THE PROCESS OF COLONIZATION IN ANTARCTIC TERRESTRIAL AND FRESHWATER ECOSYSTEMS

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Abstract: Severe and depauperate ecosystems provide excellent sites for studies of colonization. Energy and resource limitations act as effective filters to establishment and development of communities. Propagule availability must be considered from both local and long-distance sources with consequent effects on dispersion and viability. Predominant emphasis on asexual reproduction in many groups imposes a further limitation on populations at the genetic level. At present little is known of the frequency and success of individual colonization events in any Antarctic site but we can begin to identify critical factors in the process. This paper examines the key components of colonization, identifies areas in which research is lacking, and proposes some novel approaches for tackling this important issue.

1. Introduction

The continent of Antarctica has been isolated from other landmasses for over 25 million years. Further, with the exception of isolated nunataks which may have offered sanctuary to small relict populations (KAPPEN and STRAKA, 1988), most of Antarctica must have been swept clean of flora and fauna during the periods of climatic cooling and major glacial advances around 32–5 m y B.P. The modern Antarctic biota remains markedly depauperate and composed largely of immigrant species. Such a combination of circumstances is perhaps unique, on a continental scale, and makes Antarctica an especially suitable place to study colonization.

Despite this, colonization research in Antarctica has, with a few exceptions, been very limited and mainly confined to small geographical areas. Where broader-scale work has been undertaken it has been poorly coordinated. What little data is available has been mainly derived from survey work (much of the aerobiological studies *e.g.,* RUDOLPH, 1970) or locality-specific investigations of environmental constraints on development as reviewed in LEWIS SMITH (1984). Only comparatively recently have attempts been made to consider colonization as a process and to take a broader approach to the subject (WALTON, 1990).

Colonization is clearly a complex and diverse process but it can be simplified by considering the four essential components, namely:

   a) A viable propagule,
   b) A suitable transport mechanism,
   c) An acceptable new micro-habitat,
   d) Successful growth and reproduction.

Much of the research undertaken in Antarctica has, to date, been concerned with components (b) and (d) and comparatively little attention has been given to either the propagule or the nature of the potential new micro-habitat. This paper aims to examine all four components in broad terms but highlighting specific areas where more detailed research would be beneficial.

2. What Are the Attributes of a Colonizer?

A colonizing propagule is likely to be adapted for efficient dispersal. Without this strategy it is unlikely to have a high probability of reaching any new suitable habitat from its existing site, in suitable physiological condition to exploit the opportunity.

A second general attribute of successful colonizers is phenotypic flexibility, the ability not only to exist but to grow and develop in a range of habitats. This flexibility (or "weediness") attribute allows an organism to rapidly respond to the onset of favourable conditions within its habitat and perhaps produce a resistant propagule should unfavourable conditions develop. Brief periods in which free water is available characterize both hot and cold deserts and such environments tend to favour those species best able to respond rapidly to ephemeral resources.

Thirdly, a colonizer should be able to "reproduce" freely under suitable environmental conditions. There is little point in getting to a suitable site for growth if the organism is then unable to reproduce in this environment. The term "reproduce" is used here to describe any means (vegetative, asexual, or sexual) of increasing population numbers.

3. General Attributes in an Antarctic Context

These three general attributes can be readily identified in the Antarctic biota. The diversity of incoming propagules appears to be greater than the species diversity present in maritime Antarctic terrestrial and freshwater environments. This suggests that many of the incoming propagules have the wrong attributes to be successful colonizers. Winged insects are a prime example in that the most-frequented route to Antarctica for potential colonizers, namely by air currents, is barred to winged insects as they cannot fly in sub-zero temperatures (Wellington, 1945). Recent reports of colonization by winged insects have shown this to be very localized and can be largely attributed to humans, a growing alternative form of transport (Block et al., 1984). Flowering plants are another example, normally being unable to set seed at the low temperatures prevailing in most Antarctic and sub-Antarctic summers (Edwards, 1974).

On a global scale, filamentous green algae are good examples of "weedy" plants, and in the Antarctic they require only the presence of free water to establish in a range of situations from damp ground to permanently ice-covered lakes (Broady, 1989; Hawes, 1988). Cyanobacteria are a further example, but, unlike the green algae which tend to be classic annual "weeds", the cyanobacteria are usually perennial, capable of surviving dessication, and some are broadly resistant to freezing. The freezing and dessication-resistant forms (e.g. Phormidium) are therefore particularly important fell-field organisms (Davey, 1988), whilst freeze-sensitive cyanobacteria (e.g. Tolypothrix)

dominate the deep-water benthos of clear lakes (PRIDDLE and HEYWOOD, 1980).

Filamentous green algae do not tolerate freezing or dessication particularly well and for environments subject to freezing (fellfield soils and streams) only a tiny fraction of the cells in any one filament will survive the winter (HAWES, 1989, 1990). These few cells, however, develop quickly once free water is again available. It is an intriguing point, worthy of further study, that within apparently genetically identical cells of a green algal filament, some cells should have greater freezing resistance than others.

In the Antarctic context, the need to reproduce freely is generally met in plants by asexual propagules often produced by fragmentation of adult plants, despite its inevitable potential genetic consequences for new populations of founder effects and genetic drift. In the case of the ubiquitous filamentous green algae, fragmentation is the only form of reproduction ever observed (HAWES, 1989). Asexual propagules are, however, common amongst other lower plants (LEWIS SMITH, 1984). Where vascular plant sexual reproduction occurs in sub-Antarctic sites, it may be spread over two growing seasons to optimize use of the summer period (WALTON, 1982). In cryptograms there is a clear response on a latitudinal gradient northwards with increasing production of sporophytes and ascospores as the climate becomes less severe.

Although many instances of parthenogenesis have been recorded, sexual reproduction may be favored by Antarctic invertebrates. However, it seems that the terrestrial forms may vary the number of breeding events per annum depending on the severity of the habitat (USHER et al., 1989). In the freshwater environment, the physical climate is comparatively stable but food supply and quality can vary considerably. This is particularly evident in the freshwater copepod, Pseudoboeckella poppei, which shows markedly different strategies (in both male and female) of lipid storage (Fig. 1) and egg and sperm
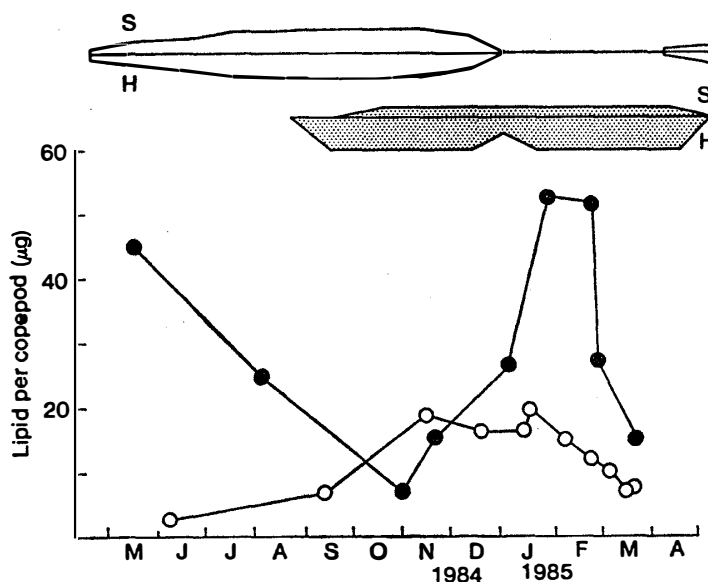

Fig. 1. Seasonal variation in lipid content of male Pseudoboeckella poppei sampled from nutrient-poor Sombre Lake (○) and nutrient-enriched Heywood Lake (●). The clear polygon shows duration of ice cover and the stippled areas show the approximate duration and size of phytoplankton development in Sombre Lake (S) and Heywood Lake (H) (after CLARKE et al., 1989).

production in lakes only 150 m apart but contrasting in the quantity and quality of substrate available (CLARKE et al., 1989). This would seem a clear example of a highly flexible strategy for colonization and undoubtedly contributes to the widespread occurrence of *Pseudoboeckella* in lakes and pools throughout the maritime Antarctic (HEYWOOD, 1977).

In addition to the above general attributes, successful colonization of Antarctica inevitably also requires tolerance of low temperatures. Most organisms appear to be psychrotolerant, *i.e.*, capable of growth at 0°C but with an optimum above 20°C (MORITA, 1975). Relatively few true microbial psychrophiles (incapable of growth at >20°C) occur in Antarctica, even in those environments that have permanently low temperatures, *e.g.*, marine and freshwater. This perhaps reflects the fact that most colonizers of the maritime Antarctic, being immigrants, are unlikely to have pre-adapted such a restrictive feature. The few studies undertaken on true Antarctic psychrophiles (see the review by HERBERT, 1981) indicate that changes in specific enzymes confer a distinct competitive edge at low temperatures, but where temperature fluctuates this advantage disappears and the more flexible psychrotrophs come to dominate (ELLIS-EVANS, 1981).

Psychrotolerance need not necessarily mean slow activity at low temperatures. Recent work on protozoa by HUGHES and SMITH (1989) indicates faster growth at low temperatures by an Antarctic strain than by its temperate equivalent and WILLOUGHBY (1971) has shown much the same for aquatic phycomycetes. Very little work has as yet been undertaken on the physiological basis of psychrotolerance in plants or microbes though it is an essential prerequisite for understanding successful colonization.

The invertebrate fauna are all small and thus able to crawl into small cracks and crevices which afford some protection from severe environmental fluctuations. Many of the simpler genera (tardigrades, rotifers) survive in the water film that is maintained on the surfaces of mosses and, in particular, algae. Nevertheless, successful Antarctic invertebrates also seem to possess various physiological features that allow them to tolerate freezing and desiccation (BLOCK, 1984). These characteristics, such as supercooling and the presence of antifreezes, appear to be distinct from the mechanisms utilized by plants and are present to varying degrees in a variety of temperate invertebrate species, suggesting a degree of pre-adaptation in some species. Such pre-adaptation is poorly documented for Antarctic plants and microbes, and is less readily demonstrated, though it is almost certainly present to varying degrees.

4. Transport to Antarctica

Whilst transport *via* drifting wood or other plant material has been recorded in the literature for the sub-Antarctic region (VAN ZINDEREN BAKKER, 1971), propagules arrive in the Antarctic almost exclusively *via* dispersal by wind or animals (including, more recently, humans). The Southern Ocean represents a major barrier to colonization and early studies concluded that the isolation factor was the major constraint (HEYWOOD, 1977). In terms of severity of habitat, there is no strong latitudinal gradient for freshwater environments as there is for terrestrial environments, and yet, even taking account of varying sampling intensity, there is a definite decline in the species diversity of lakes

with increasing distance from other continents. Recent studies (KAPPEN and STRAKA, 1988) suggest that proximity to temperate regions (South America) and more frequently favourable air currents explain the greater species diversity in modern propagule banks of the maritime Antarctic compared to continental Antarctica. They propose that not only is endemism more likely in the latter region but that the cryptogams of most of the Antarctic continent may represent a mainly relictual flora which survived in ice-free refugia. This is largely at variance with LINDSAY's (1977) view of lichen biogeography but in apparent agreement with recent work by FILSON (1982). Recent evidence that lichen species, normally found as endolithic within the Beacon Sandstone, also occur epilithically suggests that other species may have survived the last glaciation by retreating inside the rock, only emerging as conditions improved (VESTAL, 1990).

Data collected from constant pressure ballons (see Fig. 2) show that an air mass can pass over southern South America and over all the sub-Antarctic islands as well as parts of the continent in as little as 8 days, challenging the idea that aerial transport to Antarctica must necessarily involve long time intervals and that the nearest continent has to be the source of propagules. Having said this, it is nevertheless true that the flora of the nearest continent invariably dominates the propagule bank of any given Antarctic region. Generalized conclusions on transport processes based on nearest-
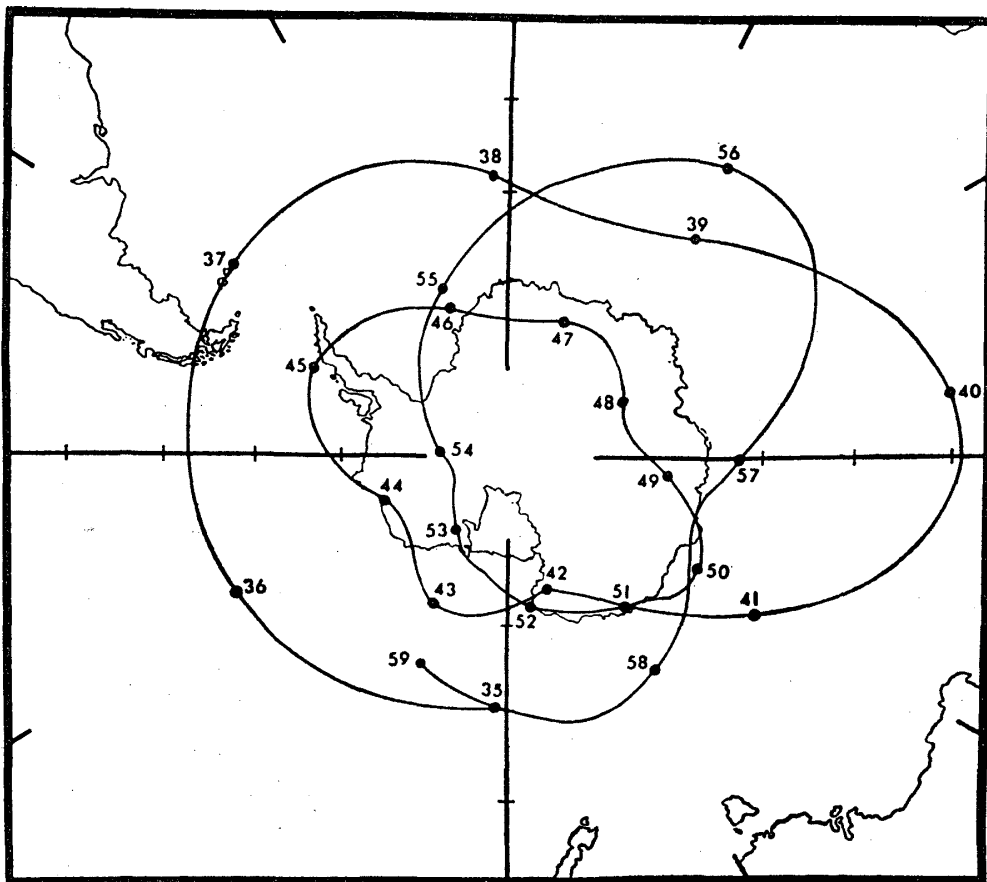

Fig. 2. Track of a GHOST ballon floating at 10–12 km around Antarctica (after SOLOT, 1967). The numbers indicate days 35–59 since release.

neighbour geography or mean weather patterns may be misleading. More attention needs to be given to the details of air movements between continents and, for that matter, between sub-Antarctic refugia. It may well be that it is the occasional contrary wind pattern, or occasional major storm, that brings an influx of biogenic material whilst prevailing winds bring little or none. We need far more detailed information on the wind patterns linking temperate and polar environments and on their composition and numbers of propagules within air masses around Antarctica. We will also need to establish if there is a seasonal component to propagule transport, although this sampling will be logistically difficult. Early work on propagule transport done with land-based samplers suggests that bryophytes in particular can be prolific local spore producers at some locations within the subantarctic and maritime Antarctic (R. I. LEWIS SMITH, pers. commun.), obscuring the long-distance component. Aerobiological sampling requires co-ordinated airborne and land-based sampling in a variety of geographical areas if we are to build up a valid picture of dispersal patterns.

Wind dispersal has been found, from studies elsewhere, to account for most of the smaller propagules whilst birds and, more recently, humans are the likely mechanism for dispersal of the larger propagules (TAYLOR, 1954; CAMERON et al., 1977). There is little evidence that invertebrates are involved in extreme long distance transport, but they clearly could be important vectors of bacteria, viruses, protozoa, etc., carried both internally and externally. Once such propagules have reached a suitable site, subsequent local dispersal may be by wind, other animals, or water.

Historical materials have revealed that a great variety of exotic propagules have rained onto Antarctica over thousands of years (LEWIS SMITH, 1984). Many have proved viable in culture conditions (LEWIS SMITH and COUPAR, 1986) but presumably these conditions of higher temperatures and abundant moisture are rarely experienced, even in the comparatively mild maritime Antarctic region. Where they do occur, around fumaroles or in geothermally warmed ground, a quite different community develops to that on the surrounding fellfield (LONGTON and HOLDGATE, 1979). What is clear from propagule bank studies is that there has been little or no significant change in the composition of Antarctic biota since the retreat of the ice sheets and onset of the Holocene.

Whilst we now have some idea of the meteorological conditions appertaining to Antarctica and can therefore begin to propose origins and destinations for dispersed material, we still know almost nothing about either the variety or rate of arrival of potential colonizers from outside to the various parts of Antarctica. Very few investigations of historical propagule banks have been undertaken and, as mentioned above, recent deposition studies have tended to be too localized to differentiate long distance from local transport. The result has been a series of often contradictory and largely qualitative studies.

Large numbers of propagules may reach Antarctica and both transplant experiments and accidental introductions have shown that a far greater range of species can survive the Antarctic environment than are currently considered native. It therefore seems that whilst transfer to Antarctica is difficult, finding a suitable habitat and becoming established is even more problematic. This is illustrated by the marked change in species diversity as one moves to higher latitudes (Fig. 3).
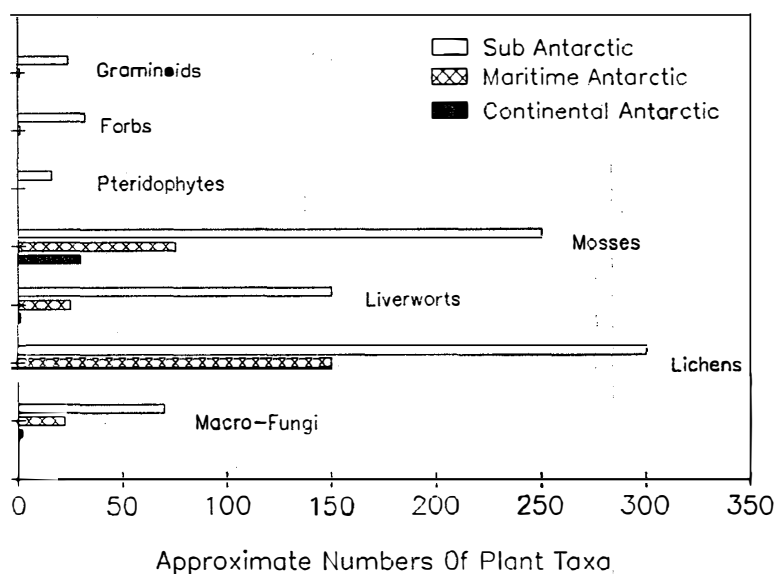
Fig. 3. Distribution of native plant taxa in the maritime and continental
Antarctic and sub-Antarctic regions (after LEWIS SMITH, 1984).

5. Attributes of Antarctic Habitats

What features of a new site make it attractive or otherwise to a potential colonizer? The substrate could be smooth rock, or volcanic debris, fragmented rock with deep cracks and fissures, or inorganic fine soil material. Clearly the scale of the site must be considered at the scale of the propagules. Using television image analysis, WYNN-WILLIAMS (1990) has found evidence to suggest that rough surface texture promotes primary colonization and that the size of particles in a matrix or the spaces between particles seems to influence the species composition of the primary community established.

The micro-climate of the micro-habitat is also important. Is the site subject to freeze-thaw or wet-dry cycles and how often do the cycles occur? Is the site subject to temperatures lethal to the propagule and, for photoautotrophs, is the site shaded? Further, is there a distinct seasonality (*e.g.*, Fig. 4) or are changes in environmental conditions largely unpredictable? There has been very little attempt to obtain realistic measures of such factors at the micro-habitat level, not least because of instrumentation problems. Without data on this it will be practically impossible to relate experimental and laboratory studies to the colonization process in the field. The pioneering work of McKay and FRIEDMANN (1985) in instrumenting endolithic habitats, however, shows that, although difficult, climatic description at this scale is possible.

Even if substrate type, surface texture and micro-climate are all suitable, nutrient availability may prove to be inadequate. Work by TEARLE (1987) and L. G. GREENFIELD (in prep.) indicate that, even in fellfield mineral soils, substantial quantities of assimilable organics occur locally as a result of freeze-thaw damage to the isolated patches of plant material (algae, moss) present. Studies of microbial populations in frost polygons revealed a rapid response by bacteria to availability of organic compounds, following freeze-thaw, and an equally rapid development of protozoa to graze on the bacteria (SMITH and TEARLE, 1985). These populations are characterized by virtual single-species
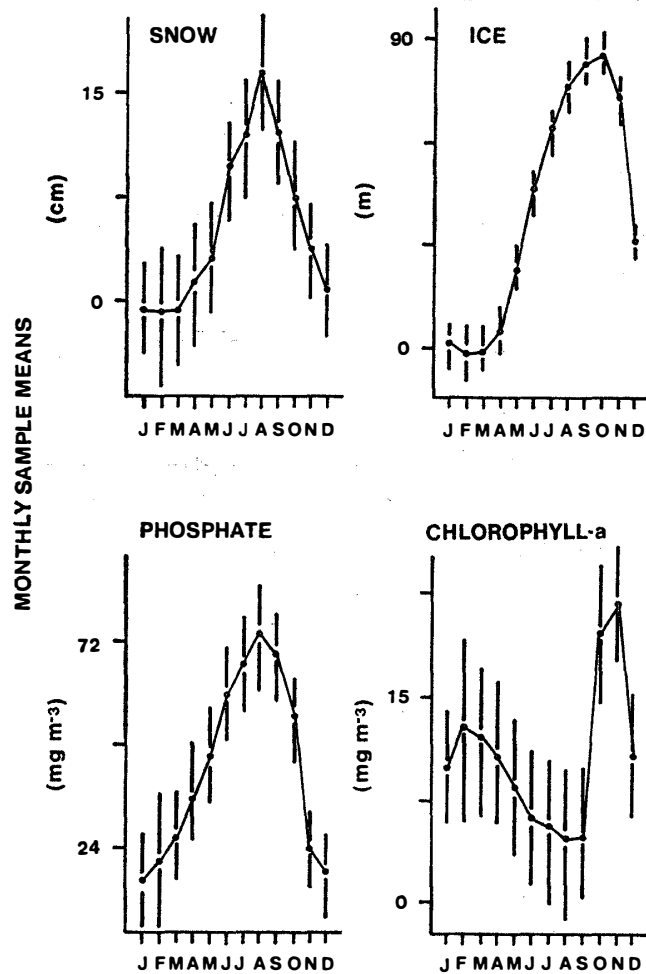
Fig. 4.   Example of a predictable seasonal pattern of change in habitat
favourableness—a freshwater lake at Signy Island.   Ice and
snow show distinct patterns which influence light availability
and nutrient accumulation and hence the seasonal pattern of
phytoplankton development.   Each data point is the mean
value for a given month of 16 years sampling at mid-depth in
Heywood Lake.   Vertical bars represent standard deviations
around the mean (after ELLIS-EVANS, 1990).

dominance, an indication of the high adversity rating of such habitats, which are common in the ice-free regions of Antarctica.

If a favourable micro-habitat does exist for a potential colonizer, what are the chances of it finding such a habitat? Does it occur extensively in a given area as is the case for the volcanic debris on Deception Island and, if not, does the habitat, small as it may be (for example moss cushions or grass clumps in a fellfield area, see Fig. 5), occur frequently enough to provide a resonable likelihood of encounter for the propagule? At the present time we lack a rationale for investigating these questions, but possibly the ideas of SOUTHWOOD (1977) offer a way forward. He proposed that favourability matrices for reproductive success could be defined on the basis of habitat factors defined in temporal and spatial modes. WALTON (1990) has suggested how these

Fig. 5.   An example of the occasional occurrence of a favourable habitat (the grass, Deschampsia
antarctica) as small patches (islands) within a large, unfavourable habitat (e.g. raised
beach, fellfield).

matrices could be applied equally well to dispersal and colonization, providing a model
approach to predict the likelihood of a propagule finding a favourable micro-habitat.
However, such modelling will require both descriptive and quantitative data for both
habitats and propagules that we do not yet possess.

The development of a general framework such as this takes time and needs a great
deal of data to validate it.   Useful preliminary descriptive work towards this could be
undertaken now.   Micro-habitat environmental parameters must be considered in inter-
active terms to establish if, when, and for how long favourable conditions can exist at
a given site.   Recent work by BÖLTER et al. (1989) on the micro-climate of a rock with
respect to lichen physiology suggests that, using this approach, periods of favourable
conditions are far more restricted than simpler studies previously suggested.   Work such
as this could be usefully directed at the limitations of the micro-habitat for colonizers
rather than at those limiting growth in established organisms, as in the BÖLTER et al.
(1989) study.   It will also be necessary to ensure that the micro-climate data covers all
seasonal changes to put any short-term studies into the proper environmental context.

6.   The Keys to Successful Colonization

It seems clear that for a species to colonize a new Antarctic site its propagule must
find a favourable habitat.   Unlike vertebrates and many invertebrates, whose offspring
can select the site they wish to colonize, Antarctic terrestrial and freshwater organisms
are dispersed entirely at the behest of physical factors outside their control.   Thus the

arrival of a viable propagule at a favourable site is a truly stochastic event. The chances of reaching a favourable site are not especially high although probably better in the maritime than in continental Antarctica. Many organisms increase their chances by producing very large numbers of propagules. Others produce fewer but longer-lived propagules which can, on arrival, wait for favourable conditions to develop. It must be mentioned, however, that certain unusual habitats, for example, fumaroles, have very special conditions and a very low frequency of occurrence and yet such sites are invariably colonized by immigrants. Possibly the time factor is important here.

The keys to successful colonization are the matching of propagule and micro-site, not only to allow the propagule to "germinate" but also to allow the organism to grow and establish. Without this latter phase, colonization cannot be said to have occurred.

Table 1 summarizes some of the key features for both propagule and habitat. Different constraints apply once the propagule has begun to grow. One feature so far not mentioned in this paper is competition for available micro-habitats. All available evidence so far suggests that, at the level of initial colonization, it is the scarcity of viable propagules that limits the rate, not competition within a micro-site.

Table 1.   Key features of propagules and habitats relevant to the colonization process.

Propagule features	Colonization features
When are they produced?	How big are the micro-habitats?
How many are produced?	How frequent are the micro-habitats?
Are they suitable for wind transport?	How long is each micro-habitat available?
Are they suitable for bird transport?	How frequently is each micro-habitat available?
How long are they viable?	How frequently is an available micro-habitat available?
How far is it to the new habitat?	How frequently do propagules arrive at an available and suitable micro-habitat?
How often do suitable transport conditions occur?	How often does colonization occur?

7.   Colonization and Climatic Change

Experimental work on the colonization of fellfields using plastic cloches and nutrient additions demonstrates that simple manipulations of micro-climate can result in markedly increased community development relative to controls (LEWIS SMITH, 1990). However, such experiments need to be repeated under more defined micro-climatic conditions to establish what factors or interaction of factors causes the observed development. Such data could form the basis of mathematical descriptions of the process of propagule development for subsequent application to the real environment.

As we are currently in a period of significant interglacial warming, glacial retreat is continually exposing more potential sites for colonization. Given the postulated major changes in CO_2, temperature, and UV levels, it would seem particularly important to establish some of the basic data on dispersal and diversity of colonization of selected study sites. Experimental manipulation of these habitats could give data on the possible long-term effects of climatic change and lead to useful predictive models. Validation of these models will need carefully planned long-term monitoring of environmental and ecological change.

8. BIOTAS Initiative

Clearly, it is not practicable for any one national group to tackle the whole subject of colonization alone. In particular, establishing the composition of the propagule rain and the spatial/temporal aspects of transport to the Antarctic is undoubtedly best undertaken at an international level. For this reason the BIOTAS programme would seem an appropriate vehicle for an international coordinated study of colonization and to this end a planning workshop for interested parties will be held in Cambridge in October 1989. This should lead to agreement on standardized equipment and experimental designs, overcoming a major weakness in earlier studies and establishing at the outset a clear framework for synthesizing the data.

Acknowledgments

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