic areas where the thickness of shore ice is less than tidal amplitude.

Detailed pollen profile sampling and palaeobotanical studies have allowed reconstruction of Pleistocene and post-Pleistocene landscapes in the North (Hopkins *et al.*, 1982; Ritchie, 1984). Ritchie (1984) studied a 220 000 km area around the Mackenzie Delta from the Alaska border to Baillie Islands in the north, to the level of about Ford Good Hope in the south. He concluded that in the past 25 000 years there were three major vegetational episodes in the area, viz.:

(1) from 25 000 to 11 000 B.P., a full- and late-glacial vegeta-

tion represented by predominantly herbaceous arctic-alpine taxa;

(2) from 11 000 to 7000 B.P., an early Holocene period of rapid change in vegetation, which in the northern unglaciated Yukon shows an abrupt change from herb tundras to dwarf-shrub tundras, and in the south of the area shows a dramatic change from tundra to forest; and

(3) 7000 B.P. to present, an abrupt increase in alder pollen followed by apparent stability of the current regional vegetation patterns.

In contrast to the full-glacial arctic-alpine vegetation envisaged by Ritchie (1984), it has been proposed that the late Pleistocene vegetation cover of Beringia was a steppe-tundra characterized by discontinuous herbaceous vegetation in which xerophytes were prominent (reviewed by Hibbert, 1982). Recent considerations suggest that there was a mosaic of vegetation, not fully analogous to modern counterparts, with a significant proportion adapted to mesic and arid conditions (Hibbert, 1982; Young, 1982). Some of the biota from this time may still occur on the arid south-facing slopes of river valleys in the Yukon and Alaska (Kassler, 1979; Yurtsev, 1982; Robinson and Scudder, unpubl. data).

The principal successional trends in modern tundra vegetation and the principal allogenic geomorphic processes controlling these successional trends have been considered by Webber (1978). Succession in unburned sub-arctic woodlands is described by Strang (1973). Viereck (1970) has investigated the forest succession and soil development in interior Alaska, and Heilman (1966, 1968) has given details of the distribution and availability of nitrogen and phosphorus in forest succession on the north slopes of interior Alaska. Bliss and Cantlon (1957) investigated the succession on river alluvium in northern Alaska, and Viereck (1966) succession and soil development on gravel outwash.

The concept of climax in the Arctic has been considered by Churchill and Hanson (1958). A biogeoclimatic zone scheme of classification based on the presumed mesic climax has shown three zones in the central Yukon (Krajina, 1975; Kojima and Brooke, 1985): a Boreal White and Black Spruce zone, a Spruce-Birch-Willow (Subalpine) zone and an Alpine Tundra zone.

The effects of human disturbance are now of major concern in the North. Observations and experiments have demonstrated the danger of surface damage and the longevity of the natural recovery process (Babb and Bliss, 1974a,b; Babb, 1977). The potential damage to plants and vegetation from oil spills has been investigated by Bliss and Wein (1972) and Freedman and Hutchinson (1976).

The effects of fire upon the native vegetation and its recovery have been documented (Bliss and Wein, 1972; Wein and Bliss, 1973; Johnson and Rowe, 1977; Black and Bliss, 1978; Viereck and Schandelmeier, 1980; Racine, 1981; Strang and Johnson, 1981). Although fire generally is not considered an important factor in tundra ecosystems (Patterson and Dennis, 1981), Bliss and Wein (1972) showed that tundra fires destroy most of the above-ground plant cover and result in significant increases in depth of the active layer. Fire stimulates the growth and flowering of *Eriophorum vaginatum* L. ssp. *spissum* (Fern.) Hult. and *Calamogrostis canadensis* (Michx.) Beauv. Recovery of dwarf heath shrubs from rhizones was relatively rapid, while lichen and mosses showed no early recovery.

Many problems relating to the physiological relationships between plants and their environment in the North, mentioned by Raup (1953), have been the subject of intensive study (e.g., Bliss, 1977; Tieszen, 1978; Chapin, 1983; Rannie, 1986). We have a good understanding of temperature sensitivity, water relations, nitrogen fixation, nutrient cycling and primary production in tundra habitats. The polar desert cushion plant morphology with tufted growth form and persistent dead leaves with consequent thick boundary layer are efficient energy trapping characteristics (Addison and Bliss, 1984). Grulke and Bliss (1985) have shown that in two high arctic grasses, *Phippsia algida* (Sol.) R. Br. and *Puccinellia vaginata* (Lge.) Fern. & Weath., adaptation to reduce the severity of the environment apparently holds a greater selective advantage than adaptation to maximize leaf orientation to a low sun angle. We now better understand life-cycle adaptations (Bliss, 1971) and the functioning of the arctic tundra ecosystem (Bliss *et al.*, 1973; Bliss, 1977; Tieszen, 1978). The distribution of peat lands and coal resources has been assessed (Sjors, 1959; Bustin, 1980).

## TERRESTRIAL ARTHROPODS

### *Objectives*

Biting flies are one of the principal obstacles to the development of the North (Sailer, 1955). The aims of the Northern Canada Insect Survey launched in 1947 (Freeman, 1952; Freeman and Twinn, 1955) were primarily to investigate life history, habits, ecology and control of biting flies; and study the systematics, distribution, relative abundance and ecology of biting flies and other insects.

### *Achievements*

The early work on biting flies carried out at Churchill, Manitoba, showed female mosquitoes can feed on nectar of flowers and are efficient pollinators of northern orchids (Twinn *et al.*, 1948). Miller (1951) showed that most species of horse flies (Tabanidae) overwinter in the larval stage and have at least a three-year life cycle around Churchill, while Jenkins and Hassett (1951), using radiophosphorus, showed that the effective range of dispersal for sub-arctic mosquitoes was about 0.4 km (0.25 mls).

An identification handbook is now available for mosquitoes (Wood *et al.*, 1979), and one is in preparation for horse flies. As a result of the many studies started in the North, we are now able to explain what is involved in black fly host location (Sutcliffe, 1986); it consists of long-, middle- and short-range phases as well as post-landing activities and is driven by olfactory, visual, anemotactic, optomotor, thermal and gustatory stimuli!

The Northern Insect Survey from 1947 to 1952 collected about 125 000 specimens each year (Freeman, 1952). These specimens and the many insects collected before and since have provided, with associated biological studies, an extensive knowledge of the fauna, its distribution and ecology. Our current knowledge of the arctic arthropods has been ably synthesized by Danks (1981a), and a bibliography is available (Danks, 1981b). Insect-plant interactions in arctic regions have also been considered by Danks (1986). However, much is still being discovered. For example, new distributions are being documented (e.g., Fjellberg, 1986), new species discovered (e.g., Behan-Pelletier, 1987), and Kugal and Kevan (1987) have recently estimated that the Lymantriid moth *Gynaephora groenlandica* (Wocke) has a 14-year life cycle at Alexander Fiord Lowland on Ellesmere Island.

## FRESHWATER ECOLOGY

### *Objectives*

Rawson (1953) observed that the vertebrate and invertebrate fauna of inland arctic lakes was largely unexplored. He also called for the study of arctic rivers and pointed out the need for general studies on the distribution of freshwater fish in the arctic.

### *Achievements*

While considerable collecting has taken place in lentic waters in the North, taxonomic inadequacies in most taxa preclude study at the present time. As noted by Danks (1981a), taxonomic, distributional and ecological knowledge in most groups of northern invertebrates is disappointingly meagre, and the life histories and ecological roles of most of these are very imperfectly known. Only in a few groups of Crustacea do we have a fair knowledge of the fauna and its distribution (Bousfield, 1958; Reed, 1963).

A number of northern and arctic freshwater lakes and ponds have been studied (e.g., Oliver, 1964; McLaren, 1964; Kalff, 1967a; Roff and Carter, 1972; Healey and Woodall, 1973; Kalff and Welch, 1974; Schindler *et al.*, 1974a; McLeod *et al.*, 1976; de March *et al.*,1978; Bushnell and Byron, 1979; Lindsey *et al.*, 1981; Hebert, 1985; Fee *et al.*, 1985). However, Char Lake on Cornwallis Island has received the most intensive limnological investigation (Kalff, 1967b; Kalff *et al.*, 1972; Welch, 1973, 1974; Rigler *et al.*, 1974; Schindler *et al.*, 1974b; Welch and Kalff, 1974; de March, 1975; Rigler, 1975; Andrews and Rigler, 1985), and studies have been undertaken on some lakes on the Truelove Lowland on Devon Island (Minns, 1977). The latter indicate that productivity in the Truelove Lowland lakes is higher than that in Char Lake. This is probably owing to the fact that Char Lake has a drainage predominantly in polar desert, while the Truelove Lowland is a low but very productive site. This supports the suggestion by Welch (1974) that the productivity of arctic lakes depends on the terrestrial productivity in their drainage basins. Kalff (1970) noted that the most important reason for low productivity during the summer in arctic lakes appears to be the low nutrient content of most arctic waters. Whalen and Alexander (1986) have shown that nitrogen and phosphorus are the most important chemical regulators of primary production in Toolik Lake, Alaska.

The limnology of tundra pools in Alaska has received detailed study (Hobbie, 1980). The studies reported in Hobbie (1980) give an in-depth account of the habitats, the biota and the processes by which organisms interact with other organisms and with their physical and chemical environments. The rooted plants in the tundra ponds provide most of the input of organic carbon, the annual primary production is low owing to the short ice-free season, and the detritus food chain is dominant in the ecosystem.

Studies on arctic rivers are still sparse (McLeod *et al.*, 1976; MacDonald and Stewart, 1980). Nevertheless, in a study of a second-order sub-arctic stream in interior Alaska, Cowan and Oswood (1983) have shown that it received and stored less energy from the surrounding forest than in temperate streams. This suggests that productive capacities (e.g., fish production) of high latitude streams may be fundamentally limited by low allochthonous input. It has a strong influence on the spatial and temporal patterns of occurrence of detritivores (Cowan and Oswood, 1984).

Since 1947, extensive collecting of freshwater fishes in the North has provided knowledge of the fauna and its distribution. The distribution of over 50 species in the North is detailed by McAllister (1965), and additional information is contained in the faunal works by McPhail and Lindsey (1970) and Scott and Crossman (1973).

The zoogeography of these northern freshwater fishes has been considered by Crossman and McAllister (1986), Lindsey and McPhail (1986) and Black *et al.* (1986). Crossman and McAllister (1986) report that there are 101 native species in the Hudson Bay watershed, but only 8 species occupy freshwater in the Canadian Arctic Archipelago: none is endemic to these areas but they have invaded the North chiefly from the Mississippi drainage system. There have been a number of assessments of the exploited and unexploited freshwater fisheries in the North (e.g., Kennedy, 1953; Johnson, 1976, 1983; McCart, 1980; MacDonald and Stewart, 1980; Stewart and MacDonald, 1981; Roberge *et al.*, 1986; Yaremchuk, 1986). Stanwell-Fletcher Lake on Somerset Island is a large, cold, monomictic, true polar lake that contains both anadromous and lake-dwelling Arctic char (*Salvelinus alpinus* [L.]) (de March *et al.*, 1978). The lake is the site of an important Inuit fishery on the char, the anadromous population of which was estimated at $9 \times 10^4$ in 1980 (Stewart and MacDonald, 1981). The food of the char in the lake consists of chironomid larvae and pupae and *Mysis relicta* Loven, while in the sea the char feed mostly on the amphipod *Parathemisto libellula* (Lichtenstein) and the Arctic cod, *Boreogadus saida* (Lepechin).

## MARINE ECOLOGY

### *Objectives*

Dunbar (1953) emphasized the sharp distinction between the biological production of the arctic and sub-arctic waters. He defined arctic waters as those in which unmixed water of polar origin is found in the surface layers (200-300 m at least), whereas sub-arctic waters are those marine areas where the upper water layers are of mixed polar and non-polar origin. Noting that it is the sub-arctic belt across the North Atlantic that is one of the richest parts of the oceans of the world and the home of fisheries of immense value, he observed that there is a much higher plankton production in these sub-arctic compared with arctic waters. Dunbar (1953) thus pointed out the need to measure this difference and understand its reasons. There was a need to measure the stability or instability of sub-arctic waters and the extent of upwelling, and measurements were required of the phosphate and nitrate concentrations in both arctic and sub-arctic waters. Plankton production needed study in Hudson Bay, the Arctic Ocean itself and the Beaufort Sea, after modern methods had been used to determine standing crop.

Dunbar (1953) called for the study of plankton biology in general, to include vertical diurnal migration, size relationships, food of zooplankton in the North and breeding cycles in planktonic animals. In the benthic and littoral fauna, there was a need to relate distribution to depth, in order to accurately determine the distribution of the North American arctic shallow-water benthos. Within the life cycles, there was a need to determine the reproductive requirements and limitations of the arctic and sub-arctic invertebrates and the presence or absence of larval stages; densities of the benthic fauna needed study by use of bottom samplers.

General collecting of the littoral fauna was called for in order to determine the distribution of arctic and sub-arctic forms. A prerequisite for this, for accurate mapping and for studies on zoogeography and life cycles was thorough, systematic investigations. The amphipod crustacean families in particular were identified for special attention. There was also a need to study the breeding seasons and cycles of littoral invertebrates at different levels of the beach and how they survive during the winter.

Noting that fishes are not abundant inside the arctic zone, Dunbar (1953) observed that the nektonic biomass in the Arctic is dominated by marine mammals. In the sub-Arctic the reverse is true, and this contrast needs to be explained.

Dunbar (1953) called for the study of the metabolism of arctic fishes at the temperature at which they live and the general relationship between temperature, reproduction and development. There was a need to study the possibility of developing fisheries in the Beaufort Sea and at the northern edge of the sub-arctic waters in Baffin Island.

Dunbar (1953) also drew attention to the urgent need to study the arctic and sub-arctic marine mammals, because of their role in the northern economy. Calculations were required on population numbers and sustainable yields. Much study was needed on the life cycles and conservation problems in the walrus, ringed seal, bearded seal, harbour seal, beluga and narwhal.

*Achievements*

Marine plankton composition and productivity has now been studied in the Beaufort Sea (Grainger, 1975a; Grainger and Grohe, 1975; Hsiao, 1976; Foy and Hsiao, 1976a; Hsiao *et al.*, 1977; Horner and Schrader, 1982), Frobisher Bay (Bursa, 1971; Grainger, 1971a,b, 1975b), Hudson Bay (Bursa, 1961), James Bay (Foy and Hsiao, 1976b; Grainger and McSween, 1976) and other areas of the North (Sutherland, 1982; Huntley *et al.*, 1983; LGL Ltd., 1983; Ratynski, 1983; Sameoto, 1984). Harrison (1986) has shown that the structure and functioning of arctic plankton communities are very similar in character to those of more southerly latitudes.

In Frobisher Bay, the phytoplankton consisted of about 50 species of diatoms, 6 species of dinoflagellates and 5 species of flagellates, while the zooplankton was composed of at least 55 species (Grainger, 1975b). Production of phytoplankton (calculated from the carbon$^{14}$ uptake method) was 40-70 $g \cdot C \cdot m^{-2} \cdot y^{-1}$ compared with 1 $g \cdot C \cdot m^{-2} \cdot y^{-1}$ or less described from the central Arctic Ocean (Grainger, 1975b). From studies in Lancaster Sound, Sameoto *et al.* (1986) have concluded that it is the thermocline that is the main physical feature that affects the depth of the chlorophyll layer and the levels of primary production, with a shallow thermocline resulting in higher primary production. The total arctic production is now calculated at $210 \times 10^6 + Cy^{-1}$ (Subba Rao and Platt, 1984).

The distinctive epontic algal community of ice edges has been described by Booth (1984) and the production in this community has been measured by Smith *et al.* (1987). The under-ice biota at Pond Inlet has been studied by Cross (1982): there is little evidence of geographic variation in this community, which is important in the food chains leading to seabirds and marine mammals.

The benthic fauna has been studied across much of the North (Ellis, 1955, 1960; Wacasey, 1974a,b, 1975; Wacasey *et al.*, 1976; Thomson *et al.*, 1979, 1986; Thomson, 1982; LGL Ltd., 1983; Martin and Cross, 1986). In the central Canadian Arctic Islands, Thomson *et al.* (1986) identified nine infaunal species assemblages that showed preferences for depth and substrate, amphipods and mysids being the dominant epibenthic animals in the subtidal zone.

Faunistically, a fair number of collections have been made and reports published on the Polychaetes (Grainger, 1954), Echinoderms (Grainger, 1955) and Pycnogonida (Hedgpeth, 1963). However, the best studied groups are the Crustacea (Dunbar, 1954; Fontaine, 1955; Squires, 1957, 1962, 1967, 1968; Johnson, 1963; Vidal, 1971; Corey, 1981) and the Mollusca (Wagner, 1977; Bernard, 1979; Lubinsky, 1980). Only in these latter two taxa do we have sufficient information on distribution to analyze the faunal composition and zoogeography. Thus, in the marine bivalve molluscs of the Canadian and Eastern Arctic, Lubinsky (1980) has shown that the 64 species occur in two zoogeographic zones, an arctic and a sub-arctic, the boundaries of which almost coincide with those of the corresponding marine waters as outlined by Dunbar (1953). Lubinsky (1967) has also studied the growth of *Mytilus edulis* L. in the Canadian Arctic. Bivalve molluscs are the primary food of the walrus, and bivalves and gastropods are important food for the bearded seal (Davis *et al.*, 1980).

In the Crustacea, some of the amphipods that Dunbar (1953) said demanded attention have now been studied (Steele, 1982, 1986). Steele (1982) has demonstrated the need for comparison with Old World material to correctly establish the identity of the northern fauna in Canada and Alaska.

In the copepods, Grainger (1963) has shown that both *Calanus glacialis* Jaschnov and *C. hyperboreus* Kroyer are arctic species that range south to the limit of penetration of arctic water, while *C. finmarchicus* (Gunnerus) is an Atlantic species that penetrates into the mixed sub-arctic zone.

Dawson (1978) has described seasonal variation in vertical distribution in *C. hypoboreus*, with females ascending to the surface in response to light and then gradually sinking by fall to about 150 m. Differential vertical distribution in *Calanus* has been reported by Herman (1983), who found that *C. finmarchicus* and *C. glacialis* occurred some 3-5 m above the chlorophyll maximum, while *C. hypoboreus* occurred at or below the chlorophyll maximum. Sameoto (1984) has also reported a diurnal vertical migration to about 20-30 m in copepodite stages C5 and C6 in both *C. finmarchicus* and *C. glacialis* in eastern Baffin Bay.

The euphausiids are not at home in arctic water, where their ecological place is taken largely by two amphipods, the hyperiid *Parathemisto libellula*, and in the Arctic Ocean itself and on the sea-ice substrate by the gammarid *Gammarus wilkitzkii* (Binula) (Dunbar and Moore, 1980). *P. libellula* is an arctic-sub-arctic species with a two-year life cycle that is a dominant carnivore in the northern food web (Dunbar, 1946, 1957) and forms a very important food species for the ringed seal and the harp seal (Dunbar, 1941; Davis *et al.*, 1980). *G. wilkitzkii* has colonized sea ice in the Arctic and exploits the diatoms on the under surface of the ice (Dunbar and Moore, 1980).

The number of marine fish species in arctic waters is very small (Dunbar and Hildebrand, 1952; Dunbar, 1968; Stewart and MacDonald, 1981). As yet there is no large faunal synthesis with keys and descriptions for the Canadian North, but there is a list of species (Steigerwald and McAllister, 1982), a distributional atlas (Hunter *et al.*, 1984), and a bibliography (McAllister and Steigerwald, 1986). Two of the species in the North, the Bering wolffish (*Anarhichas orientalis* Pallas) and the blackline prickleback (*Acantholumpenus mackayi* [Gilbert]), are on the rare and endangered list in Canada (McAllister *et al.*, 1985).

While 104 species of fishes are reported from the marine and brackish waters of arctic Canada, the number of species whose biology is even moderately well known can be listed on the fingers (McAllister, 1977). The biology of the Arctic cod is the best known of these fish (Bain and Sekerak, 1978; Bradstreet *et al.*, 1986). This species occurs as far north as 88°N and feeds primarily on copepods (Bradstreet and Cross, 1982; Bradstreet *et al.*, 1986). It is now known to be the most important food organism for sea birds feeding in near-surface waters along or just under the ice-edge (Sekerak and Richardson, 1978; Bradstreet and Cross, 1982; Cairns, 1987) and is the principal food of Thick-billed Murres (Gaston and Nettleship, 1981; Gaston and Noble, 1985). Arctic cod is often the main food of belugas, narwhals, ringed seals and harp seals, and it is occasionally an important food for bearded seals and, less frequently, walruses (Davis *et al.*, 1980; Finey and Evans, 1983).

With respect to the adaptation in fishes for life in the North, arctic species have larger orbits (McAllister, 1977) and tend to replace the system of neuromast-containing canals by a system of free neuromasts on the body and the head (Andriashev, 1970). We now also know that many species rely on antifreeze polypeptides to confer freezing resistance (DeVries, 1984; Fletcher *et al.*, 1982, 1986; Kao *et al.*, 1986).

As one might imagine, the marine mammals have been a major focus throughout the last 40 years in the North. The literature is vast, and our current knowledge is well summarized by Davis *et al.* (1980) and Malouf *et al.* (1986). Although the ringed seal (*Phoca hispida* Schreber) is the most abundant of the arctic seals, little is known of its population biology (Malouf *et al.*, 1986); the bearded seal (*Erignathas barbatus* [Erxleben]) is much less numerous, but few quantitative estimates of abundance are available. Davis *et al.* (1980) expressed concern about the declining beluga population in Cumberland Sound, noted that the Lancaster Sound narwhal population estimates need verification, and pointed out that the current status of the Baffin Bay walrus population was unknown and that there are no estimates of the size of the Foxe Basin population of this species.

## TERRESTRIAL VERTEBRATES

### *Objectives*

Research needs on arctic vertebrates were outlined by Rausch (1953) and Clarke (1955). In the early 1950s faunal inventory was still needed on the arctic mainland west of Hudson Bay and on many of the arctic islands (Clarke, 1955).

Forty years ago, study of the lives of arctic birds and mammals was just at a beginning (Clarke, 1955). Clarke (1955) noted that the great sea bird colonies of the North offered unrivalled opportunities and could also be studied profitably; there was a clear need to follow up any lead on the life of the Whooping Crane.

The social behaviour of the muskox was cited for study, and there was a need for life-cycle studies on the caribou (Clarke, 1955), with particular reference to the structure of the populations, their dynamics, migration, food and conservation (Rausch, 1953).

Rausch (1953) called for more investigation of the predator-prey relationships involving wolves, the rationale behind wolf-kill programs and the methods of killing. Clarke (1955) noted that the larger bears must be studied also, or the opportunity may be lost.

Clarke (1955) finally pointed out that there is no other biological problem in the North more important and more challenging than the periodic fluctuations in the numbers of northern animals. While there was a substantial outline of the population cycles of arctic mammals and birds, most details were lacking, and these he thought could only be filled in by field work in the North using large-scale marking of individual animals.

### *Achievements*

Our information on the distribution and ecology of arctic and northern birds has increased markedly over the past 40 years. The ornithological knowledge for the North to 1973 was summarized by Davis *et al.* (1973), who called for more information on numbers of birds in various areas, their occurrence, migration and susceptibility to human disturbance. Additional data on numbers and distribution have subsequently been obtained (e.g., Parker and Ross, 1973; Smith, 1973; Davis *et al.*, 1975; Johnson and Adams, 1975; Richardson *et al.*, 1975; Searing *et al.*, 1975; Barry, 1976; Curtis, 1976; McLaren *et al.*, 1976, 1977; McLaren and Holdsworth, 1978; McLaren and McLaren, 1978; Maltby, 1978; Nettleship, 1974, 1977; Patterson and Alliston, 1978; Richardson and Johnson, 1981; Johnson and Richardson, 1982; LGL Ltd., 1983; Boyd *et al.*, 1982; Martell *et al.*, 1984; Alexander, 1986; Gaston *et al.*, 1986; Hawkings, 1986; Smyth *et al.*, 1986). Although the northern avifauna is well known, sizes of populations of many species are still poorly known (Hawkings, 1986). Impressive bird books dealing with the northern fauna are now available (Snyder, 1957; Gabrielson and Lincoln, 1959; Godfrey, 1986).

The highly colonial Thick-billed Murre (*Uria lomvia* [L.]) is the most abundant species of bird breeding in arctic Canada and has been studied in depth (Gaston and Nettleship, 1981; Gaston *et al.*, 1983). The Blue Goose and Lesser Snow Goose are now known to be forms of the same subspecies *Chen c. caerulescens* (L.) (Cooke and Cooch, 1968), whose migration has been studied by radar (Blokpoel, 1974; Blokpoel and Gauthier, 1975) and whose nesting colonies and numbers in the Arctic have been investigated (Boyd *et al.*, 1982; Geramita and Cooke, 1982; Kerbes *et al.*, 1983; Davies and Cooke, 1983). Hanson and Jones (1976) have shown that it is possible to determine the origin of both Snow Goose and Ross' Goose (*Anser rossii* Cassin) populations by studying the mineral composition in the vane portion of primary feathers grown on the breeding grounds. Kerbes *et al.* (1983) found that from 1967 to 1976 numbers of Snow Goose increased fivefold, while the numbers of Ross' Goose doubled; nesting resources did not appear to be limiting.

The Ivory Gull (*Pagophila eburnea* [Phipps]), confined to the High Arctic, is the most northerly breeding of all birds and favours nunatak nesting sites (Frisch, 1983). With no more than 1500 breeding pairs in North America (Brown and Nettleship, 1984), it is rarely seen far from pack ice and has been shown to differ markedly from both the Sabine's Gull (*Xema sabini* [Sabine]) and Ross' Gull (*Rhodostethia rosea* [MacGillivray]) in resource exploitation (Blomqvist and Elander, 1981). In contrast to most birds, the southern breeding Ross' Gull has the largest clutch size, while the most northern Ivory Gull has the smallest (Blomqvist and Elander, 1981). In his recent study of the breeding biology of Sabine's Gull, Abraham

(1986) has shown that the timing and duration of breeding effort is confined to just over seven weeks, the rapid rate of growth being an adaptation to the short arctic summer.

Clarke (1955) called for more study on the life of the endangered Whooping Crane (*Gus americana* [L.]), and this objective has been fulfilled (Novakowski, 1966; McNulty, 1966; Miller *et al.*, 1974; Kuyt, 1976; Binkley and Miller, 1980, 1983). The population has risen erratically from a low of 15 in 1941 to 78 in 1980 (Binkley and Miller, 1983) and now stands between 110 and 130 (G. Archibald, International Crane Foundation, pers. comm. 1987). The breeding area of the migratory population was discovered in Wood Buffalo Park, N.W.T., in 1954, and since then the Whopping Crane has been found nesting in the Klewi River area and elsewhere (Kuyt, 1976).

Banfield (1974) has provided a popular account of the mammals of Canada, including notes on the species in the North. The intriguing Muskox (*Ovibos moschatus* [Zimmermann]) has now been studied intensively (e.g., Tener, 1965; Miller and Russell, 1974; Wilkinson *et al.*, 1976; Miller *et al.*, 1977a; Parker, 1978; Thomas *et al.*, 1981; Vincent and Gunn, 1981; Urquhart, 1982; Klein *et al.*, 1984; Latour, 1987), and studies continue. Although there is no reason to consider any major population in danger of extirpation (Lent, 1978), only at a few localities are muskox densities high and populations stable (Thomas *et al.*, 1981). However, on the mainland and Banks and Victoria islands in the N.W.T., rapid expansion of muskox populations has been observed over the last decade or so (Gunn, 1984; Gunn *et al.*, 1984).

Investigation of the social organization and behaviour of the muskox shows that the species is a very social animal, with the herd as the social unit with a hierarchy within (Tener, 1965); the typical defensive circle, formed when under wolf attack, with adults and immatures facing outwards and with yearlings and calves sheltered, suggests a long association of muskox with wolves (*Canis lupus* L.).

Many of the caribou studies suggested by Rausch (1953) and Clarke (1955) have now been completed, although disturbance and conservation are still of major concern. Large-scale scientific study of caribou started in 1947, just 40 years ago (Kelsall,1968). Banfield (1961) clarified the systematics and recognized three tundra caribou subspecies, namely Grant's Caribou (*Rangifer tarandus granti* Allen), which occurs in the Yukon and Alaska, the Barren-ground caribou (*R.t. groenlandicus* L.), which occurs from southern Hudson Bay to the Mackenzie, and the Peary Caribou (*R.t. pearyi* Allen), found in the Canadian Arctic Archipelago and northwest Greenland; another subspecies, the Woodland Caribou (*R.t. caribou* [Gmelin]), is a forest dweller and occurs in the boreal forest region from Newfoundland to the Yukon, while the European Reindeer (*R.t. tarandus* [L.]) has been introduced to the North, and the Dawson's caribou (*R.t. dawsoni* Seton) on the Queen Charlotte Islands in British Columbia has been extinct since 1910. The origin of the different subspecies of *R. tarandus* in North America is still largely unknown (Roed *et al.*, 1986). The most favoured hypothesis is that the continental tundra forms evolved in the Beringian refugium during the Wisconsin glaciation, the Woodland Caribou south of the ice sheet and the Peary Caribou in a western Queen Elizabeth Islands refugium (Banfield, 1961) or a Pearyland refugium in northern Greenland (Manning, 1960; Manning and MacPherson, 1961; MacPherson, 1965). The large genetic distance in the transferrin locus between continental and island populations of caribou suggest the isolation of a High Arctic population in a northern refugium during the Wisconsin glaciation (Roed *et al.*, 1986).

There have been considerable fluctuations in populations of the Peary Caribou, the Peel population declining from 24 000 in 1961 to about 2700 in 1974 (Miller *et al.*, 1977a). In Peary Caribou starvation related to weather conditions is assumed to account for the high die-off (Thomas, 1982). There is evidence for inter-island movements of the Peary Caribou (Miller *et al.*, 1977b; Miller and Gunn, 1978), and morphological variations support the notion of genetic mixing (Thomas and Everson, 1982).

Following the first aerial census of the major herds of barren-ground caribou and the publication by Banfield (1954), the biology of this subspecies has been studied in detail (summarized in Harper, 1955; Kelsall, 1968; Banfield and Jakimchuk, 1980; Calef, 1981). Calef (1981) outlines the range of the major barren-ground caribou herds and their calving grounds. Bergerud (1974) has argued that predation has been a potent force in calving behaviour, the caribou migrating to certain calving grounds to reduce this predation. The location of these calving grounds seems to depend on the interaction between plant phenology and predator avoidance (Fleck and Gunn, 1982).

It is clear that barren-ground populations are seldom stable in numbers (Banfield, 1954; Kelsall, 1968). It has been proposed that wolf predation, rather than starvation from absolute shortage of food, is the main factor limiting population growth (Miller, 1975; Bergerud, 1980, 1983). According to Bergerud and Elliott (1986), the recruitment and mortality rates of caribou in North America are correlated with the abundance of wolves in those systems where wolves have been censused. By ear-tagging wolf pups, Kuyt (1972) has shown that wolves follow the migrating caribou, while Miller *et al.* (1985) have shown they do prey on newborn caribou. Walters *et al.* (1975) carried out a computer simulation of the Kaminuriak barren-ground caribou herd dynamics and showed that there was no reason to suspect that food supply currently limits population size; hunting pressure appears to be the critical variable. Haber (1977) has argued that the major declines in Grant's Caribou populations in Alaska over the past 10-20 years have been triggered by excessive human harvest. It seems that hunting and predation are additive and together can result in major declines of caribou populations (Bergerud, 1978).

Haber and Walters (1980) have pointed out that the prevailing model for the dynamics of caribou herds in the Alaska-Yukon population in essence visualizes a limit cycle in which wolf predation is seen as a primary factor causing caribou declines from large herd sizes. However, they show that an alternate "multiple equilibria" model appears to portray more accurately the observed changes in the wolf-caribou system; according to this model, population densities can be held down by predation for extended periods until dispersal among herds releases population increases. This has far-reaching implications with respect to hunting regulations and controversial wolf control measures.

Between 1979 and 1985 pronounced increases in numbers have been recorded in several large North American caribou herds. The seven largest herds (George River, Bathurst, Beverly, Western Arctic, Kaminuriak, Porcupine and Northeastern Mainland) consist of over 2 million animals, or 80% of the North American population (Williams and Heard, 1986). However, almost 20% of all herds are declining, and some small herds that exist as isolated gene pools are in danger of extinction.

Within historic time, moose (*Alces alces* [L.]) have extended their range in both Alaska and northern British Columbia (Kelsall and Telfer, 1974; LeResche *et al.*, 1974). Since moose serve as food for wolves where they co-exist (Frenzel, 1974), wolf numbers have tended to increase following expansion of moose (Bergerud and Elliot, 1986). Such increased wolf populations can impact on the local populations of other animals and cause their decline, as suggested in woodland caribou in northern British Columbia (Bergerud and Elliot, 1986).

The life of the polar bear (*Ursus maritimus* Phipps) is now better understood, and much has been discovered about the biology of this top predator in the arctic ecosystem. Polar bears are intimately associated with arctic sea ice, and their distribution is approximated by its winter extent (Ramsay and Stirling, 1986). Polar bears on sea ice are typically solitary (Latour, 1981a); however, aggregations of polar bears may occur either when sea ice completely melts, forcing all bears ashore (Latour, 1981a,b), or when bears scavenge at large food sources, such as at whale carcasses and dumps (Lunn, 1986).

Ringed seals and to a lesser extent bearded seals are the predominant prey of polar bears (Stirling and Archibald, 1977; Smith, 1980). The seasonal and local abundance, as well as the vulnerability of this prey, is also strongly influenced by sea ice conditions (Stirling and Archibald, 1977; Smith and Stirling, 1978). Bears tend to eat only the calorie-rich blubber of seals, leaving the carcasses for scavenging by the arctic fox and ravens (Stirling, 1974; Smith, 1980).

Within Canada, polar bears are distributed in a number of relatively discrete populations (Schweinsburg *et al.*, 1982; Furnell and Schweinsburg, 1984; Ramsay and Stirling, 1986), but bears move considerable distances in some years to locate suitable regions of seal abundance (Lentfer, 1983; Schweinsburg *et al.*, 1982).

There is competition among male polar bears for breeding females, but established dominance hierarchies are unstable (Ramsay and Stirling, 1986). Polar bears have low natality rates and high cub survival to the age of weening. Females give birth at an advanced age, litter size is small and the interbirth interval is a minimum of two years (Ramsay and Stirling, 1982). Female bears with young are very aggressive (Lunn, 1986) and generally avoid associating with adult males (Stirling, 1974; Taylor *et al.*, 1985).

Similarly, in the grizzly bear (*Ursus arctos* L.) adults avoid close proximity to each other, and females are generally intolerant of males (Murie, 1981). The minimum breeding interval for females is three years but is usually at least four years (Murie, 1981). In contrast to the polar bear, the grizzly bear is omnivorous, relying on a vegetarian diet (Murie, 1981; Miller *et al.*, 1982). Miller *et al.* (1982) have calculated that the average minimum home range size of females in the Mackenzie Mountains of the N.W.T. is 265 $km^2$.

The brown lemming (*Lemmus sibiricus* [Kerr]) and collared lemming (*Dicrostonys richardsoni* Merriam) of the central Canadian Arctic have been shown to have a classic 3- to 4-year cycle (Krebs, 1963, 1964). The ability of lemmings to breed in winter under snow is a spectacular biological accomplishment (Krebs, 1988). Winter breeding is always associated with cyclic increases and lack of winter breeding with the decline phase (Krebs, 1988). The physiological mechanisms of how winter breeding is achieved have yet to be studied.

While the easiest interpretation of this cycle is migration from areas of increase to more sparsely populated areas (Butler, 1953), there is no good evidence of any oriented long-distance group movements of lemmings (Krebs, 1964, 1988), although migration has been suggested by Pitelka (1973) for lemmings in northern Alaska. Although there are changes over the cycle in reproduction, mortality and the properties of individuals, these changes are not brought about by starvation or nutrition, nor are there obvious signs of physiological stress (Krebs, 1963, 1964).

Krebs (1963, 1964, 1985, 1988) hypothesizes that population changes in lemmings are driven by changes in social behaviour and genetics. However, since Pitelka (1973) postulates that each lemming cycle may have a different set of causes, much more experimental research is needed on field populations in the North.

While it has been argued that there is competitive interaction between small rodents (*Clethrionomys*, *Microtus* and *Peromyscus*) in some southern situations (Grant, 1972), studies

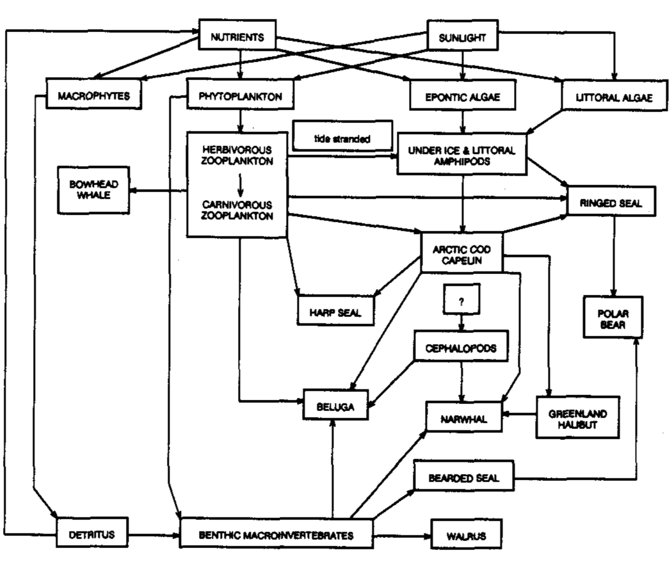


FIG. 1. Conceptual view of major energy flow pathways in arctic marine waters. Redrawn after Davis *et al.* (1980).

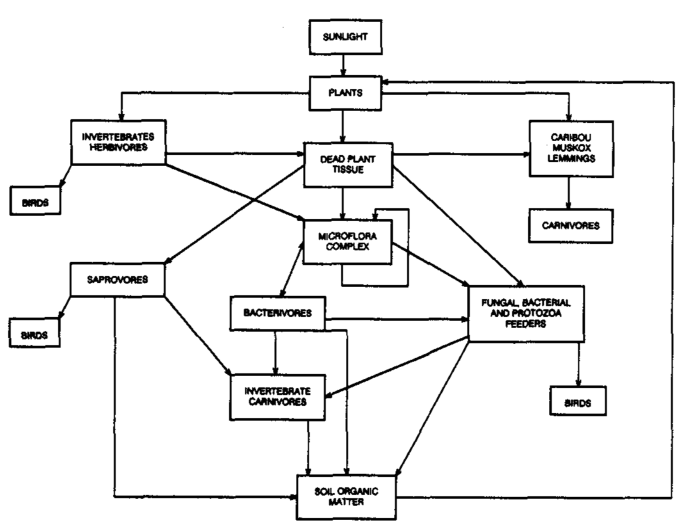


FIG. 2. Conceptual view of energy flow on the arctic tundra. Redrawn from Bliss (1975).

in the southern Yukon have shown no competitive interaction between deer mice (*Peromyscus maniculatus* [Wagner]), meadow voles (*Microtus pennsylvanicus* [Ord]) and northern red-backed voles (*Clethrionomys rutilus* Pallas) (Gilbert and Krebs, 1984; Galindo and Krebs, 1985). These three species also show no evidence for a 3- to 4-year population cycle (Krebs and Wingate, 1985). However, there appears to be an 11-year interval between high populations of *C. rutilus* (Gilbert *et al.*, 1986). Gilbert *et al.* (1986) suggest that the outbreaks of *C. rutilus* are linked to the 10-year cycle of the snowshoe hare (*Lepus americanus* Erxleben) and tend to occur two years after the peak of the hare cycle.

The 10-year population cycle in the snowshoe hare is being studied by field work in the North using large-scale marking of individuals. Using radiotelemetry to monitor the proximate causes of mortality, Boutin *et al.* (1986) have demonstrated that both starvation and predation are proximate causes of the decline at Kluane Lake in the Yukon. However, Krebs *et al.* (1986a,b) have shown that shortage of food is not necessary for cyclic decline. Sinclair *et al.* (1988) suggest that predation is a necessary cause of the hare cycle, and in some circumstances, it may be the only cause.

Thus research over the last 40 years has shown that the population cycles in the various mammals in the North are controlled by rather different factors in the different taxa. However, most proposed hypotheses have not been experimentally tested, so much research remains to be done.

## THE ARCTIC ECOSYSTEM AND FOOD CHAINS

The long-term studies that are essential to the understanding of any ecosystem (Kalff, 1970) have now been undertaken in the North over the past 40 years. They show that although the arctic ecosystem may be relatively stable and have certain resilience (Bliss, 1977), major interference with the food chain or interruptions in energy flow can have serious consequences. While the primary producers and the whole decomposer component on land appears to be rather stable and conservative in growth and development, there are certain critical times of year for vertebrate herbivores and carnivores when the food supply or habitat can be rapidly altered.

Figure 1 summarizes the major food chains and energy flows to marine mammals in arctic marine waters, with the polar bear as the top predator. The interrelationships are clear. Figure 2 presents a similar summary for the major food chains and energy flows in the terrestrial tundra habitat. The terrestrial ecosystem is largely a detritus system in which solar radiation → plants → decomposers and organic matter storage is the main pathway; herbivores and carnivores form a small biomass and energy flow component (Bliss, 1977).

## CONCLUSION

While most of the objectives outlined in the early 1950s have been achieved and we now know much more about plants, terrestrial arthropods, freshwater ecology, marine ecology and terrestrial vertebrates, it is not these new discoveries that are the main accomplishment. Instead, the real triumph of the research has been the discovery of how the organisms fit together in the natural ecosystem; the five fields of investigation considered in this paper should no longer be considered independently.

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