PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Discussion on the Papers on Life Sciences

R. M. Laws, M. W. Holdgate, Van Zinderen Bakker, N. J. Collins, S. Z. El-Sayed, G. E. Fogg, R. E. Longton, R. B. Heywood, E. D. Hollowday, W. R. Piggott, R. J. H. Beverton, I. Everson, W. Block, M. R. Payne, W. N. Bonner, D. W. H. Walton, W. C. Young, B. B. Roberts, George Deacon, L. Davies and M. J. Roobol

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R. M. Laws

Would Dr Holdgate amplify his brief comments on time as a factor? Can we expect these simple ecosystems to become more diverse and complex?

M. W. Holdgate

These ecosystems may be impoverished for two reasons: the harsh polar environment and the difficulties of colonizing the habitats available across the wide sea barriers of the Southern Ocean. I believe that the Antarctic does present some of the features of an oceanic island in this respect. Probably more species will succeed in invading habitats in the maritime Antarctic as time goes by, assuming that the climate does not deteriorate. Experimental introductions suggest that more vascular plants could probably live in the most favourable places if they could reach them, and I would expect the same to apply to invertebrates.

Bryophytes, on the other hand, seem to disperse fairly easily, judging from the rich vegetation around transient fumaroles on the young volcanoes of the South Sandwich Islands, and the high proportion of South American species along the west side of the Peninsula. I would not be so confident of great increases in their diversity with time: indeed there might be losses as vegetation moved more towards a climax.

Superimposed on these successional and distributional changes we must expect short-term cyclical changes and losses due to local catastrophe like glacial surge, climatic oscillation or volcanicity. Many successful Antarctic species may have strategies involving high reproductive and dispersion rates that are adaptive to such stresses.

Van Zinderen Bakker

What methods were used for measuring bryophyte production?

N. J. Collins

Dry matter production in bryophytes has been assessed by cutting across cores of known area at the level of the clear innate markers of growth. These arise in most species as a result of the death of many of the shoot apices at the end of season. New growth in the following season is initiated by sub-apical branching. In certain species, most noticeably in species of *Polytrichum*, there is variation through the season in the size to which successive leaves grow, with the result that the shoots have a segmented appearance, each segment corresponding to one season's growth. In those species lacking innate markers against which growth may be assessed some form of artificial marker (such as the cranked wire of Clymo (1970) *J. Ecol.* **58**, 13–49) has been introduced.

S. Z. El-Sayed

Would Professor Fogg care to comment on the reasons for the great differences between the productivity of the coastal and oceanic waters in the Antarctic, noting that the levels of the nutrient salts in the latter are just as high as in the former?

G. E. Fogg, F.R.S.

We need more information on the chemistry and biological properties of Antarctic seawaters before a definite answer can be given but my feeling is that turbulence prevents growth in

oceanic waters and that the relative stability of the water column necessary for phytoplankton growth only occurs in coastal sea areas.

R. M. Laws

You mentioned that the productivity of some coral atolls may be largely sustained by nutrients transported in Antarctic bottom water. Would you amplify this, particularly concerning how relative quantities were estimated?

G. E. Fogg, F.R.S.

Sorokin (1973) assumed dark uptake of ^{14}C from bicarbonate to be a measure of bacterial productivity in seawater samples. This assumption is open to question but if it is accepted then his results would indicate that in waters over and around coral reefs the production of bacterial cell material exceeds by several-fold the primary production of photosynthetic phytoplankton. The carbon source for this bacterial production must be dissolved organic matter and in the sea areas in question the ultimate origin of this is probably in the Antarctic.

R. E. Longton

I was interested in Professor Fogg's comment that the rates of net photosynthesis in Antarctic marine algae at temperatures close to freezing may be increased by a reduction in the respiration rate at low temperatures as compared with temperate forms. Recent reports have suggested that a similar situation may also exist in certain Antarctic lichens, in which the temperature optimum for net photosynthesis may be at or below 0 °C, again due in part to depressed respiration rates under cold conditions. It is not yet clear, however, whether this mechanism operates in bryophytes, as for the few Antarctic species so far reported upon the optimum temperatures for net photosynthesis have generally been in the range 10–20 °C. Are any more recent results available on the physiology of Antarctic bryophytes which may help to clarify this point?

N. J. Collins

Most mosses studied recently with the use of infrared gas analysis techniques have been found to have optimum temperatures for net photosynthesis at saturating light intensities that correspond well with tissue temperatures prevailing in the field. For example, in material of *Polytrichum alpestre* grown under a temperature régime similar to that in the field, the optimum temperature at 1000 μE† m^{-2} s^{-1} was 10 °C and in *Drepanocladus uncinatus* was 15–20 °C. However, at lower light intensities the temperature optimum shifts to lower temperatures; at 100 μE m^{-2} s^{-1} the optimum is at 5 °C in *Polytrichum alpestre* and at 50 μE m^{-2} s^{-1} as low as 0 °C. Although the optimum temperature is 10 °C at saturating light intensities for *Polytrichum alpestre*, the rate of net photosynthesis falls only slightly down to 0 °C, to two-thirds of the optimal rate. The decrease in rate at temperatures up to 20 °C was much less than one-third. It appears therefore that both of these species are capable of carrying on high rates of net carbon fixation over much of the day on Signy Island, often at rates as high as those observed in mosses in temperate habitats. Although some earlier published work reports much higher optimum temperatures for Antarctic mosses, these were based on respirometric methods with inherent problems of interpretation as far as field behaviour is concerned. There seems, therefore, to be little evidence for mosses being less capable than algae or lichens of sustaining growth at low temperatures.

† E = einstein.

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M. W. Holdgate

Are any animals known to eat the bryophytes forming the luxuriant lake-bottom communities Dr Heywood described? The evidence seems to indicate that Antarctic moss vegetation on land is virtually ungrazed by invertebrate herbivores, and it would be interesting to know whether the same holds for the aquatic system. Presumably this vegetation supports a substantial decomposer community.

R. B. Heywood

The limited evidence available suggests that the herbivores associated with the mosses are grazing the epiphytic algae. However, current and proposed detailed studies on tardigrades, nematodes and an enchytraeid worm may reveal that certain species use the cell sap of the mosses as a food source. Research on decomposition forms part of a current bacterial study but no results are available yet.

G. E. Fogg, F.R.S.

Has Dr Heywood any indication of the rate of growth of aquatic mosses?

R. B. Heywood

The growth of aquatic mosses is being studied during a current ecological investigation of benthic flora in Signy Island lakes by J. Priddle, British Antarctic Survey. Preliminary results indicate an annual mean shoot extension in *Calliergon sarmentosum* of about 13 mm (range 11–25 mm). These values are of course provisional. Considerable detailed information on both growth and ecology should be available when the study is completed in 1978.

E. D. Hollowday

Apropos Dr Heywood's remarks to the effect that organisms adapted to a very rigorous environment might not do so well in less severe conditions, I think it possible that Bdelloid Rotifera, which appear to form an important part of the Antarctic micro-fauna, might lose fecundity if not subjected to alternate freezing and thawing, in the case of polar species, or alternate desiccation and immersion in temperate and tropical regions.

I have observed on several occasions that the Bdelloid rotifer *Philodina roseola*, which normally inhabits very shallow habitats such as gutters and bird-baths, will remain in large numbers for many years in such an environment, but appear to die out if placed in such a depth of water as precludes frequent evaporation and subsequent desiccation in summer and freezing solid in winter.

W. R. Piggott

Have you considered seeding uninhabited lakes, ponds or pools with species from inhabited ones or from elsewhere in Antarctica? This might give more exact information on the problems of colonization and growth. If this type of experiment is desirable and were to be allowed, the wording of the Agreed Measures under the Antarctic Treaty would need careful consideration.

R. B. Heywood

This type of experiment is generally discouraged for very good reasons – the effect of introduced species in various areas of the world has often been to upset the balance of nature with disastrous consequences. For this reason the Antarctic Treaty attempts to prohibit the introduction of alien species. Containment of organisms apparently suited to Antarctic freshwaters would

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be particularly difficult because all could easily be transported by wind and birds into adjacent areas. Extermination or removal at the end of the experiment would be impossible.

The feasibility of such an experiment is questionable. The success of any organism within an environment is the product of a complex interaction of physical, chemical and biological factors – and the latter are the most difficult to assess. Such an experiment would currently be of dubious value therefore, and add little to the knowledge being gained from laboratory experiments and field observations.

Present knowledge clearly indicates that it is not the severity of the physicochemical environment which restricts colonization in the majority of instances. Many animals, from temperate and tropical as well as polar regions, actually require periods of extreme stress to maintain vigour and fecundity.

R. J. H. Beverton, F.R.S.

Is Dr Everson suggesting that Scholander's cold adaptation theory is no longer valid; is that a fair summary?

I. Everson

I would not be quite as dogmatic as that. With the limited results available at this time we cannot be definite but the implication is clearly that as far as the marine environment is concerned there is little to support the theory and a great deal against it.

W. Block

In relation to Dr Everson's comments on the lack of evidence for cold adaptation in Antarctic marine poikilotherms, I would like to suggest that terrestrial poikilotherms may be different in this respect. For the terrestrial mite *Alaskozetes antarcticus* we have measured individual rates of resting metabolism at low temperatures in a study at Signy Island. These are elevated by a factor of between 3 and 5 compared to data for temperate species of mites over a similar temperature range. So there is some evidence for higher levels of resting metabolism in these terrestrial arthropods.

It may be that such a phenomenon is restricted to terrestrial poikilotherms, which in the maritime Antarctic are subject to large variations in habitat temperature both diurnally and seasonally. In contrast the marine ecosystem is a relatively stable thermal environment as Dr Everson has shown. I wonder if the speaker would like to comment on these differences?

I. Everson

The evidence I have presented is only concerned with the marine environment which as you point out is a far more stable thermal environment and it may be that cold-adapted metabolism is a result of eurythermality (although that is only a spontaneous idea). In the defence of Scholander I would point out that his paper does include results obtained from terrestrial Arctic species so it is possible that your results are confirming his original impression.

R. M. Laws

The staple food of the fur seals during the breeding season at Bird Island is krill. Is it known what they feed on during the rest of the year?

M. R. Payne

No. Since the wintering grounds of the seals are not known, I can only point out that I believe fur seals to be rather opportunistic feeders, not as highly specialized as the baleen whales

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for instance. Thus, if a migration into South American coastal waters does occur, one would predict that fish would be a significant part of the diet.

W. N. Bonner

Would Mr Payne like to speculate on the original size of the South Georgia fur seal population in its virgin state, prior to 1775? And could he further speculate on the possible density of colonies at that time?

M. R. Payne

Mr Bonner is rather better placed to assess the original size of the South Georgia fur seal population than I, and all the historical information of which I am aware is summarized in his 1968 publication. However, my personal feeling is that the original size of the stock was similar to that of *Callorhinus ursinus* on the Pribilof Islands today. If this number of animals occupied the area on South Georgia that the old records suggest, this might be taken as an indication that the density at that time was somewhat lower than is the case now. The evidence is of course totally inadequate to reach any meaningful conclusions.

D. W. H. Walton

In view of the reduction in whale numbers and the consequent increase in available krill and your statement that many suitable beaches on South Georgia remain unoccupied by fur seals, surely we might expect that the population will not stop expanding within the next ten years?

M. R. Payne

I agree. However, I would expect the rate of increase to fall significantly, within about ten years, due to growing intra-specific competition for food within the feeding range of lactating cows.

Mrs W. C. Young

I would like to ask Dr Laws the very simple question – where can one buy krill?

R. M. Laws

The simple answer is – in a Moscow supermarket, where it is sold as 'ocean paste'. I understand that the Japanese operations are about to go commercial within a few years; all other groups are conducting experimental fishing operations.

B. B. Roberts

When boiled or fried, as we might cook shrimps or prawns, krill are almost tasteless; certainly without any attractive flavour or appearance. But when it has been properly processed and cooked by, say, a skilled Japanese cook in Tokyo, it can become a delicious food for humans. What I think is important is that raw wet krill contains about 15% protein and 5% fat. I have little doubt that in times of increasing food shortages, it will not be beyond the ability of our food technologists to use this raw material for the production of either pastes or 'ocean fingers' of the right texture and flavour to make them popular.

I. Everson

From my experience also krill can be made into very acceptable food items although I would not like to consider any of them as the major part of my diet. The resource we are considering is of enormous magnitude, which means that the food technologists must be looking for a generalized type of food product.

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M. W. Holdgate

Did I understand Professor Dunnet to challenge the established concept that research on ecosystems in the Antarctic was especially appropriate because they were uniquely simple? If so, I have some sympathy with the view. The Antarctic has no monopoly of simple ecosystems: we can find them, nearer at hand, on mountains (for example the Cairngorm plateaux), in tree holes, or in the laboratory. I think it is important that we try to resolve in discussion just what it is about Antarctic systems that justifies the effort and expense of studying them!

D. W. H. Walton

There is no doubt that some of the Antarctic ecosystems are exceptionally simple by comparison with their temperate and tropical counterparts. Some may offer us a halfway house where model systems developed for artificial crop situations may be tested in natural communities of only one or two species. The occurrence of large areas of simple plant species stands on the subantarctic islands, offers great possibilities for investigation of the basic mechanisms of competition and the relationships between growth and environment.

W. N. Bonner

I agree with Professor Dunnet that one must examine the blocks in order to understand the building, or the species in order to understand the ecosystem. This has been the traditional approach of B.A.S. or its predecessor, F.I.D.S. I am sitting next to Bernard Stonehouse, who was one of the early workers on the autecology of the emperor penguins at the Dion Islets.

Yet it will always be the biologists' aim to understand the system, though we accept that the system must be too complex for a complete understanding. In the Antarctic we shall perhaps come closest to our ambition in the inland waters where restricted and relatively simple systems can exist. Dr Heywood has made great progress here in his work on the Signy Island lakes.

But basically I agree with Professor Dunnet – we need to make a careful study of the blocks before we attempt to synthesize the system.

M. W. Holdgate

May I ask Dr Walton whether he can confirm or refute an observation I made in South Georgia during a brief visit ten years ago? I had come from Signy Island and was interested to find that many of the dominant bryophytes occupied similar situations: turf species on well-drained, sunny, stable slopes; carpet communities in moist seepage zones and the like. The vascular plant layer in the vegetation appeared to be superimposed, with its components again behaving broadly similarly to their habit in Fuegia, the Falkland Islands or Gough Island. No doubt there was some modification in bryophyte pattern due to the presence of the vascular plant layer – and to species differences – but it was not evident: does more detailed knowledge alter this conclusion?

D. W. H. Walton

In general the bryophytes do occupy similar habitats on both islands but modification by the phanerogams on South Georgia can be very important. *Acaena magellanica*, a deciduous dwarf shrub with a high leaf area index, effectively suppresses moss growth throughout much of the summer whilst litter production in some of the grasslands may also have a significant effect on cryptogam growth. A further important difference is the direct colonization of bare ground on South Georgia by several phanerogams. Examples of competition between phanerogams and

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cryptogams are clearly visible in some communities whilst the much deeper layer of vegetation on South Georgia provides quite different microclimates for cryptogams than exist on Signy.

G. E. Fogg, F.R.S.

As far as I am aware, no poisonous or symbiotic species have been reported from Antarctic waters. If this is correct it would support Dr Holdgate's contention that the influence of the physical environment is of greater importance in Antarctic ecology than interactions between species.

Sir George Deacon, F.R.S.

We ought to know more about climatic changes round the Antarctic Continent. Early observations, such as those of Wilkes, d'Urville and Ross, indicate that there has been little trend in the mean sea temperature over the past century, but we begin to be aware of considerable changes from year to year. In November 1930, an exceptionally cold year, the *Discovery II* had to push through very heavy ice to reach South Georgia from the northeast – more than may be seen later in the summer in exceptionally warm years on the way to Halley Bay. The voyages of supply ships over the past 20 years must have provided much more data.

L. Davies

In connection with the subantarctic islands north of 60° S, I would like to ask you, Dr Roberts, whether you think that we have adequate machinery to protect the scientifically valuable animals and plants of these islands. I sometimes think that perhaps a Subantarctic Treaty is called for, to produce the international cooperation necessary not only to implement agreed conservation measures, but also to produce the research and development work needed perhaps to attempt reduction or elimination of harmful introduced forms.

B. B. Roberts

As I have said already, these islands are all subject to national jurisdiction, and it is not to be expected that all governments will approach these problems in the same way. I believe that there is great scope here for S.C.A.R. to make a useful contribution in coordinating and making proposals through their own National Committees for conservation policies in the subantarctic islands. Perhaps Dr Davies would comment on the situation in the islands where he has personal experience?

L. Davies

Certain of the Îles Crozet contain virtually untouched native vegetation that happily escaped the damaging exploitation of subantarctic islands of the late eighteenth and early nineteenth centuries. Now these priceless natural systems are threatened with damage from a recently introduced herbivore. It would be tragic, in conservation terms, if steps are not taken quickly to remove the still small sheep-flock at large on the Île de la Possession, Îles Crozet.

B. B. Roberts

I certainly agree with Dr Davies about the unfortunate consequences which may result from the introduction of sheep to Île de la Possession. I do not think this particular introduction was deliberate French policy and we can only wish them quick success in their subsequent efforts to destroy these sheep. Much more controversial, I think, are the introductions of several herbivores and carnivores, ducks and salmonid fish to Îles Kerguelen. Some of these have been planned,

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others – like cats and rats – have been accidental. There is no doubt that they have had considerable impact on the local ecology. It is not only in the French subantarctic islands that these introductions have been taking place. In the Falkland Islands, for example, salmonid fish have been introduced without any serious consideration of the possible ecological consequences. Still more disturbing are the recent irresponsible proposals to introduce Alaskan salmonids into the Southern Ocean to feed on the 'surplus' krill.

M. W. Holdgate

Responsibility for damage to the ecological systems of subantarctic islands is sometimes divided: for example the rabbit, which is one of the most destructive herbivores on Îles Kerguelen, was introduced by a British expedition sent to observe a transit of Venus in 1874, probably with Royal Society backing!

May I report a more encouraging recent development? Within the past month a new Conservation Ordinance has been enacted for the four islands of the Tristan da Cunha–Gough Island group (Wace & Holdgate 1976). This Ordinance has much in common with the Agreed Measures for the Antarctic and with the South Georgia laws that Dr Roberts described. The Tristan da Cunha Islands are the least altered of all the oceanic islands in the southern temperate zone, and the new measures, which have the warm support of the islanders, should help secure the future for their unique plant and animal communities.

We cannot expect to rely on controlling alien herbivores or predators once they have been established. It is true that shooting campaigns have eradicated goats on Tristan and some islands near New Zealand, but generally control measures are ineffectual, especially for damaging predators like cats or rats that can cause havoc in the great seabird colonies. The best course is to take all possible steps to see that such animals are kept off the islands altogether.

Reference

Wace, N. M. & Holdgate, N. W. 1976 *Man and environment in the Tristan da Cunha Islands*. Monograph Series, International Union for the Conservation of Nature and Natural Resources.

M. J. Roobol

As a geologist I can see no reason why sulphide deposits such as copper and tin should not occur along the Antarctic Peninsula and the possibility of oil and gas in the continental shelves should be taken seriously. Would Dr Roberts care to comment on the implications of these possibilities on existing efforts of coordinated research as well as future plans?

B. B. Roberts

There may well be significant minerals in the Antarctic Peninsula, but the discovery of oil or gas in the continental shelf area at present seems likely to become an earlier problem. It is important that some way be found to ensure that no exploitation takes place in the Antarctic except in conformity with the agreements concluded under the Treaty. We do not want two separate groups of visitors to arise – one group subject to internationally agreed restrictions and obligations while the other might wish to operate without any restraint or exchange of information. The Antarctic Treaty had, of necessity, to avoid any mention of mineral resource exploitation. During the past few years the Treaty Consultative Meetings have been giving much anxious consideration to these problems. There is at present no agreed way to regulate

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mining or drilling for oil which would not seriously disturb the working of the Treaty. Much would depend on the area involved and consequently which existing legislation might be relevant. It is, perhaps, rather doubtful whether any company would be willing to put much money into a very expensive project where they could not be assured of protection by their own or any other government. If I may express a purely personal opinion on this matter, I would say that any practical licensing system applicable anywhere in the Treaty Area will have to operate on behalf of all the parties to the Treaty, or at least all the nations which are active in the area.

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