Environmental Change: Possible Consequences for the Life Histories of Antarctic Terrestrial Biota

Peter Convey*

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, United Kingdom

ABSTRACT. Awareness of environmental change in Antarctica centres on two areas of potentially great biological significance - the consequences of a clearly demonstrated trend of regional climate warming, and those related to the recent and large seasonal increase in ultra-violet radiation levels experienced as a result of stratospheric ozone depletion. As yet, little hard evidence exists as to the effects of these changes on the depauperate terrestrial biota of the region. This paper considers the likely effects of environmental change on the major groups of maritime Antarctic terrestrial biota. Life history strategy studies have demonstrated great flexibility in areas such as growth and reproductive rates, and the use of physiological mechanisms to allow tolerance of (extreme) cold and desiccation. Increased plant growth and colonisation rates, combined with evidence of increasing length of summer seasons, and physiological data indicating longer periods of water availability to terrestrial invertebrates, are used to suggest that a general shortening of life cycle duration will be expected. Parallel studies in the Arctic suggest massive population increases of some species are likely, which may destabilize simple polar food webs. Conversely, high spring UV loads may act to reduce colonization opportunities, habitat area and growing season for some plants and microbiota.

Key Words: Antarctica, environmental change, life history, terrestrial biota

Introduction

Antarctica, by virtue of its geographical isolation and atmospheric circulation patterns, has provided some of the most significant evidence relevant to discussions of global environmental change. This has included the discovery of the stratospheric ozone "hole" (Farman *et al.* 1985), the correlation of climate and chemical composition of the atmosphere as revealed by deep ice cores (Lorius *et al.* 1985), and recent rapid break-up of Antarctic Peninsula ice shelves (Doake and Vaughan 1991; Vaughan and Doake 1996).

Antarctica has experienced climate change in the past. On a geological timescale, the formation of the present continental ice cap commenced after the separation of Antarctica from the rest of Gondwana during the Miocene. Antarctica supported rich plant and animal communities during the Palaeocene and Eocene, now preserved as fossils, which were obliterated by expansion of the continental ice cap. Separate ice caps also destroyed terrestrial habitats on maritime and sub-Antarctic island groups (including South Shetland and South Orkney Islands, South Georgia, Heard Island) (Sugden and Clapperton 1977). Only a tiny remnant portion of the pre-glaciation fauna is now thought to survive as relict species on inland nunataks of the Antarctic continent (Marshall and Pugh 1996). The majority of the current biota must have arrived as post-glacial colonists, as no appropriate refugia are likely to have remained, at least on the Antarctic continent and islands of the maritime Antarctic. Even as ice retreated following Pleistocene glacial maxima, fluctuations in climate and ice extent were experienced

*corresponding author (peter.convey@bas.ac.uk)

on shorter (decades to millennia) timescales (Clapperton and Sugden 1982, 1988; Smith 1990). Although large in scale, it is important to note that these fluctuations occurred more than an order of magnitude more slowly than rates of temperature change predicted by current global circulation models. Both the magnitude and rate of change are significant to biological communities (Huntley 1991).

A common feature of global circulation models is a prediction that any warming effects will be most pronounced in high latitude regions (Maxwell and Barrie 1989; Maxwell 1992; Meehl and Washington 1990; Mitchell et al. 1990). Despite this recognition of the importance of Antarctic regions in providing geophysical evidence to help understand the processes of climate change, the terrestrial biological consequences of global change in Antarctica are only now beginning to attract serious attention, with limited data obtained or published as yet (see Kennedy 1995a). Antarctic terrestrial ecosystems have not attracted research interest on account of their low diversity and biomass, intrinsic sparse distribution and low abundance, and lack of economic incentives (Kennedy 1995a; Roberts 1989; Smith and Steenkamp 1990). The potential deleterious effects of increasing levels of ultra-violet (UV) radiation are thought to be a threat to all Antarctic ecosystems (Wynn-Williams 1994), while terrestrial systems "may be the first to be affected by increased UV-B radiation caused by ozone depletion" (Voytek 1990).

In this paper I consider the limited evidence currently available for the effects of environmental change on Antarctic terrestrial organisms. Applying knowledge of the life history strategies of Antarctic terrestrial invertebrates and plants, combined with parallel studies of Arctic species, I attempt to make broad predictions of the likely effects of environmental changes on life histories of specific groups, and consider possible wider-scale implications for food web interactions and ecosystem processes.

Antarctic Terrestrial Environment

Terrestrial habitats and communities

Antarctica is a continent of extremes. Considerably

larger than Australia (14.4 x 10⁶ km²), over 99% of the continental area is permanently covered by ice or snow, with an average depth of about 2 km, and maximum of over 4 km (Fox and Cooper 1994). It has the highest average altitude of any continent, and is the windiest and coldest. Much of the continental area is classified as a cold desert, with very low precipitation rates (Walton 1984; Sømme 1995). Areas south of the Antarctic Circle experience periods of up to several months of permanent darkness during winter, alternating with continuous exposure to solar radiation during summer.

Terrestrial environments in Antarctica are conventionally considered in three separate biogeographical zones (continental, maritime, sub-Antarctic; boundaries indicated by Smith (1984a) and Longton (1988)). These zones have distinct but overlapping terrestrial fauna and flora (Smith 1984a; Longton 1988; Greenslade 1995; Marshall and Pugh 1996), also falling along a temperature gradient (Holdgate 1977; Walton 1984; Convey 1996a, 1997). Antarctic terrestrial communities are species-poor relative to those found in similar habitats and latitudes in the Arctic (Sømme 1979; Danks 1990; Convey and Block 1996). This is largely a function of their extreme isolation. Intentional transplant experiments (e.g. Edwards 1980), an increasing number of natural and human-mediated introductions (e.g. Block et al. 1984; Chown and Language 1994; Pugh 1994; Smith 1996), and the presence of exotic cryptogamic plants and microbes on volcanically-warmed ground (Longton and Holdgate 1979; Smith 1984b; Bargagli et al. 1996; Broady et al. 1987) have demonstrated that there is a potentially large pool of species with appropriate ecological and physiological characteristics to allow survival should colonization opportunities occur.

Antarctic terrestrial communities, with the exception of snow algae, and the microbial communities found in glacial cryoconite holes (Broady 1989; Broady and Kibblewhite 1991; Vincent 1988; Wharton et al. 1981), are limited to areas permanently or seasonally free of ice and snow. Arctic and alpine cryoconite faunas also include tardigrades (e.g. Dastych 1993), but no published records exist

from Antarctic cryoconites. The fauna (Block 1984) is dominated by micro-arthropods (Acari and Collembola), with higher insects (particularly Coleoptera, Diptera) only forming a significant component in the sub-Antarctic. More extreme habitats of the maritime and, especially, continental Antarctic may harbour only microscopic invertebrates such as nematodes and tardigrades (Dastych 1984; Dastych and Harris 1994; Freckman and Virginia 1991, 1997; Powers *et al.* 1995; Schwarz *et al.* 1993). The vast majority of the fauna of continental and maritime zones is composed of mixed algivores, microbivores and detritivores, with no obligate herbivores. Terrestrial predators exist in the form of mesostigmatid and prostigmatid mites (*Gamasellus* and *Rhagidia* spp.), which take mostly Collembola (Lister *et al.* 1987, 1988) and have a minimal impact on their prey populations, and probably nematophagous Collembola (*Friesia* spp.). Despite the increase in importance of phanerogams on sub-Antarctic islands, most invertebrates remain in the detritivore category.

True non-marine vertebrates (dependent on the terrestrial or freshwater environments for resources other than breeding or moult sites) comprise a few species of duck and passerine bird found only in the sub-Antarctic, where they have very limited impact. However, the influence of marine birds and seals, particularly in terms of nutrient input and physical trampling, may be very important in both the development and destruction of certain terrestrial ecosystems (Smith 1988a; Ryan and Watkins 1989).

Likewise, floral diversity and community complexity decrease down the gradient from sub- to continental Antarctic (Smith 1984a; Longton 1988). Thus, phanerogams (flowering plants) form a major component of low altitude ecosystems of the sub-Antarctic, but contribute only two localized species in the maritime zone, and are not present in the continental zone. Algal and cryptogamic (bryophyte and lichen) communities reach a level of importance rarely found elsewhere in all three zones. In the extreme conditions of the McMurdo Dry Valleys of Victoria Land, microbes and lichens retreat to an endolithic habitat (Friedmann 1982), existing in the interstitial spaces between crystals of porous rocks such as sandstone.

A range of inter-related environmental stresses will be experienced by any terrestrial Antarctic organism. These, and their potential influence on life history attributes, have been discussed by Convey (1996b, 1997), and are summarized here, in order to provide a baseline from which the potential effects of environmental change may be considered.

Temperature

In contrast to the thermally-stable Antarctic marine environment, terrestrial habitats experience widely varying temperature regimes both on short-term (daily) and longer-term (seasonal/annual) time-scales. Daily ranges of 25-50°C are not unusual in vegetation and on rock surfaces, with seasonal variation in the range 50-100°C (refs. in Convey 1996b). Absolute values experienced are also of great significance to physiology and life history. Air temperature ranges vary between zones, being less extreme in the sub-Antarctic (c. -15 to +20°C (Holdgate 1977)), intermediate in the maritime Antarctic (c. -40 to +20°C (Walton 1982, 1984)) and most severe in the continental Antarctic (c. -40 to +5°C at coastal sites, c. -89 to -10°C inland (Phillpot 1985; Jones and Limbert 1987; Smith 1993a)). Importantly, microhabitat temperatures (at a scale relevant to terrestrial biota) are often higher than those of the air due to absorption of solar radiation, and buffered from extreme lows by seasonal snow cover (e.g. Davey *et al.* 1992; Kennedy 1995b). However, certain habitats such as exposed rock surfaces and ablation zones will track winter air temperatures very closely.

Freeze-thaw events

Closely related to temperature variation, the formation of ice crystals poses dangers to living tissue, and has led to the use of a wide range of physiological and behavioural cold tolerance strategies by Antarctic invertebrates (see reviews by Block 1990; Cannon and Block 1988; Convey 1996b). In practical terms, use of these strategies means that, in their normal habitats, Antarctic terrestrial invertebrates can survive the range of temperatures experienced,

either avoiding or controlling the formation of ice crystals within the body so as to avoid damage. The potential frequency of and danger from microhabitat freeze-thaw events may be minor in the sub-Antarctic (Convey 1996a), and limited in moister habitats of the maritime Antarctic (Davey *et al.* 1992), but may be of daily occurrence in drier sites and in much of the continental Antarctic (Kappen 1985; Longton 1988; Smith 1988b). Freeze-thaw events also influence the formation and stability of soils via frost-shattering and cryoturbation (Chambers 1967; Hall and Walton 1992), processes which may limit the survival and establishment of colonizing propagules (Smith 1993; Wynn-Williams 1993).

Water availability

Where free water potentially occurs, its availability to biota is again closely related to patterns of environmental temperature. However, much of the continental Antarctic is a cold desert, with very low precipitation levels. Even in the moister summer climate of the maritime Antarctic, periods of low precipitation (or snow melt) are experienced which, combined with the poor water-holding capacity of many substrates, leads to water stress for both plants and animals (Block and Harrisson 1995; Longton 1988). During the maritime Antarctic winter terrestrial organisms are inactive and surrounded by ice crystals. In these circumstances desiccation becomes a purely physical process with no biological control, a function of vapour pressure difference between body fluids and surrounding external ice (Worland 1996). Water availabiltiy is recognized as one of the most important limits on the distribution of terrestrial organisms in Antarctica (Janetschek 1970; Kennedy 1993). Again, physiological responses to water stress (which are closely related to those allowing tolerance of cold) are well-developed in Antarctic terrestrial invertebrates (Block 1996; Ring and Danks 1994).

Nutrient availability

Levels of soluble nutrients are related to the availability of water and therefore, at least in part a func-

tion of temperature. Nutrients are generally thought to be superabundant for Antarctic invertebrate communities (mostly or completely decomposer-based) (e.g. Block 1985; Convey 1997), although it should be noted that very few data exist. Conflicting evidence exists from Antarctic plant and microbial communities - the cyanobacterium *Phormidium* sp. shows physiological and behavioural responses to nitrate and phosphate shortage (Gapp 1995), and nitrate shortage may limit the growth of terrestrial algae in some circumstances (Davey and Rothery 1992), but other studies of stream and pond algae give no evidence of nutrient limitation (Davey 1993a, b). More widely, plant tolerance of nutrient stress is closely related to tolerance of other environmental stresses (Grime 1988, 1991). The distribution of many plant species and occasionally communities (most noticeably calcicole species) is closely-related to underlying soil/rock chemistry and nutrient status (Smith 1972).

Light availability

Levels of incident solar radiation vary on a seasonal timescale (modulated by meteorological effects, especially cloud cover). At latitudes south of the Antarctic Circle the sun remains below the horizon for a period of weeks to months during the winter while, conversely, radiation receipt during summer may be higher than experienced in temperate or tropical regions (Gates 1972). Levels of visible light may have little direct effect on Antarctic terrestrial invertebrates, as they will be protected in their typical interstitial microhabitat. However, the indirect effect on microhabitat temperatures may be of great significance. The dominant cryptogamic plant (Callaghan *et al.* 1992) and cyanobacterial communities are generally adapted to function efficiently at low light intensities, and some show photoinhibition at the light intensities experienced during the Antarctic summer (Adamson *et al.* 1988a; Kappen *et al.* 1989; Post *et al.* 1990). The potential consequences of seasonal increase in receipt of ultra-violet radiation, as a consequence of the spring depletion of stratospheric ozone, are discussed below.

These stresses will often act in combination, and

will be of varying importance to each situation considered. The level of pressure exerted also varies widely (and unpredicatably) between years. With specific relevance to life history strategies, their joint action will lead to three general consequences (Convey 1997):

" - short, cold summers will impose limits on physiology, growth and reproduction

- windows for colonization and establishment will be rare and short-lived

- the long winter may lead to a requirement to budget for significant physiological costs".

Life history strategies

Recent studies of the life history strategies of Antarctic terrestrial invertebrates and plants have identified little evidence of evolved adaptation to local environmental pressures (Convey 1996b, 1997). In general, life histories are described well by the features of adversity (A-) selection (Convey 1996b; Kennedy 1995a; strategies after Greenslade 1983; Southwood 1977), with long life cycles, slow growth rates, low reproductive output, low dispersal ability and high investment in survival adaptations. Although all Antarctic species examined have features which allow survival of the likely stresses experienced, individually their possession is a plesiotypic character of the taxonomic group concerned. The ancestral possession of several such features is likely to have aided colonizing species pass selective filters imposed by the Antarctic environment (Convey 1997), as terrestrial habitats became available after the recent retreat of ice sheets following Pleistocene glacial maxima.

Very few invertebrates of the maritime and continental Antarctic zones show a phenology dependent on season. Indeed, although the life cycle of most involves repeated overwintering in several life stages (e.g. Burn 1984; Convey 1994a; Marshall and Convey, in press), there is little evidence of true diapause mediated by environmental cues (Convey 1996a, b). The lack of a true diapause has also been noted in Arctic and alpine invertebrates (Sømme 1995), and is thought to be due to disadvantages consequential on any incorrect "switching on or off"

of the diapause state (for a different reason, *viz.* reduced seasonality due to limited temperature variation on isolated oceanic islands, many invertebrates of the sub-Antarctic also show little seasonal structure to their life cycle). Antarctic invertebrates have essentially free-running life cycles with asynchronous population development and extensive overlap of generations. This situation is parallelled by soil-dwelling (detritivorous) arthopods of the Arctic (Addison 1977, 1981; Sømme and Block 1991), but contrasts with the life cycles of many Arctic above-ground herbivores, which are closely synchronized with the phenology of their host plants (Bale *et al.* 1997). Bryophytes and lichens are usually very long-lived, reproducing vegetatively throughout their life. In many cases spores or sexual propagules are not produced.

The typical free-running life cycle of Antarctic terrestrial invertebrates introduces a large element of flexibility and opportunism. The thermal constraints of the short, cold summer impose a requirement on most species to overwinter more than once during development. Beyond this constraint, individual organisms can take opportunistic advantage of any periods suitable for feeding, growth or reproduction, while retaining the capability to re-enter a tolerant quiescent state rapidly when needed. Life cycle duration and structure can vary widely, with apparently very little cost to the individual. The degree of variation in environmental conditions experienced throughout an organism's life is far greater (in most cases) than changes predicted by models of global climate change. This may lead to difficulties in identifying reponses of organisms to small but consistent changes, when their physiology and life history are already well-tuned to survive and take advantage of much larger and unpredictable variations.

Environmental Change in Antarctica

Climate warming
There can be little doubt that climatic warming is already tangible in Antarctica (Jones 1990; Kennedy

1995a), although it is not yet clear whether warming trends observed are a consequence of global or regional processes (King 1994). In each of the three biogeographical zones warming trends have been identified over the last 30-50 years. An increase in mean daily temperatures of c. 1°C has been observed on sub-Antarctic Macquarie Island (Adamson et al. 1988b), and recent monthly air temperature observations made during summer on South Georgia (Convey 1996c) were c. 1.4°C above the mean values reported between 1905 and 1973 (Smith and Walton 1975). Similar trends have been reported in the maritime Antarctic from sites on the Antarctic Peninsula (Fowbert and Smith 1994; King 1994; Smith 1994; Stark 1994) and the South Orkney Islands (Smith 1990), and at two coastal stations in the continental Antarctic (Adamson and Adamson 1992). Accepting the level of uncertainty in predictions of the magnitude of climate warming, especially with reference to Antarctica (Kennedy 1995a), the observed data are at least consistent with these predictions (Maxwell and Barrie 1989).

Increased temperature is often associated with more rapid loss of snow or ice cover. In particular, recent well-documented break-up of floating ice shelves along the Antarctic Peninsula (Doake and Vaughan 1991; Vaughan and Doake 1996) has focused attention on large-scale changes expected to be associated with temperature amelioration. However, large-scale loss of coastal ice shelves may be limited initially to the relatively small and thin shelves of the maritime Antarctic. Changes in annual patterns of seawater flux associated with reduced winter sea ice formation may act to thicken the much more extensive ice shelves of the continental Antarctic, and even increase their longevity (Filchner-Ronne Ice Shelf - Nicholls 1997).

On a smaller scale, rapid reduction in area of snow and ice fields has been documented on Signy Island, South Orkney Islands and elsewhere in the maritime Antarctic (Corner and Smith 1973; Fenton 1982; Fowbert and Smith 1994; Smith 1990), with ice margins receding over 100 m and glacier thickness being reduced by 7-8 m over a period of c. 20 y, and total ice area decreasing by 35% over 40 y. The small

increase in mean temperatures observed at Signy Island, probably associated with changes in precipitation, insolation and ablation patterns appears to have been sufficient to alter the mass-balance of the relatively thin Signy Island glaciers and ice cap in favour of rapid retreat. Block & Harrisson (1995) postulate that recent rates of glacial ablation on Signy Island are primarily due to increased wind speed and irradiance, and have led to greater availability of water in terrestrial habitats.

Increasing temperature and life histories

In simple terms, any increase in mean temperature will result in greater total thermal energy being available within an ecosystem. Furthermore, theoretical models suggest that a given level of increase in temperature will have proportionally greater effects on high latitude ecosystems, where growing seasons are short and annual temperature budgets low (Strathdee et al. 1995, and refs. therein; Woodward 1987).

It is likely that any increase in temperature will have an immediate effect on the growth rates of poikilothermic organisms, through Q_{10} effects. Predictably, growth rates of many Antarctic invertebrates increase as culture temperature is increased (e.g. Burn 1982, 1986; Convey 1994b; Nicolai and Droste 1984; Young 1979), as do those of moss shoot fragments and developing propagules (R.I.L. Smith, pers. comm.). Invertebrates also show adaptation to their low-temperature environment, with low optimum temperatures for feeding and growth, and evidence of thermal stress or an inability to complete the life cycle at temperatures above c. 15°C. Low enzyme activation energies and enhanced metabolic rates in response to temperature increase at low positive temperatures are postulated to allow some Antarctic micro-arthropods to take maximum advantage of their current thermal environment (Block 1977, 1979, 1982; Block and Young 1978; Crafford and Chown 1993; Sømme et al. 1989; Young 1979). Such features pre-adapt these species rapidly to take advantage of small thermal increments in their habitats.

Very few pertinent field data are available from

studies of Antarctic invertebrates. Field manipulation experiments at Signy Island (maritime Antarctic) utilising plastic cloches (greenhouses) to mimic temperature increases expected as a result of global warming demonstrated consistently greater microarthropod populations, with the greatest effect (as predicted above) at more extreme sites where thermal amelioration was greatest (Kennedy 1994). Similar large increases in micro-algal and bryophyte populations have also been obtained by the use of passive greenhouses on Antarctic fellfield soils (Smith 1993; Wynn-Williams 1990, 1993, 1996a, b). However, great care must be taken in the interpretation of such experiments, as the greenhouse methodology often affects variables other than temperature, and may cause patterns of temperature variation contradictory to those predicted by climate change models (Kennedy 1995b, c).

If increasing temperature leads to concomitant increases in growth rates, then a shortening of life cycle duration would be predicted for invertebrates with free-running life cycles (i.e. containing no seasonally defined cues, see above). In the short term this has the potential to lead to rapid increases in population. Such a situation has been demonstrated recently in field experiments on the aphid *Acyrthosiphon svalbardicum* on Arctic Svalbard (Strathdee *et al.* 1993). Using a different greenhouse methodology, temperature elevations in the aphid's natural habitat of 2.8°C were achieved, equivalent to an increase in thermal budget over the entire summer period of 215 day degrees (c. 50% of the non-manipulated control). This led to an eleven-fold increase in the number of overwintering eggs, by allowing completion of an extra generation during the summer. Such rapid population increase has serious implications for the food web of which the aphid forms a part. In the short term, increased impact on the host plant (*Dryas octopetala*) is inevitable. However, long term effects are less clear. Resource limitation may stop population growth of the aphid or, alternatively, as yet unquantified responses of natural predators and parasitoids to either the increase in prey population or directly to change in climate may come into play. It is clear that

trophic interactions may be seriously altered, potentially leading to significant changes to the food web. Parallel studies on closely related *Acyrthosiphon* species from lower latitudes in Scandinavia have also confirmed the prediction of proportionately greater effects being observed at more thermally-limited high latitude sites (Strathdee *et al.* 1995).

A recent study of the predatory diving beetle *Lancetes angusticollis* on sub-Antarctic South Georgia has indicated similar potential (Fig. 1; Arnold and Convey, in press). Unusually for an Antarctic invertebrate, this species exhibits a temperature-mediated overwintering state (Nicolai and Droste 1984) and is unable to complete development at water temperatures below 7.5°C. With a thermal constant for development of 380 degree days above this threshold temperature, the beetle has a minimum life cycle duration of two years on South Georgia, as recent summers have provided only c. 170-290 degree days above the threshold. The effective length of the development season (days above the threshold temperature) is currently up to 123 d. An increase in mean summer temperatures of only 1°C (i.e. of the level already experienced in many Antarctic sites) would in some years, therefore, be sufficient to allow development to be completed within a single season, by providing at least a further 123 degree days above the threshold temperature. Again, far-reaching consequences on food web and ecosystem function can be predicted. *Lancetes angusticollis* is one of only two predators present in sub-Antarctic lake ecosystems on South Georgia. Currently, predators are thought to be functionally insignificant in the trophic interactions within these lakes, which therefore consist of two trophic levels (primary producers and unregulated grazers) (Hansson and Tranvik 1996; Tranvik and Hansson 1997). With a potentially large increase in predator population, as would be expected with a switch from a biennial to annual life cycle, a third functionally important trophic link would be introduced to the lake ecosystem (Hansson and Tranvik 1996; Arnold and Convey, in press), with unknown but likely major consequences on interspecific interactions and lake ecology. Lake communities in the maritime and con-
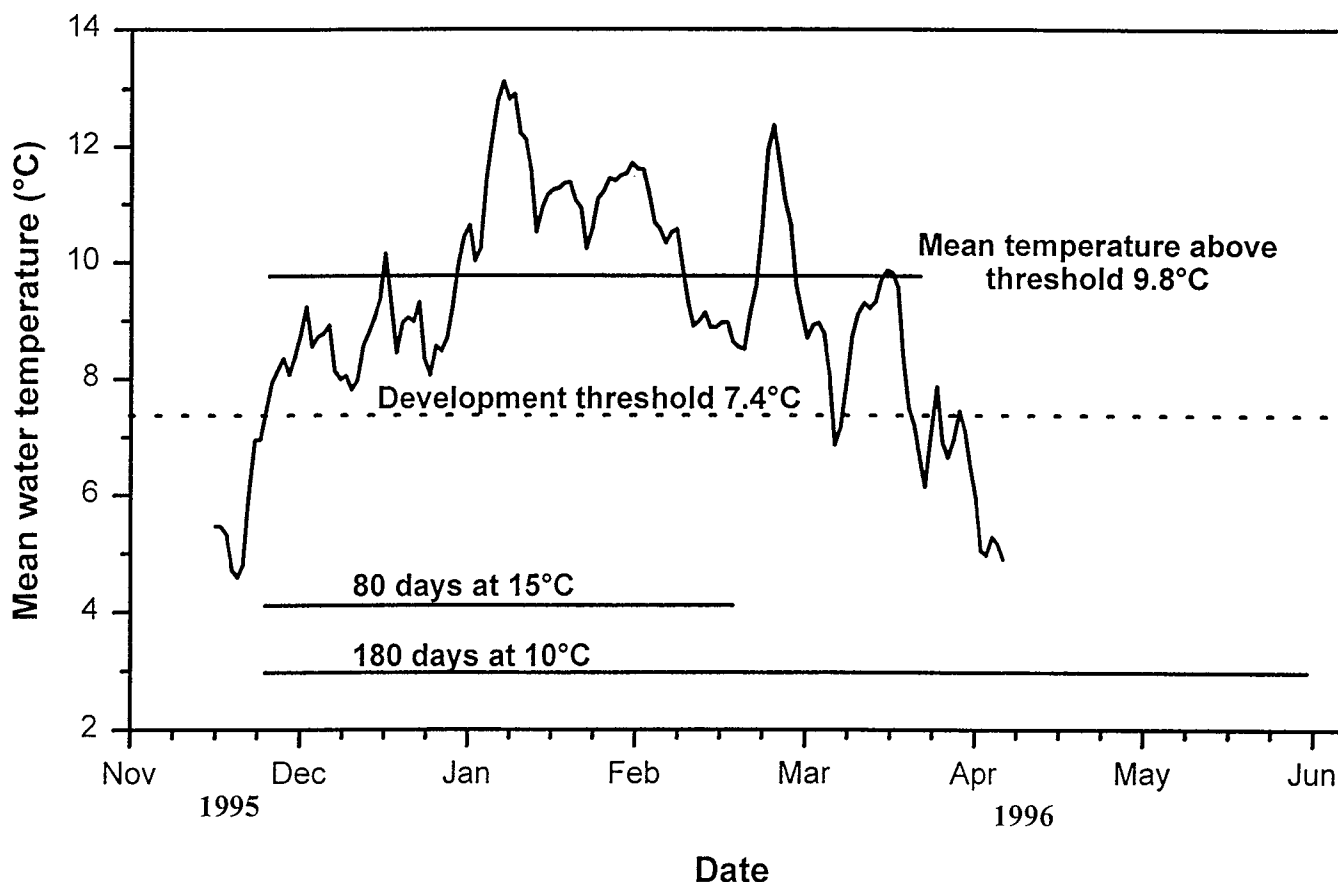
Fig. 1. The potential influence of increasing water temperatures on larval development of the dytiscid water beetle *Lancetes angusticollis* on sub-Antarctic South Georgia. Mean daily water temperature data from the 1995/96 austral summer are presented, with life cycle developmental threshold temperature and the duration of larval development (oviposition to adult emergence) at constant culture temperatures of 10 and 15°C indicated (see Arnold and Convey, in press; Nicolai and Droste 1984).

tinental Antarctic zones are even simpler, characterized by short food chains and dominance of microbes (Ellis-Evans 1996; Laybourn-Parry *et al.* 1996). Any inclusion of higher trophic levels in these lake ecosystems would alter their trophic dynamics drastically.

The flexibility inherent in the life history strategies of many Antarctic terrestrial organisms (Convey 1996b), combined with the "free-running" nature of high latitude detritivore life cycles (Bale *et al.* 1997), means that many species of all major groups represented (invertebrates, plants, microbes) are well-placed to show similar reduction in life cycle duration and increase in population in response to small changes in temperature, well within the predictions of global circulation models. How such immediate life history responses to warming will translate into medium- and long-term

consequences for food web and ecosystem structure and function is unknown.

Colonization

Two consequences of warming processes are likely to have important indirect effects on life histories: the rapid decrease in permanent ice cover exposes new areas of uncolonized ground, while patterns of water availability are likely to change (typically increasing) either as a direct result of ice and snow melt (e.g. Block and Harrisson 1995) or as a result of increased precipitation predicted as a result of global warming (Schlesinger and Mitchell 1987).

Abundant evidence demonstrates the existence of plant propagule banks in Antarctic habitats (Smith and Coupar 1986; Smith 1990, 1991, 1993a; McGraw and Day 1997). Not surprisingly, due to the extreme isolation of these habitats from non-Antarctic

sources of propagules, the majority are thought to be of local origin (e.g. Marshall 1997; Marshall and Convey 1997). However, immigration of exotic propagules undoubtedly occurs (Kappen and Straka 1988; Marshall 1997; Marshall and Chalmers 1997; Smith 1991) encouraged by unusual but recurring weather patterns (Marshall 1996). Communities of exotic bryophytes have developed on volcanically-warmed ground (which is both moist and buffered from low temperatures) in continental Antarctica (Bargagli *et al.* 1996; Broady *et al.* 1987) and in the maritime Antarctic South Shetland (Smith 1984b) and South Sandwich Islands (Longton and Holdgate 1979; Convey and Smith, unpubl.). Records of exotic species on non-heated ground elsewhere in the Antarctic are much more limited. However, at least two bryophytes new to the region and probably of South American origin have been found on recently-exposed ground on Signy Island, South Orkney Islands (Convey and Smith 1993; Smith 1993).

As discussed earlier, many sub-Antarctic and even temperate invertebrate and plant species already possess sufficient physiological and ecological plasticity to allow survival in the more extreme habitats of the maritime and continental Antarctic zones. The only limit to their establishment is appropriate colonization opportunity (Ellis-Evans and Walton 1990). Climate amelioration will serve to increase this pool of potential colonists, while increasing human presence and ease of access is likely to provide a major means of transport (Smith 1996). Initial colonization processes for newly-exposed substrates are stochastically likely to be dominated by species and communities already present locally. However, in the medium to long-term, invasion (either natural or with human assistance) by exotic microbes, bryophytes, lichens and higher plants is inevitable, increasing both species and structural complexity of communities. An analogous process is also predicted within invertebrate communities. This may involve the inclusion of a specifically herbivorous trophic level, concomitant with the increase in importance of phanerogams, with life histories much more closely tied to host phenology than found in the current detritivore-based community

(c.f. Bale *et al.* 1997).

Although most introductions of exotic species so far documented have had little obvious effect on the natural ecosystems involved, a number of exceptions highlight the potential of immigrants to disturb and even destroy pre-existing food webs. Vertebrate introductions (in particular of cats and rodents) have led to extinction of sub-Antarctic ground-nesting birds, while alien herbivores (e.g. rabbits, reindeer, moufflon) have largely restructured ecosystems, favouring the spread and dominance of alien grass species over the native vegetation (Vogel *et al.* 1984; Leader-Williams 1988, and refs. therein). Such introductions of mammals occur only with human assistance. However, their subsequent establishment following introduction is rendered more likely within a scenario of climate amelioration. Furthermore, records of adventitious migratory birds (including Turkey Vulture, Starling, Cattle Egret, Black-necked Swan and various wading birds) are a regular occurrence on sub-Antarctic islands, and occasional in the maritime Antarctic. Establishment of any of these is now a real possibility, and could introduce a new trophic level to existing terrestrial food chains. The impact of an introduced invertebrate predator (the carabid beetle *Trechisibus antarcticus*) on endemic herbivorous beetles has already been demonstrated on sub-Antarctic South Georgia. In the presence of the carabid, herbivore populations are significantly reduced, with evidence of a shift in larval phenology favouring more rapid development to enable avoidance of predation (Ernsting *et al.* 1995). Introduced detritivorous Collembola (*Hypogastrura viatica, H. purpurescens*) are also established on several sub-Antarctic islands, where they have displaced naturally-occurring species and become numerically dominant in many habitats (Deharveng 1981; Deharveng and Travé, 1981; Greenslade 1990).

Water availability

Water availability plays a pivotal role in limiting the distribution of Antarctic terrestrial biota (Janetschek 1970; Kennedy 1993). Fine-scale distributions are obviously closely correlated with sources of water

(e.g. Light and Heywood 1975; Schwarz *et al.* 1992). Changes in water availability will alter the pattern of microbial and plant community development (see flow diagrams in Smith 1990). Increases, in particular, will promote the development of more complex plant communities. Invertebrates, which depend on primary producers for food (often via detritus), are likely to mirror the increase in complexity as the majority of their microhabitats are associated with plant and/or microbial communities. Species which are able to tolerate extreme desiccation are well-represented in Antarctic ecosystems, including cyanobacteria (Davey 1991), lichens and xerophytic mosses (Longton 1988) and microscopic invertebrates (Pickup and Rothery 1991; Sømme and Meier 1995). The Arctic collembolan *Onychiurus arcticus* can survive gradual desiccation and loss of c. 75% of its initial body water content (Worland 1996), but the capabilities of Antarctic micro-arthropods are unknown. Characteristic of all these organisms is a very rapid recovery of water content and return to normal activity when exposed to free water. If environmental change in Antarctica leads to longer periods of water availablility in terrestrial habitats than at present, the consequence could be a further reduction in life cycle duration, by acting additively with the increasing thermal budget discussed above.

Recent evidence suggests that some Antarctic micro-arthropods may exist in a permanent state of water stress (Block and Harrisson 1995) - in a four-year study, the body water content of field-collected springtails (*Cryptopygus antarcticus*) varied seasonally within the range 57-66% of fresh weight, consistently below the 74-85% typical of laboratory cultures, and therefore suggested to be suboptimal. Controlling for seasonal variation, the same study also found a trend of increasing water content over the period, which was correlated with environmental variables resulting in increased rates of glacial melting/ablation, hypothesised to lead to increased water input to the terrestrial habitat. Further analysis of a longer (11 year) dataset obtained at the same site on Signy Island (Convey and Block, unpubl. data) also gives evidence of changing environmental water status (Table 1). These results confirm the sea-

Table 1. Direction of trends in monthly mean water content of the maritime Antarctic springtail, *Cryptopygus antarcticus*, over the period April 1984 to November 1995 (Convey P. and Block W., unpubl. data). Trends each month over the 11 y period (+ve, -ve) are presented as regressions of (1) water content as a proportion of fresh mass (WC/FW) and (2) water content per gram dry mass (g g⁻¹ dry mass) on month of collection. NS = regression not significant. Springtails, n = 10-50 animals per sample (usually 25), were collected each month from the same site on Signy Island, South Orkney Islands; individuals were weighed separately after November 1997, and in groups of 5-10 animals before that date

Month	WC/FW	$g\ g^{-1}$ dry mass
January	NS	NS
February	NS	NS
March	NS	NS
April	(+ve, p = 0.081)	+ve, p = 0.011
May	+ve, p = 0.003	+ve, p = 0.001
June	NS	NS
July	(+ve, p = 0.075)	NS
August	+ve, p = 0.007	+ve, p = 0.003
September	NS	NS
October	NS	NS
November	-ve, p < 0.001	-ve, p < 0.001
December	(-ve, p = 0.098)	NS

sonal pattern of changing water content in *C. antarcticus*. Although no overall trend was found in the longer study, analysis of water content data by collection month showed a striking seasonal pattern. In most winter and summer months, no trend is apparent. However, during early spring and late autumn (August, April, May), significant increasing trends were found, with a decrease during one month in summer (November). Although not offering proof, these observations are consistent with an increase in effective summer length that is expected as a consequence of climate amelioration, which will result in the spring thaw commencing earlier and autumn freeze completing later.

The midsummer reduction in water content is indicative that the direct association of warming, water availability and community complexity is too simplistic (see Kennedy 1995a). Earlier spring melt, or complete loss of permanent snow or ice, may result in water shortage later in the season.

Furthermore, melting of permafrost may increase drainage, and increased numbers of freeze-thaw cycles may promote soil disturbance via cryoturbation. The net effect of these processes would be to limit rather than encourage the development of bryophyte communities (and associated invertebrates) that currently dominate Antarctic vegetation (Kennedy 1995a).

Separately, increased water flow through particular soil substrates may result in more leaching of nutrients. Primary stabilization and colonization of Antarctic soils occurs via the formation of microbial crusts or mats (Wynn-Williams 1993). Gapp (1995) demonstrated that, under conditions of nitrate or phosphate limitation, the common Antarctic cyanobacterium *Phormidium* sp. showed reduced ability to attach to hydrophobic substrates. This result implies that increased throughflow of water and associated leaching of nutrients may actually reduce the rate of stabilization of some Antarctic soils, hence retarding community development.

Ultra-violet radiation

The discovery of the Antarctic ozone "hole" in 1985 (Farman *et al.* 1985) led rapidly to realisation that increased levels of ultra-violet (UV) radiation would reach the earth's surface. Ozone depletion (from > 300 Dobson Units (DU) to < 100 DU) occurs early in the austral spring (September), with the hole persisting until November/December (Frederick and Lubin 1994; Kerr 1994; Voytek 1990). As the efficiency of UV absorption by ozone varies with wavelength, increases in irradiance at ground level vary widely (Frederick and Snell 1988), between factors of 2 and 14. The biological damage caused by UV radiation is also a function of wavelength (Dahlback *et al.* 1989), while susceptibility to damage varies between species (Vincent and Quesada 1994). Finally, the UV dose received at any location is modulated by meteorological conditions (e.g. cloud cover), and the pattern of movement of the ozone hole (Gautier *et al.* 1994).

The potential biochemical consequences of exposure to UV radiation (especially shorter wavelength UV-B, 280-315 nm) are well-documented, and the general subject is not considered further here. Enhanced UV radiation is considered as a potential threat to all Antarctic ecosystems (Wynn-Williams 1994), with terrestrial ecosystems likely to be the first to be affected (Voytek 1990). As recognized by Voytek (1990) and Kennedy (1995a), little research activity has been directed towards evaluating the biological consequences of global change (including increasing UV radiation) on Antarctic ecosystems. Both authors draw general conclusions that community composition, life history characteristics and trophic dynamics are expected to change.

Direct effects of increased UV radiation are predicted to be limited to primary colonizers of the surface layers of Antarctic soils (algae, bacteria, cyanobacteria), along with the bryophyte communities that develop subsequently, and lichens that colonize bare rock surfaces directly. Associated detritivorous invertebrate communities are likely to receive little direct exposure, spending most or all of their life cycles within the soil or vegetation matrix. However, a suggestive increase in the proportion of individuals of the maritime Antarctic mite *Magellozetes antarcticus* carrying "faulty" patterns of setation at sites on Alexander Island (exposed to ozone depletion for longer periods than more northerly sites in the zone) has been noted (J. Stary, pers. comm.).

Micro-organisms can use four lines of defence against UV exposure (Vincent and Quesada 1994) - avoidance, screening, quenching and repair. Many cyanobacteria synthesize pigments capable of absorbing harmful UV radiation (Ehling-Schulz *et al.* 1997; Garcia-Pichel and Castenholz 1991, 1993). In *Nostoc commune*, the pigment scytonemin is responsible for UV-A absorption, while exposure to UV-B induces production of mycosporine-like amino acids (MAA's), a specific UV-B sunscreen (Ehling-Schulz *et al.* 1997). Scytonemin is produced by many cyanobacteria and is contained within an extracellular mucilage sheath. This sheath is believed to play several overlapping roles of ecological relevance, including attachment to substrate, modulation of environmental stress, protection against desiccation, concentration of nutrients and prevention of UV

damage, and represents a major investment of energy and biochemical resources (Hill and Potts 1994; Potts 1994). In the extreme, the level of investment in sheath production may result in growth cessation. Scytonemin and other pigments such as flavonoids, carotenoids and MAA's are known to be present in cyanobacteria-dominated microbial mats in Antarctica (Vincent et al. 1993). However, it is not yet known whether Antarctic species actively produce additional pigment in response to increased UV radiation levels. Any such diversion of resources will reduce that available for other processes such as growth and reproduction. One possible consequence of a switch in resource use will, therefore, be to reduce the rate at which soil stabilisation (and hence colonisation by macroscopic plants) can occur.

Protective pigments also are found in algae and bryophytes (Markham et al. 1990; Post 1990; Post and Larkum 1993; Webby et al. 1996). However, evidence for their role in Antarctic species is fragmentary at best. The foliose alga Prasiola crispa contains high levels of a single UV-absorbing pigment, varying in a manner consistent with the level of UV exposure; however, experimental exposure to enhanced UV-B resulted in a decrease in chlorophyll content without changing the ratio of UV-absorbing pigments to chlorophyll (Post and Larkum 1993), suggesting that the exposure was stressful and the alga had little ability to respond. A somewhat speculative analysis of flavonoid content of preserved bryophyte herbarium specimens collected in the Ross Sea area between 1957 and 1989 (Markham et al. 1990), revealed a trend approximating to measured changes in ozone levels at the South Pole.

In the absence of data, it can be speculated that two likely components of the response to increasing UV levels will be important within the life history strategies of Antarctic microorganisms and plants. Any associated increase in production of protective pigments will divert resources away from other processes. Repair processes following damage to photosynthetic or genetic apparatus will similarly divert resources, in addition to a direct reduction in primary production (the latter effect has been demonstrated in marine, but not terrestrial, ecosys-

tems (Holm-Hansen et al. 1993)). As the period of increased UV exposure is currently limited to the spring and early summer, it may result in an effective reduction of growing season length (thereby acting in a contradictory manner to the effects of climate amelioration and water availability discussed above). In an extreme scenario, seasonally-increased UV radiation may be sufficient to prevent colonization or continued existence of certain species at a given site.

With the exception of exposed lichens and the near-surface biota of ablation areas such as the Dry Valleys, many communities may be partially protected from the effects of increased UV exposure for some or all of the duration of ozone depletion. Throughout the maritime and continental Antarctic zones, many terrestrial and freshwater communities do not emerge from winter snow or ice cover until late November or December. Although visible and ultraviolet radiation can penetrate through snow (indeed snow cover can effectively form a "greenhouse", with significant photosynthetic activity possible well before completion of snow melt (Longton 1988), no data exist on the magnitude of exposure of terrestrial biota, and hence the potential of snow cover to give protection.

Conclusions

Environmental change is a reality in Antarctic terrestrial environments. Factors of immediate relevance to life history strategies of the biota include increasing mean temperatures, with associated changes in water availability due to ice recession and altered precipitation patterns, and seasonally-increased levels of UV radiation caused by spring ozone hole formation.

The terrestrial environment already provides an inter-related range of stresses to the resident biota. The level of variation in most of these stresses is considerably greater than the predicted change resulting from global circulation models. These changes lie comfortably within the physiological and life history characteristics of the resident biota.

Life history strategies of Antarctic terrestrial biota are generally "free-running", characterized by a large degree of flexibility, lack of environmentally-cued diapause and lack of synchronization (both within species and with season). These features allow opportunistic advantage to be taken of ameliorated environmental conditions.

Resident species are therefore well-placed to respond rapidly to climate warming. In the short-term, parallel changes to those found experimentally in the Arctic are predicted. Rapid population growth will occur, leading to changes in trophic interactions, which may involve inclusion of new (higher) trophic levels and the destabilisation of current food webs. Community structure will increase in complexity where plant communities develop further than at present. The precise trajectory of change is unknown, depending on the balance of interactions between primary producers, detritivores, herbivores and carnivores, and the response of any/all of these to climate change. Virtually no data are available in these areas.

Correlated changes in water availability may act additively with warming effects, allowing further decrease in life cycle duration and contributing to population increase and community development. Conversely, through increased drainage, leaching, cryoturbation and/or desiccation, the potential of terrestrial habitats for colonization or community development may decrease. Again, the precise consequences remain to be quantified at any specific site.

In the middle- to long-term, climate amelioration will provide greater opportunity for colonisation by exotic taxa, by increasing both the area available for colonization and the duration of field conditions suitable to permit establishment. Human intervention is likely to increase the rate of arrival of exotic species, but is not the only available route. The trajectory of community development following colonisation of exotic species is not predictable in detail. However, increasing trophic complexity is again likely, with expansion of phanerogam communities, the arrival of obligate herbivores with life cycles synchronized with season and host plant phe-

nology, and increasing importance of higher trophic levels in food chain regulation. Populations of some resident species may be driven extinct by this process.

Deleterious effects of increased UV-B receipt during spring and early summer are likely to have a greater effect on microbial communities (especially primary colonizing micro-algal phototrophs), along with exposed bryophytes and lichens, than on soil-dwelling invertebrates. Survival of this stress will necessitate significant additional diversion of resources to the manufacture of protective pigments, thereby reducing individual and population growth. The ability of microbial groups to act as primary colonizers and stabilizers of Antarctic soils may be seriously impaired which may, in turn, limit the subsequent colonization and development of macroscopic plant and animal communities, independently of the direct effects of UV on the latter groups.

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