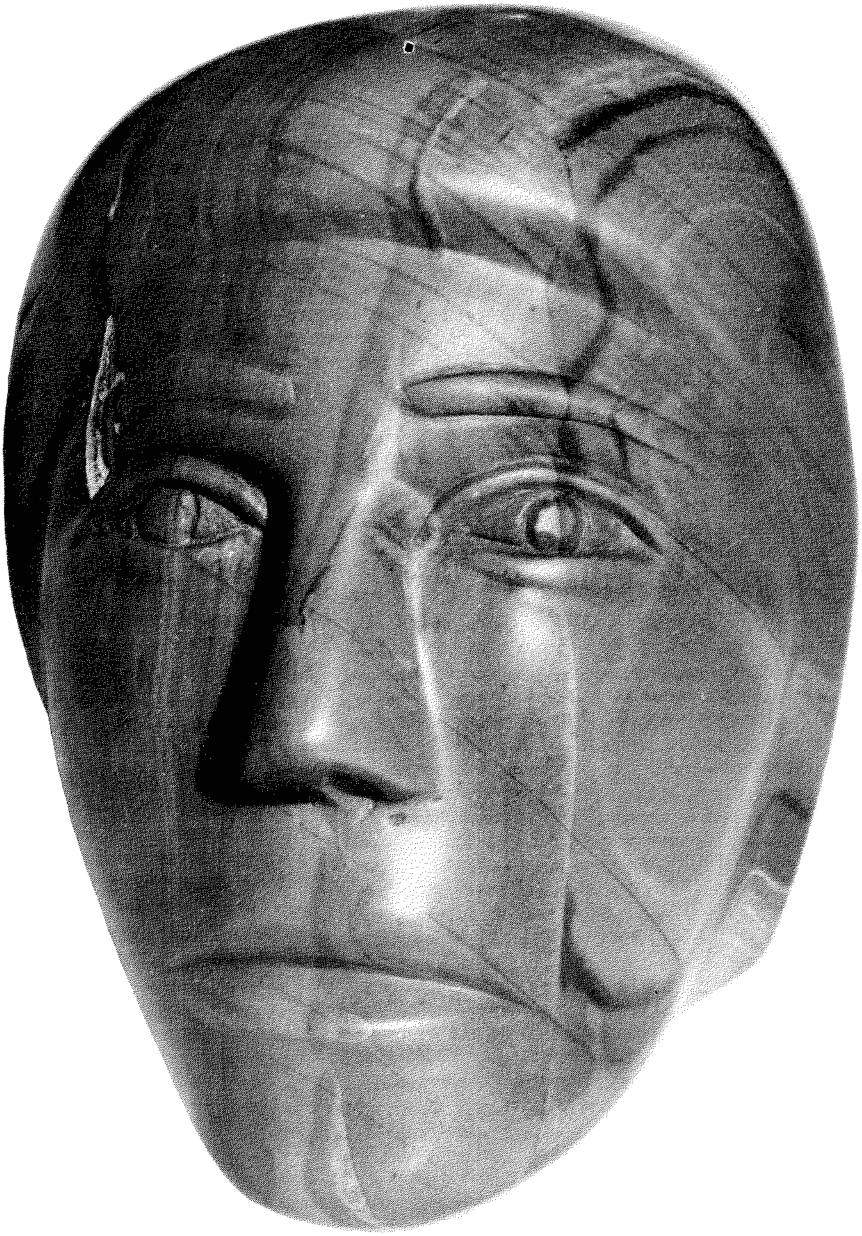

Soapstone carving by Martha of Arctic Bay, Northwest Territories.
Courtesy of J. Graham Cogley. Photograph by Robert Bignell.

Stability and Fragility in Arctic Ecosystems[1]

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Four years ago (Dunbar 1968) I proposed that the instability of arctic ecosystems in terms of the oscillation of the populations of their constituent species, which was itself a result of ecosystem simplicity, must be dangerous to the systems themselves leading perhaps to their extinction, at least to their local extinction. Therefore we should expect evolutionary adaptation of the ecosystem leading to its greater diversity and hence greater stability. I suggested that this would set up selection in two conflicting directions: toward adaptation to the highly oscillating arctic environment (characteristic of most high latitude habitats), which would favour the development of simple systems of low diversity; and toward greater stability, which would favour the development of higher diversity.

This argument needs qualification and greater precision. Northern forests, and the tundra vegetation itself, appear to be rather stable in their natural state, and arctic lakes seem to have reached a remarkable stability in spite of low system diversity. The definition of stability is important. In the particular study quoted stability was defined as the continued existence of the system without significant oscillation in the total mass of living material or in population numbers of the species which form the communities contained in the system. This definition does not adequately take into account the ability of the system to adjust to perturbation, obviously an important point in a naturally oscillating environment. One definition which does emphasize the power of the system to recover from stress is expressed by Conrad (1971) as follows: "I shall assume that the stability of the ecosystem increases as the number of essentially similar states which it can assume increases, i.e. as its ensemble of functionally equivalent states increases . . . This increases the system's resistance to perturbation. Perturbing influences of the environment will alter the state of the ecosystem. If these alterations make no essential difference, the ecosystem is by definition more stable."

This is not the definition adopted by Benninghof (1968) who uses "stability" in the literal sense of "not changing", and points out the danger of such a condition: "The stable system (as in the low latitudes), when confronted with a sudden and extreme shift in environmental conditions, may not be able to adapt or migrate in sufficient time and thus becomes extinct. On the other hand, the strongly oscillating system stands a good chance of finding itself in harmony, even pre-adapted, to the new environmental condition" (Benninghof 1968); the point being that regulatory mechanisms need oscillation, or "error", in order to function.

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[1]Slightly modified version of a paper read at the AAAS Meeting in Washington, December 1972.

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The relation between stability (by any current definition) and diversity has recently become controversial. Mathematical ecologists find that they are unable to demonstrate a necessary connection between the two phenomena in mathematical terms, and if they finally fail to do so then we are left with the choice of accepting that decision or going on without them. Mathematics, after all, are open to much the same semantic difficulties as ordinary language is, since we begin by defining our mathematical symbols in words, and conclude by putting the mathematical results back into words. In pragmatic terms, there are no doubt different kinds of diversity, and the important thing is the pattern of energy flow through the system. In that case a system which channels all the energy between plants and carnivores through one key link, or through a very few herbivores with different predators depending upon them, must be considered to be vulnerable, prima facie, for if that link disappears there is bound to be serious dislocation. This is precisely what happens on the arctic tundra, and yet the system as a whole survives. The answer to this riddle may lie simply in the very large spatial scale involved. Lemmings, in years of low population, virtually become extinct within quite large areas; if they do disappear completely within any region, then their population must obviously be reseeded from outside the area of extinction, and the temporary balance is restored. On the large geographic scale, therefore, the system is stable in the sense that it survives, in spite of great instability on the smaller scale.

This oscillation of the lemming populations constitutes a very considerable "stress" upon the ecosystem, and it is a natural stress entirely independent of human activity. To quote from a position paper recently sent to the Stockholm Conference on the Human Environment by the Arctic Institute of North America (AINA 1972): "This suggests that the system is much tougher than is popularly supposed, and it is as yet an open question whether oil development could do more than the system itself does in its natural oscillation. Certainly there is very little chance of the extinction of the lemmings, so long as they have free range over very extensive territories".

One source of strength, then, of arctic systems is their very large spatial scale, which provides for the mending, or reestablishment, of regions of perturbation or distress. It follows, of course, that to reduce the areas available for system development may be hazardous, but such spatial restriction is less likely to happen in the arctic tundra, or in the subarctic forest, than in many smaller-scale systems in lower latitudes. It is unlikely to happen, that is, under normal present-day conditions, but in the past such restriction has undoubtedly occurred during glacial periods, and the restriction of habitat area is probably one important factor in the extinction of northern animals, especially herbivores and especially mammals, during such periods. Even today it might well occur on islands so that lemmings, for instance, might be intermittent on certain islands. There are at present no lemmings on Coats Island, the Ottawa Islands or the Sleeper Islands in Hudson Bay, and no lemmings or mice on the Twin Islands in James Bay (T. H. Manning, personal communication). There are lemmings on the Belcher Islands.

Arctic ecosystems must have space. They must also have time. Metabolic rates of arctic poikilotherms are often regulated with respect to temperature, that is, the metabolism/temperature curves are shifted to the left, toward the low temperature end of the horizontal axis, when compared with similar organisms in temperate or tropical environments. If they were not, life in Arctic environments would be impossible to sustain. This has been elaborately documented (for a summary, see Dunbar 1968, and note also certain exceptions recently published, in which metabolism is not regulated with respect to temperature, such as in *Mysis relicta* (Lasenby and Langford 1972)). Growth rates of arctic poikilotherms are normally not so regulated, or much less so. Low growth rates are in fact the energy price that is exacted for the regulation of the metabolism. In special circumstances, where the evolutionary advantage is great, growth rates may also be regulated, as in the case of larval forms of certain benthonic invertebrates in which the larval life must be completed before the brief period of phytoplankton bloom is over, but such regulation is rare. The female arctic char, for instance, in the Frobisher Bay region of Baffin Island, takes twelve years to reach maturity, and after that first maturity normally spawns only every second or third year (Grainger 1953). Trees in the subarctic forest may take a century to achieve a diameter of four inches at breast height. Large lake trout in northern lakes may be up to forty years old. These slow growth rates obviously introduce a vulnerability into the system, especially where the activities of man in the north are concerned. It is worth noting here that slow growth rates, leading to longevity, are normally cited as conferring stability, in the "little change" or "non-oscillation" sense, upon the ecosystem. High growth rates and short life-spans foster the development of oscillation in the tundra (lemming) community, and it has recently been shown that the tropical marine planktonic systems, also characterized by high turnover and rapid growth, which hitherto have been considered to be rather stable, non-oscillating systems, do in fact exhibit quite significant oscillation (Steven and Glombitza 1972). Clearly slow turnover systems are the more vulnerable to perturbation. If an arctic lake full of char or lake trout is fished out in a season or two, which has happened many times, the damage is either permanent or will take many years to repair; the same principle applies to subarctic forests.

Lakes, especially small lakes, in the Arctic, are probably the most vulnerable part of the landscape, except perhaps to controlled eutrophication. Again, the spatial scale is important. Many of them harbour only one species of herbivore (a copepod crustacean), and one species of primary carnivore, usually a Mysid or an Amphipod. These are analogous to the lemming of the tundra, but without the protection of large geographic scale. They represent extreme cases of ecosystem simplicity, in which the removal of one species means ecological disaster. Copepods in small lakes are more vulnerable than lemmings on the barren grounds. In fact, owing to the slow growth rates and long life spans of arctic fishes, lake ecosystems approach the non-oscillation stability of the tropical rain forest, in spite of the low diversity and the oligotrophic condition.

Arctic lakes are young, poor in nutrients, and most of them are therefore oligotrophic. The low nutrient capital invites experimentation in fertilization; in fact, up to a carefully controlled point, the dangers of eutrophication in the Arctic are less than elsewhere.

Thus we have reached the preliminary, and obvious, conclusion that the definition of "stability" is important. A second conclusion must be that "no oscillation" stability (definition 1) and extreme oscillation are both hazardous states in terms of the survival of the system, and that one defence against extreme oscillation is large spatial scale. Selection should operate in the direction of the middle road, that is, toward stability in the "recovery from perturbation" sense of the word (definition 2). The goal is the achievement of sufficient diversity to avoid the hazard of channeling too large a proportion of the energy through single trophic links, together with the retention of sufficient oscillation, or "error", to preserve elasticity and the ability to recover equilibrium. Fragility is thus defined as the state of inability to recover, the state in which perturbation leads to disintegration of the system.

The confusion caused by the haphazard use of these two definitions of stability has been pointed out by Margalef (1968), who relates the two types of stability to the constancy, or predictability, of the environment. The "definition 1" stability achieves a steady state under constant conditions; "definition 2" stability gives greater resistance to changes that are external to the biotic system. Margalef also points out that in the latter type, "resistance is paid for through a higher energy flow and a smaller number of interacting elements." The production/biomass ratio is thus involved, the ratio being higher in the second type of stability. This question has also been discussed by Dunbar (1972); it follows from the argument that the tendency to increase the information content of the system, leading to stability type 1, as in the tropical rain forest, is advantageous only in the absence of serious perturbation or environmental change. Gómez-Pompa *et al.* (1972) have recently brought this point home in their description of the great vulnerability of the rain forest to the predatory activities of industrial man, a matter which lies very close to the subject of this present paper. These authors also point out the importance of geographic scale. The rain forest has adjusted successfully in the past to the small-scale primitive agriculture of native peoples, but is destroyed by modern methods. To quote from their paper: "We cannot overstress the importance of the space factor in these considerations, because it makes an enormous difference if we use or destroy thousands of square kilometres or if we destroy one or two".

While on the subject of the definition of stability I should add yet a third type of stability which is different but related, and which can add to the confusion. This is the vertical stability in aquatic environments, a consequence of the density stratification in the water column. Upon this stability, or the lack of it, depends very largely the productivity of the water, so that the production/biomass ratio is also involved. The term "stable tropics" can thus mean two things — the rain forest type of stability and the physical condition of the sea. It may not appear likely that this should lead to confusion, since the environments are quite different, but experience shows that it does.

The strategy of the evolution of arctic ecosystems has two sides to it, as I have already indicated. One reflects the necessity to adapt to an environment which, either in terms of climate (physical environment) or in terms of food supply (biotic environment), or both, oscillates with large amplitude on the annual time-scale. The other is the evolution towards greater diversity which would dampen population oscillations on a time-scale greater than the annual. The first process seems to be well advanced, and demands few species and large numbers of individuals (see Dunbar 1968); the second, which is to some extent in conflict with the first, is still, in my view, in an early phase of the process of development toward greater stability (type 2). In parenthesis, it should be pointed out that the northern environments oscillate also on a much larger time-scale still: that of the amplitude of climatic cyclical changes; to this oscillation the biotic system responds by migration, by geographic shift, as is demonstrated for example in the recent changes in the marine populations in West Greenland waters, involving cod, halibut, etc., (in fact the system as a whole), and very probably including the Atlantic salmon as well.

The popular reputation for fragility which the Arctic has achieved in the daily, weekly, and monthly press appears to be based entirely upon the damage that heavy vehicles and miscellaneous engineering activities can wreak on permafrost terrain, on the tundra. This is a very specialized and local sort of fragility, but where such damage has occurred the effects are spectacular enough to cause widespread horror and alarm, reactions which are quickly recorded and amplified by the "news media". Once the active layer of the tundra, the layer of soil and vegetation which freezes and thaws seasonally, is removed or seriously damaged, the frozen ground below begins to melt, and the ditch so produced will continue to deepen and widen for several years; may in fact never heal. This is now a well-known phenomenon, and suitable precautions are now taken in the running of seismic lines, in building and other industrial operations, to avoid it. If they are not taken, they can be enforced by appropriate legislation.

This "thermokarst" effect, as it is called, is one form of environmental damage that is peculiar to the Arctic. In many ways it is analogous to the effects of strip-mining. There are very few others that are special to the Arctic; the effect of wood-cutting and overfishing of lakes, a consequence of slow growth, is no doubt another, and possibly special attention should be paid to oil in arctic seas.

Not much is known about the behaviour of the various grades of industrial oil in sea water of arctic temperatures, and indeed this is an area urgently needing research. A large oil spill in the Arctic would undoubtedly be very messy, and not easy to get rid of. The facilities available under special mobilization at Chedabucto Bay in February 1970 would not be available at random points in the North. It is apparently possible to burn off some types of oil on ice surfaces, but a large spill would spread under the ice, be contained by ice, mix with the water, and according to one authority could form a layer of oil emulsion up to 12 inches thick. Mammals, and more especially birds, would be very badly hit in the regions of such spills. The effects on the plankton are simply not known, nor is there any information as yet on the key problem, namely the rate at which bacterial degradation of oil at arctic temperatures would proceed. If the bacteria involved obey the common rule of cold-water poikilotherms of adapting their metabolism with respect to temperature (that is, shifting the Q-10 relation to the left or toward the lower temperature condition) then the rate might be the same as for temperate regions. But this is a point requiring research and I believe some work is now being done on it.

The dangers of other pollutants, such as pesticides, heavy metals, radioactive substances, and so on, have no special reference to the North but exist everywhere, although in the case of pesticides the concept of the "rule of the cold wall" should be mentioned, according to which pesticides tend to concentrate in high latitudes, both because of the condensation effect and because of the assumed low rates of degradation. The significance of this effect still has to be established. Concentrations of pesticides in herrings, for example, are reported to be significantly higher in the Gulf of Bothnia than in the Baltic proper, and pesticides appear to be accumulated in snow during the winter.

To return to the ecosystems themselves: There has been much discussion in the literature of the difference between high and low latitude environments in the imposition, on the biotic phase, of intense physical stresses (high latitudes) and intense biotic stresses (low latitudes). I have never been very impressed by this argument, because the biota in all regions is obviously adapted to its own normal environment. This is surely axiomatic; the native is most comfortable in his natural habitat. And on the biotic side, the mayhem that concentrated amphipod populations in arctic and subarctic seas can stir up constitutes, I would imagine, as stressful a situation as the close quasi-urban life of the jungle. Both concepts are subjective, and whereas I agree with Benninghof (1968) that animal and plant species are often separable into what he has called "multiversant" and "pauciversant" species according to the breadth of the spectrum of conditions they can deal with, it seems to me that this dichotomy has more to do with the maturity of the system and the subdivision of niches than with physical or biotic stress. I agree also with Benninghof, however, that an oscillating system, whatever the causes of its existence may be, is in a sense "pre-adapted", to use another doubtful term, to changing and changeable environmental conditions; and that this is a strength rather than a weakness of arctic ecosystems, always with the reservation, made above, that extreme oscillations of extremely simple systems are dangerous unless they are buffered by large geographic scale.

Marine ecosystems in the Arctic (and Antarctic) call for further consideration, but I think it is too early in the history of research into them to draw conclusions about their state of evolution or their resilience. One thing is clear — it would be difficult to find a more stable or more predictable environment than the intermediate and deep waters of the Arctic Ocean, in which the system diversity is not large. But on the question of its evolutionary history and its state of stability as an ecosystem we have very little information.

SUMMARY

The conclusions reached in this paper, concerning the "Fragile Arctic" are the following:

1) Two definitions of ecological stability are in use, and it is essential to keep them separate and explicitly stated. "Type-1 stability" is the condition of non-oscillation, or nearly non-oscillation and steady state found in certain

tropical situations, the result of continued evolution toward greater economy of energy and involving high information content and low production/biomass ratio. This type of stability is highly vulnerable to serious perturbation, to which it cannot adapt. Such systems may thus be called "fragile" and they are found in the tropics and perhaps in certain parts of high latitude systems, such as lakes, subarctic forests and perhaps the tundra vegetation itself. "Type-2 stability" is the condition of ability to absorb serious perturbation and return to a stable state, usually the *status quo ante*. This involves system oscillation, smaller information content, higher production/biomass ratios, and lesser economy of energy use. This type is found in mid and high latitudes, in which the physical environment itself oscillates considerably.

2) In tundra environments, extreme ecosystem simplicity in the animal communities leads to extreme oscillation, and it is suggested that such oscillations can be tolerated only if the geographic scale is large, which it is in the Arctic.
3) "Thermokarst", or damage to tundra terrain by damage to, or removal of, the active layer, is a serious hazard which is well understood and can be easily avoided. It is upon this that the "fragile Arctic" reputation is founded.
4) Oil in arctic sea water constitutes a serious hazard, probably more serious than in warmer waters.

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