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## Discussion on the Preceding Papers

J. E. Smith, R. B. Heywood, G. E. Fogg, O. W. Heal, J. E. Hey, M. W. Holdgate, J. P. Harding, S. E. Allen, J. H. Price, M. H. Thurston, T. J. Hart, F. C. Fraser, C. H. Gimingham, R. E. Longton, P. J. Tilbrook, G. M. Dunnet, S. W. Greene and N. A. Mackintosh

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*Discussion on the preceding papers*

- J. E. SMITH. The Anostraca, following the classic studies of Cannon & Manton, are commonly regarded as filter feeders, yet there is evidence that some, including *Branchinecta* on Signy Island, feed on the bottom. What mechanism is involved and what kind of food is being taken?
- R. B. HEYWOOD. In calm weather few *Branchinecta giani* are visible at the surface, or in mid-water in the Signy Island lakes. They all seem to be browsing on the benthic felts of blue/green algae. The thoracic appendages show slight modification for scraping and Dr Ralph has observed this process in the laboratory. Large masses of blue/green alga are common in the fore-gut of the animals, and we can only conclude that they are general and detritus feeders whose diet is limited largely by particle size. Large pieces of crustacean exoskeleton have been seen in some specimens but these were without musculature and were probably taken in with detritus rather than as the result of predation.
- G. E. FOGG. Having seen these lakes I agree that the blue/green algal felt on the bottom is the main primary producer in summer. Results so far available suggest that a good deal of the photosynthetic products are liberated into the water and hence dissolved nutrient organic matter may be available for utilization by the phytoplankton in spring.
- R. B. HEYWOOD. Phytoplankton samples certainly do tend to confirm an increase at about the time I have suggested.
- O. W. HEAL. Dr Ralph has suggested that adult *Branchinecta* are taken by few predators. But predators take the larvae, and surely this could limit the population?
- R. B. HEYWOOD. Numbers of *Parabroteas sarsi* are more or less the same in all lakes whether *Branchinecta gaini* is there or not. The numbers of the latter fluctuate in a manner not clearly related to the fluctuations in the former.
- J. E. HEY. Studies at Cape Royds, Ross Island, confirm the importance of air flows in creating turbulence. A strong circulation can prevent ice formation on the bottom of lakes and must have marked effects on the phytoplankton.
- R. B. HEYWOOD. At Signy Island anchor ice forms only on shallow shelves. In summer variations in temperature with depth are very slight—differences ranging over less than 0.5 degC—undoubtedly because of vigorous turbulence. This mixing may cut down summer phytoplankton densities and production because the cells are dispersed over the whole water column and hence carried into levels with too high light intensities.
- J. E. HEY. At Cape Royds a 4 degC temperature gradient can be present over a 1 m vertical range, and this is significant ecologically.
- R. B. HEYWOOD. On Signy Island the greatest temperature gradients are horizontal rather than vertical. On shelf areas in summer the water may warm to 7 or 8 °C but the central areas remain substantially cooler.

M. W. HOLDGATE. Savich-Liubitskaia & Smirnova (1964, *Sovet. Antarkticheskaia Eksped. Inform. Bull.*, no. 7, 34–9) have described other, deeper lakes in the Bunger Hills where water at 33 to 36 m has a near-constant temperature of 3·3 to 3·4 °C in summer and 2·3 to 2·7 °C in winter. Consequently there are evidently deep stratified lakes in some parts of the Antarctic.

R. B. HEYWOOD. I was unable to investigate the deepest lakes on Signy Island.

J. P. HARDING. *Pseudoboeckella* species in Lake Titicaca show a marked size range, and the number of eggs produced also varies with the dimensions of the female, the largest individuals carrying about 15 eggs and the smallest only 1 or 2. The eggs, however, and the nauplii are the same size irrespective of parental dimensions.

R. B. HEYWOOD. *Pseudoboeckella silvestris* shows bimodality within Signy Island lakes at different seasons of the year. Animals maturing in the early winter are small, while those derived from nauplii feeding on the phytoplankton bloom are much larger. This size difference can be followed through the age classes.

Egg numbers are not, however, related to parental size. Some large animals bear few eggs, and conversely. But the eggs are all the same size: the differences become first apparent in the nauplii and are conspicuous in the copepodids. The adults are very distinct indeed.

*Parabroteas sarsi* also seems to show size variation, but its cause is not clear: it could relate to prey availability. *Branchinecta gaini* is different again, between the larger lakes and the pools in Paal Harbour. Much more work is required to elucidate the causes of these variations.

J. E. SMITH. We now need to look at the Antarctic ecosystem as a whole, as presented in Dr Holdgate's paper, and examine its several aspects.

S. E. ALLEN. I am unhappy about the mixture of static and dynamic factors in this paper. Some parts of the chain—such as those in the sea—are displayed as changing, and others (like the plants) as static. Even the carbonaceous material temporarily accumulated in the peat is not static, and is available for later circulation.

J. H. PRICE. As a minor point, rasping by the limpet *Patinigera polaris* can bring benthic maritime material back into the system via the gulls and sheathbills.

M. H. THURSTON. Benthic biomass in the Weddell Sea appears to be much less than the Soviet figures—perhaps only 10% of their average.

M. W. HOLDGATE. There is certainly a good deal of place to place variation, induced for example by ice scour. Locally, the standing crop is very high indeed, but it shows wide regional variation, as is typical of the Antarctic.

G. E. FOGG. The phytoplankton probably release about 25% of the gross photosynthetic product extracellularly, so that Ryther's average figure may be increased to an actual total of 125 g C/m<sup>2</sup> y.

J. E. SMITH. It is also important to be precise about the organisms included in the phytoplankton. Are the smaller flagellates accounted for?

- T. J. HART. In the early phytoplankton collections, where the pigments were estimated using Harvey's units, micro-flagellates were not included, because of the mesh size of the plankton nets.
- O. W. HEAL. There seems to be a valid point of contrast between sea and land ecosystems, in that the former has a very full series of food chains embracing primary and secondary carnivores, while the latter has food chains stopping at the herbivore or decomposer level. The question is whether the food chain can or cannot support primary and secondary carnivores, or whether these larger animals cannot occur on Signy Island because there is insufficient time to complete their life cycles.
- F. C. FRASER. Biogeographical limitations are also involved. Large secondary carnivores like polar bears or Arctic fox do not occur in the southern hemisphere, and were they to succeed in getting there, the effect would be dramatic.
- O. W. HEAL. I was really thinking in terms of invertebrate predators, which do succeed in reaching the southern temperate zone.
- M. W. HOLDGATE. Staphylinidae and Dytiscidae have succeeded in colonizing several southern islands, including South Georgia. They could probably reach Signy Island equally well. The limitations are probably ecological rather than biogeographical.
- C. H. GIMINGHAM. The true gap in the terrestrial food chains seems to me to be at the herbivore level. There is a mass of plant material, with almost nothing eating it.
- J. E. SMITH. This is the kind of situation in which the effects of introducing alien species have an attraction, provided they are done as carefully controlled experiments. There is also a great opportunity for the study of energy flow in these relatively simple ecosystems—both in relation to ecological factors limiting distribution and in relation to actual metabolic rates under different conditions.
- F. C. FRASER. The successful introduction of reindeer to South Georgia—more successful than that into the Scottish Cairngorms—is of great interest. Are the food requirements of this species met better at South Georgia than in Scotland—or is the climatic difference significant?
- R. E. LONGTON. In 1963/64 Mr R. W. Vaughan carried out a survey, recording some 2000 animals in the two herds. These animals are restricted in their range by glaciers and in some areas have grossly modified the vegetation, especially the grass heaths. Certain associations are lacking altogether in areas grazed by reindeer, and fruticose lichens are notably less common.
- M. W. HOLDGATE. One of the most interesting things about the South Georgia reindeer is that their diet is remarkably wide, including flowering plants as well as lichens.
- P. J. TILBROOK. An interesting question has been raised by the discovery on Signy Island and the South Shetland Islands, six specimens of two species of lathridiid beetle. One of these species is a typical synanthrope, but the other is a southern temperate insect collected both from apparently undisturbed habitats and from the base itself. Further collecting will show whether the species has established itself. Among the predators there are only one or two carnivorous mites among the microfauna. The limiting factor in my view is the limited period of their activity and not food availability.

- G. M. DUNNET. Ordinarily, one tries to relate the abundance of animals to the primary producers. Here, however, it does not apply because the animals are feeding on the decomposers, not the primary producers. The availability of substrate for the decomposers is the critical factor, and it is important that this aspect of the ecosystem receives study. It is an interesting thought that there may be a general parallel with a tropical rain forest where the high primary production is not immediately utilized by herbivores.
- T. J. HART. Decomposers are also important in the supralittoral drift line zone in the Subantarctic where quantities of seaweed are cast up and utilized by micro-organisms and by dipteran larvae. This is a far less important habitat in the Antarctic because of the reduced algal growth by ice scour.
- S. W. GREENE. It is interesting to compare the situation in South Georgia, where the reindeer has attained some balance with the vegetation and that at Macquarie Island where rabbits have created devastation which has led to severe erosion. In neither case is food limiting: why is one population uncontrolled and the other not?
- M. W. HOLDGATE. Especially when one remembers that the Macquarie rabbits have a predator—the cat. The situation on Macquarie appears to arise largely because the dominant tussock grass, *Poa foliosa*, is grazed preferentially and killed out and there is no other species in the vegetation equally capable of stabilizing the soil on the steep coastal slopes. On South Georgia there is presumably a less critical balance.
- J. E. HEY. In New Zealand upland country grazing by imported herbivores has also caused great damage to vegetation and has led to erosion. There is no question that, in view of the evidence, any experimental introduction to the Antarctic islands must be very strictly controlled.
- J. E. SMITH. But before one can properly understand the normal working of a balanced ecosystem it is often necessary to disturb the balance experimentally. I agree that great care is, however, needed.
- Behavioural studies of activities of species in the field are also of very great importance, and these illuminating the selection of habitats and food by animals, will help to elucidate food chains and energy flow.
- R. B. HEYWOOD. Could behavioural factors in part limit the South Georgian reindeer herd?
- N. A. MACKINTOSH. Winter keep is far more likely to be limiting. Snowfall is heavy on South Georgia and the animals feed at times along the beaches, where food must be short.
- G. M. DUNNET. Deer as a group notoriously fail to adapt their numbers to their food supply in the absence of predators. Though the South Georgia herd has so far done little damage, it would be unwise to assume that it is in a state of genuine balance and direct human control may well prove necessary.
- S. E. ALLEN. The most attractive thing to me about the Antarctic ecosystem is its suitability for efficiency studies. This is in contrast to more complex environments such as British woodlands. Odum has demonstrated how closed and simple systems such

as coral islands and deserts can be used for such studies and the Antarctic is analogous in its ecological simplicity. The balance of herbivores and carnivores is an interesting aspect in that whole stages may drop out rather than becoming uniformly attenuated along the producer and consumer chain.

- O. W. HEAL. The absence of herbivores which eat mosses is surely a general feature even in temperate woodlands? In such habitats much of the primary production probably still goes straight to the decomposers?
- C. H. GIMINGHAM. Nematodes gall some mosses.
- O. W. HEAL. But N. N. Smirnov (*Hydrobiologia* 17, 179) found no invertebrate grazer of *Sphagnum* except for one chironomid whose impact was very small.
- J. E. SMITH. Rather similarly, the algae on Signy Island coastal rocks do not seem to be exploited.
- P. J. TILBROOK. Micro-arthropods may graze algae on the rocks, and from among soil and moss, although I have never observed this directly.
- R. B. HEYWOOD. The mosses might be considered a 'temporary halt' in the food chain, but surely not a 'dead end'?
- S. E. ALLEN. On Signy Island there is a lack of intergradation between the peat layers and mineral soils below. However, most peats do show some evidence of continuing chemical and structural changes so the 'halt' may be indeed a temporary one.
- M. W. HOLDGATE. And, although the moss peats may be deep and frozen there are evident changes with depth. The old, dark, compact permafrost peat has a striking and offensive smell when freshly cut and then thawed, and this may well indicate that the decomposers can be active even under these conditions.
- O. W. HEAL. Is there any evidence that the more mature *Deschampsia* patch 'brown earth' soils develop from pre-existing moss peats?
- C. H. GIMINGHAM. There is no indication that an earlier moss stage is essential for the establishment of grass, and seedlings are visible both on bare ground and among bryophytes.
- S. W. GREENE. Certainly on South Georgia, *Deschampsia antarctica* is quite capable of establishing itself without a preceding bryophyte stage, as indeed probably most of the island's native vascular plants can at low altitudes. But, with increase in altitude or increase in exposure most species show a conspicuous fall off in this capacity and the development of some form of bryophyte turf—often with *Tortula robusta* as one of its important constituents—seems a necessary prerequisite before phanerogamic communities can get established.