The Antarctic Ecosystem

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Introduction

The aim of the present paper is to summarize the broad scope of this Discussion and to attempt to draw certain final generalizations about the Antarctic as a biological zone.

It is almost impossible to omit all mention of the sea from a discussion of Antarctic biology, and consequently a review of Antarctic oceanography and of food chains and biomasses at the various marine trophic levels will be given first. This leads in turn to a consideration of the interrelationships between sea, land and fresh water, and thence to an assessment of the total ecosystem.

The marine ecosystem

1. *The habitat*

The circulation and physical characteristics of the Antarctic Ocean have been reviewed briefly by Deacon (1964), and the environmental features considered as ecological factors by Currie (1964). As the latter author points out, the Antarctic Ocean is essentially a deep oceanic environment. The continental shelf is narrow, and depressed by ice loading to abnormally great depths (cf. Adie 1964), and the submarine ridges such as the Scotia Ridge, the Kergeuelen–Gaussberg Ridge and the Balleny–Macquarie Ridge, provide important dispersal routes but no very great areas of shallow water.

The southward boundary of the Southern Ocean is the Antarctic Continent: its northern boundaries have been equated with the Subtropical Convergence (or, in the case of the Antarctic Ocean *sensu stricto*, with the Antarctic Convergence). However, as Currie (1964) point out, these lines of demarcation are in the surface layers and consideration of the basic circulation makes it plain that the Antarctic Ocean is not an isolated entity but an integral part of the world oceanic system.

As Deacon (1964) demonstrated, there are three major ocean currents in the Antarctic Ocean. Cold water and ice spread outwards as a surface current about 100 to 150 m thick in summer, and this upper layer is of fairly low salinity and at temperatutes close to freezing point. The water has a northward and eastward movement, except close to the continent south of about 63° S, where the winds have a westward tendency and impart a similar drift to the surface waters. There is also a northward-flowing cold saline layer forming the Antarctic bottom current. Between these two layers there is a compensating southward movement of relatively warm and saline water and this is drawn from beneath the waters of the world ocean, some of it being traceable from sources as far away as the Mediterranean or the north Atlantic. It rises nearer the surface south of about 50° S, and upwells into the cold surface current about the periphery of Antarctica where it is cooled and diluted, though where it is cooled without dilution, as under great ice shelves, it feeds the cold bottom current. In its upwelling this warm deep water brings dissolved salts continuously into the surface waters.

The Antarctic Convergence is demarcated by a sharp temperature change where the cold surface current sinks below warmer mixed water in the Sub-Antarctic zone. The Convergence itself has some of the characteristics of an atmospheric frontal zone, varying somewhat in position and showing a complex eddying phenomena. Within the whole broad zone south and north of the Convergence the surface waters have a wind-impelled movement from west to east averaging about 13 km/day.

The surface waters immediately south of the Antarctic Convergence have an average temperature of about 1 to 2 °C in winter and 3 to 5 °C in summer, while the sea is significantly colder farther south, being at about $-1\cdot0$ to $-1\cdot9$ °C about the shore of the continent. North of the Antarctic Convergence there is an abrupt temperature rise of about 2 degC. These latitudinal differences are paralleled by differences with depth, between the 'cold' and 'warm' currents, but as Currie (1964) points out these amount only to a total of a few degrees centigrade. Near the continent, as at McMurdo Sound, the sea temperature varies little over the year, remaining within a few tenths of a degree of the mean figure of $-1\cdot9$ °C. The same is true off the ice shelf at Halley Bay, Coats Land (Thurston, private communication).

The area of open water surface south of the Antarctic Convergence is halved when the sea ice reaches its maximum extent in winter and this has a profound biological impact by reducing by some 90% the light penetration to the water below. Ice formation also causes a rise in salinity, reduced at the time of the spring break up. There is a substantial diatom flora attached to the floating ice (Bunt 1964*a*, *b*) and the pack ice zone may be an important source of photosynthesizing organisms in spring.

During summer, with a long day, there is abundant incident radiation reaching the surface of the Southern Ocean. In the far south there is almost continuous illumination during the summer months, while the extension of the pack ice in winter causes a deepening of the winter darkness in southern waters. The result is a strongly seasonal light regime. Beneath the ice shelves and old fast ice the total light reaching the sea floor or the water above the sea bed is perpetually kept to low levels.

Extensive nutrient analyses by Clowes (1938) have demonstrated that phosphate and silicate at least are unlikely to be limiting to phytoplankton growth and production, even at the peak of the summer 'bloom', although these salts do show some seasonal periodicity. This unusually abundant nutrient supply results from the pattern of water movement. Below the Sub-Antarctic zone there is a region of extensive decomposition and regeneration, which releases nutrients to be transported southward in the warm deep current and so restored by upwelling to the surface layers.

The Antarctic marine environment is thus a deep oceanic system with a strongly marked circulation. Upwelling brings nutrients into the surface waters in considerable quantity. The light regime is seasonal, with abundant light for photosynthesis in summer but very low illumination in winter. The temperatures are consistently low throughout the zone. As with many productive oceans, there is considerable turbulence in summer, but stability in winter under the protective ice cover. Granted tolerance of, or physiological adaptation to, the low temperatures, habitat conditions are favourable for life in summer, but owing to the low light intensities, become markedly less so in winter especially in the most southerly areas.

2. *The phytoplankton*

Biomass and standing crop

Hart (1942) examined the phytoplankton standing crop over the season over a wide area of the Southern Ocean south of the Antarctic Convergence, which he subdivided into 'northern', 'intermediate' and 'southern' regions, taking the waters offshore from South Georgia as a fourth category. In these areas he assessed phytoplankton density in terms of Harvey's units of pigment intensity, and calculated minimum crops from nutrient levels, comparing these with actual average standing crops to get a measure of grazing intensity. Later workers (El Sayed & Mandelli 1965; El Sayed, Mandelli & Sugimura 1964; Bunt 1964*b*) assessed chlorophyll *a* levels as a measure of standing crop, and Bunt (1966) has converted some of these to organic carbon on the basis that 1 mg chlorophyll *a*, represents 50 mg organic carbon.

TABLE 34. CALCULATED MINIMUM AND AVERAGE STANDING CROPS IN ANTARCTIC SEAS

	calculated minimum crop (g/m^3)		average standing crop (g/m^3)	
	maximum	minimum	maximum	minimum
English Channel	20·1	1·06	0·48	0·025
South Georgia	61·5	15·5	1·10	0·28
North Region–Indian Ocean	28·9	16·7	0·23	0·13
North Region–Atlantic Ocean	36·2	10·1	0·14	0·04

Taken together, these results show that Antarctic waters are comparatively rich in phytoplankton, and that the waters off South Georgia are exceptionally so. Hart's data in this respect are summarized in table 34, and more recent chlorophyll *a* and organic carbon figures in table 35.

TABLE 35. ORGANIC CARBON AND CHLOROPHYLL *a* IN ANTARCTIC SEAS (SUMMER)

area	chlorophyll *a* (mg/m^3)	organic carbon (g/m^3)	author
McMurdo Sound	37·5	1·875	Bunt (1964*b*)
Deception Island	14·2	0·710	Burckholder & Sieburth (1961)
N.E. of S. Orkney Islands	4·3	0·215	El Sayed & Mandelli (1965)
Bransfield Strait	2·4	0·120	El Sayed, Mandelli & Sugimura (1964)
Drake Passage	0·73	0·036	El Sayed, Mandelli & Sugimura (1964)

The results in tables 34 and 35 demonstrate the extreme variability in standing crop in the Southern Ocean. For example, there is a progressive increase in plankton southwards across Drake Passage, with higher values still in Bransfield Strait (El Sayed *et al.* 1964) and there is also substantial point-to-point variation within the Weddell Sea (El Sayed & Mandelli 1965). Higher standing crops still have been recorded from Deception Island

and, at peak, McMurdo Sound waters have strikingly great chlorophyll levels (Bunt 1964*a*, *b*). These last, however, are probably inflated by the release of under-ice diatoms following the summer break-up. In contrast to the high oceanic and southern inshore values, coastal waters about South Georgia are deficient in phytoplankton (Hart 1942), probably because of turbulence and the effect of detritus in the land drainage. Investigations in 1965/66 suggest that the same poverty of inshore waters may exist in the South Orkney group.

The phytoplankton of the Southern Ocean is also variable with time. Hart (1942) demonstrated a pronounced annual cycle, the peaks of which occurred earlier in northern areas, where the productive period was also rather longer drawn out. Bunt (1964*a*, *b*) has shown that at McMurdo Sound the rise in plankton density is extremely rapid following the break up of the ice, and that the productive period is even briefer than in Hart's southern oceanic region.

Production rates

In parallel with the variation in standing crop, productivity by the plankton shows wide point-to-point variation in the Antarctic. Thus El Sayed *et al.* (1964) recorded uptake rates of 8·2 mg C/m^3 h in Bransfield Strait, and 3·5 mg/m^3 h in Drake Passage. El Sayed & Mandelli (1965) obtained a higher value, of 10 mg C/m^3 h in the richest part of the Weddell Sea, but elsewhere in the same waters rates of production were down to from 0·18 to 0·53 g C/m^2 surface day. They computed an annual production of 84 g C/m^2 surface, based on data for the four summer months, a result which compares well with the estimate of 100 g C/m^2 surface y computed by Ryther (1963) for the Southern Ocean as a whole (on the basis of Hart's earlier data). Both these figures are significantly above the 43 g C/m^2 surface y calculated by Currie (1964). In contrast, at McMurdo Sound, Bunt (1964*a*, *b*) obtained fixation rates *in vitro* of only 2·0 to 1·7 mg C/m^3 h and *in situ* rates (below ice) of 0·01 to 0·05 mg C/m^3 h. These latter values reflect the low light penetration below the ice cover. Another basis for comparative assessment has been provided by Bunt (1966) who points out that, taking Ryther's 100 g C/m^2 surface as a target, the standing crop of plankton over the general oceanic area might be expected to produce this quantity in about 90 days while the standing crop in Gerlache Strait would attain it in 170 days and the under-ice flora in McMurdo Sound would require 13000 days. Bunt makes the important point that in several areas, such as Gerlache Strait and McMurdo Sound, heavy standing crops have relatively low assimilation numbers, while the highest activity is to be found in rather less dense populations.

Taken as a whole, despite the high standing crop in many areas, the Antarctic oceans do not show an outstandingly high rate of primary production. The importance of the steady and non-limiting nutrient supply and of the high summer illumination has already been mentioned. Temperature is likely also to have a significant influence. Bunt (1964*b*) has demonstrated experimentally that carbon fixation by Antarctic phytoplankton is temperature dependent in the range from 1·5 to 5 °C and that maximum production is reached at 10 to 15 °C, well above ambient limits. Thus, while at very low light intensities this temperature response is slight or absent, at high summer values it could play a significant part in causing regional variations over the Southern Ocean. It is also interesting as suggesting that Antarctic microalgae (in contrast to krill and fishes) are not adapted to work with maximal efficiency at actual ambient temperatures. In McMurdo Sound, under field conditions, the rates of primary production are only about 10% of the potential maximum (but see Fogg, this Discussion, p. 210).

Despite the importance of these variables and of zooplankton grazing as a further influence, Bunt (1966) considers that the ice regime is of even more importance in determining regional differences in phytoplankton standing crop and production. Not only may the ice layer at its break-up release a significant number of organisms to the water column, but the period of time for which the seas are open is of critical importance in controlling the rate of build up of the standing crop and hence of the total seasonal production. A short season may permit only a partial build up of standing crop, or may mean that the standing crop has only reached its optimal level and commenced to produce at maximal rate by the time the ice closes again. A long season allows plenty of time for the phytoplankton to build up and to continue production at a high level. Under 'long season' conditions, grazing by the zooplankton probably becomes the most important factor regulating plant cell numbers.

3. *The Zooplankton*

Grazing of phytoplankton

Hardy & Gunther (1935) demonstrated directly that in the waters about South Georgia there was an inverse correlation between phytoplankton density and the numbers of herbivorous zooplanktonts (table 36). Because the numbers of phytoplankton in turn could be correlated inversely with nutrient levels there was a further relationship in which *high* phosphate (and low pH) were associated with *low* phytoplankton and *high* krill densities (and, at a further stage in the food chain, with *high* whale densities) (figures 72*a*, *b*). A comparable inverse relationship between zooplankton and phytoplankton was noted in the Weddell Sea by El Sayed & Mandelli (1965), and these authors point out that this pattern holds also for Arctic waters. Marr (1962) demonstrated that the plankton diatom *Fragilariopsis* does in fact form from 18 to 80% of the diet of *Euphausia superba*.

TABLE 36. PHYTOPLANKTON AND ZOOPLANKTON NUMBERS IN SOUTH GEORGIA WATERS

(From Hardy & Gunther 1935)

phytoplankton (cells $\times 10^9$)	*Euphausia superba*	*Euphausia frigida*	*Salpa fusiformis*
3–112	289	3	38
139–341	1913	44	1781
358–608	951	47	1051
800–3328	859	76	675
4643–97230	31	15	246
99050–531200	41	2	49

Hart (1942) also considered that zooplankton grazing was the main factor controlling Antarctic phytoplankton, after comparing average standing crops of the latter with calculated minimum crops (based on nutrient availability) (table 34). In the northern region of the Antarctic he concluded that grazing might be 3 to 5 times as intense as in the English Channel, while at South Georgia it was comparable with the level in the English Channel. Foxton (1964) and Currie (1964) demonstrated that the zooplankton population showed an increase closely following the phytoplankton peak and that, on more detailed analysis,

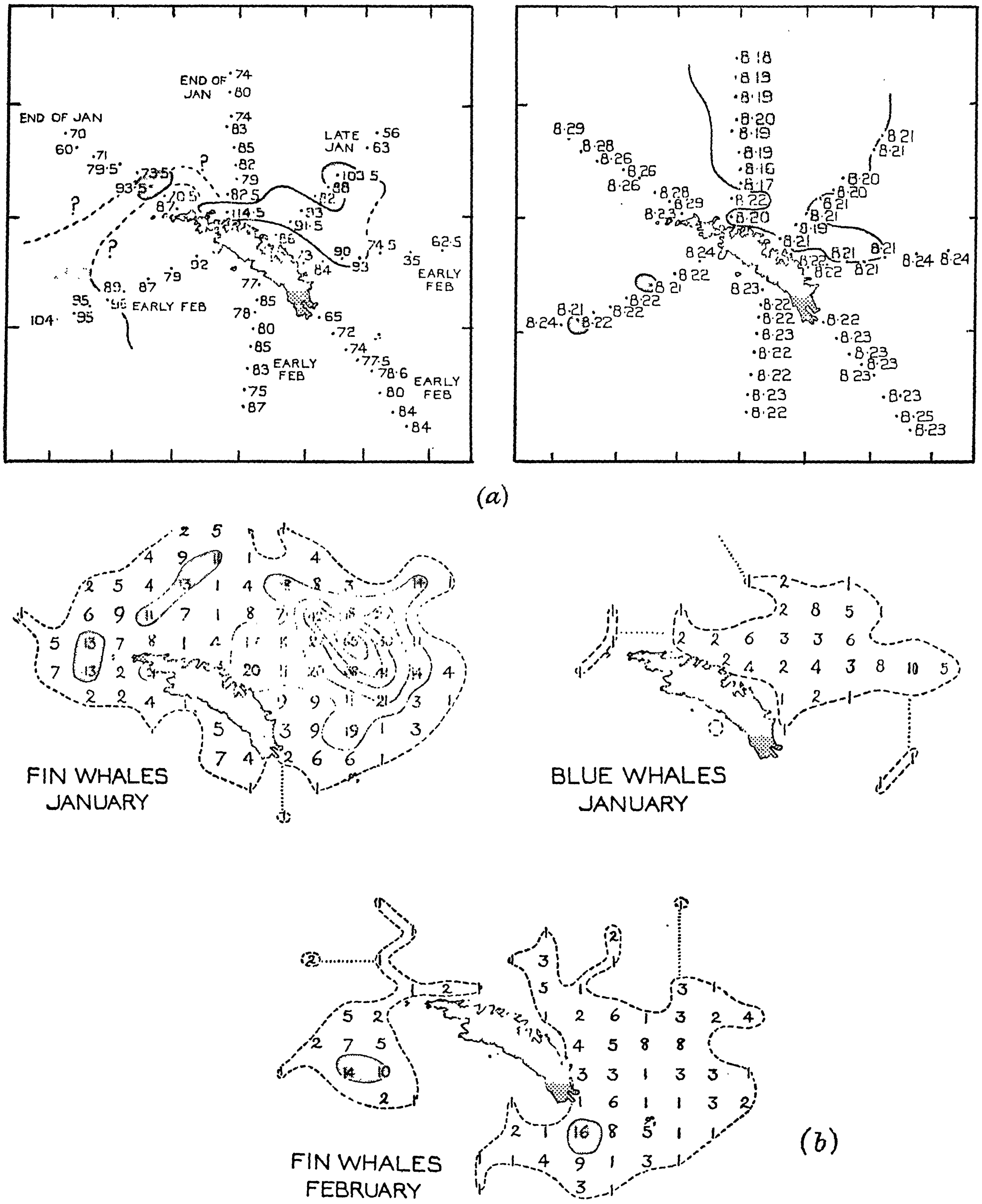

Figure 72. The correlation between (*a*) phosphate and pH (indicators of phytoplankton density) and (*b*) whale numbers, in the waters about South Georgia. Whales are concentrated in areas of high krill density, which in turn have low phytoplankton levels and high phosphate. (After Hardy & Gunter 1935.)

herbivorous organisms could be shown to increase first, carnivores building up as a later stage. Little is known of the detailed food chain sequences involved but this broad pattern is likely to be of general significance. There is an approximate doubling of the biomass of herbivore carbon in the upper 250 m between September and February (Currie 1964), but this reflects vertical migration as well as secondary production and no figures for the latter can as yet be given.

Standing crop of zooplankton

Foxton (1956) summarized information about the standing crop of zooplankton in different zones of latitude in the Southern hemisphere and confirmed that Antarctic waters supported significantly more organisms than tropical or temperate regions (table 37). The peak of abundance occurs very near the Antarctic Convergence. These results have been extended by Vinogradov & Naumov (1958) who examined inshore waters as well as the open ocean. These authors report that below fast ice the plankton totals are small, although zooplankton, especially copepods and euphausiids, increases below 25 to 50 m. Ice free water, however, supports abundant plankton with many immature copepods. The total plankton biomass in the upper 50 m was found to range from 1 to 20 g/m^3, while at 100 to 200 m it was 100 to 150 mg/m^3 and at 200 to 500 m, about 50 mg/m^3.

TABLE 37. STANDING CROP OF ZOOPLANKTON IN THE SOUTHERN OCEAN (AFTER FOXTON 1956)

(Data expressed as mg/m^3)

	Antarctic	Sub-Antarctic	tropical	sub-tropical
0–50 m	55·2	55·8	33·1	40·5
0–1000 m	25·6	20·9	9·8	9·0

As Foxton (1956) emphasized, the standing crop of zooplankton over the whole water column from 0 to 1000 m shows surprisingly little variation over the year, oscillatin about 8 to 14 ml. in volume/m^2 surface. However, because of the marked seasonal migration made by many species, there is a substantial variation in the standing crop in any particular layer, the upper zones showing a summer peak and winter minimum and the deep waters an inverse pattern. Table 38 summarizes the standing crop in the 0 to 5 layer (the feeding zone for birds) and the 0 to 250 m layer which might be considered as the potential seal and whale feeding zone. It is well known (cf. Currie 1964) that these vertical migrations may be of great biogeographical significance since the fauna will spend the summer in a northward-moving cold surface layer and the winter in a relatively warmer southward-moving layer: over the year as a whole temperature oscillations will be damped down and species tend to remain in particular latitudinal zones. The mechanism may explain how it is that many species of Southern Ocean plankton (such as *Euphausia* spp.) do retain characteristic rather narrow zones despite the continuity of the oceanic environment (cf. Mackintosh 1960; Baker 1954).

Just as it is difficult, because of local variability, to indicate one 'typical' figure for phytoplankton biomass over Antarctic waters as a whole, so zooplankton 'typical values' are difficult to assess. Taking Foxton's data as representative, however, a value of 55 mg/m^3 appears reasonable for the upper 50 m. This figure may be compared with the mean of Hart's 'average standing crops' in table 34 for phytoplankton, which is 320 mg/m^3. The combined total of 373 mg/m^3 is still less than the standing crop for the uppermost layers indicated by Vinogradov & Naumov (1958), but is of the same order of magnitude. Moreover, the zooplankton:phytoplankton gross ratio emerges as close to 1:6 which is at least plausible. The zooplankton figures do, however, require qualification in two respects. First, they include both herbivorous and carnivorous species. Secondly, they do not include the largest organisms, notably adult *Euphausia superba*, which were not caught at a representative level in the 70 cm net used by *Discovery* Investigations. As to the former problem, there is no detailed evaluation of the proportion of carnivores in the Antarctic zooplankton although some are known to be very abundant (Littlepage 1964). In the present assessment it will be assumed that these organisms contribute 10 % of the zooplankton biomass (other than krill). Estimations of the biomass of *Euphausia superba* have been made by Marr (1962) who arrives at figures in the range between 2·5 and 29·3 g/m^2. These data apply, however, to aggregations and the average standing crop spread over the whole Southern Ocean certainly cannot approach the higher estimate. To make them comparable the lower of Marr's figures will be accepted as the general average, and it will be assumed that this standing crop is concentrated in the top 50 m. The biomass per cubic metre would then be 50 mg/m^3, which implies that *E. superba* alone has a standing crop equivalent to that of all other zooplanktonts put together. This may well be the case, for there is no doubt that it is far and away the staple Antarctic food organism, only *Munida* spp. approaching it in temperate waters farther north (Marr 1962). The resulting total herbivorous zooplankton biomass of 108 mg/m^3 is, however, high in proportion to the phytoplankton.

TABLE 38. VOLUME (ml./m^2 SURFACE) OF ZOOPLANKTON OVER THE YEAR IN UPPER WATER LAYERS OF THE SOUTHERN OCEAN

0–5 m level (available to birds)

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Sub-Antarctic	2·35	6·05	4·60	1·50	1·80	0·85	1·17	0·92	1·40	1·78	3·20	2·50
Antarctic	2·25	4·32	4·82	5·30	2·50	1·58	1·23	1·88	1·35	0·92	1·30	2·40

0–250 m level

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Sub-Antarctic	5·22	9·80	9·88	3·58	3·82	2·27	3·15	3·40	3·17	5·05	7·60	9·45
Antarctic	5·32	9·05	9·60	9·02	4·85	4·20	3·82	3·70	3·17	4·52	6·35	8·00

HIGHER TROPHIC LEVELS IN THE OPEN SEA

It is well known that baleen whales graze predominantly upon krill and that birds, crabeater seals and fish all take appreciable numbers of this species. Whales, according to Mackintosh & Brown (1956), have (or had) a biomass of 0·28 g/m^2 surface if averaged over the Antarctic Ocean south of the Convergence as a whole, or 0·56 g/m^2 within the inner zone of '1° ice'. Even this second figure may be an underestimate, for if the population of baleen whales in 1933–39 is taken as 300000, of mean weight 50 metric tons, then the biomass averaged over the 9×10^6 square miles ($2·34\times10^7$ km^2) of Antarctic Ocean open in summer would be 0·64 g/m^2 surface. Crabeater seals, according to Laws (1964) and to census results obtained by Eklund & Attwood (1962), have a total population of 5 to 8 million, and taking the mean body weight as 300 kg the biomass over the same area would be 0·06 to 0·1 g/m^2 surface. In practice the species is notably aggregated in the pack ice zone and locally must reach quite high biomass for short periods.

It is more difficult to assess the biomass and role of plankton-eating birds over the

Southern Ocean. Different species are well known to have different feeding ranges, and even juveniles and adults of the same species may have differing migration paths (as in giant petrel discussed, for example, by Tickell & Scotland 1961). The complexities of food preference in southern seabirds have only recently been explored (Tickell 1964), making it apparent that many species are selective feeders and that the spectrum of species encountered in their crops will differ substantially from that taken in plankton nets (while many species may not be exclusively plankton eaters). Census data for bird populations at sea are virtually nonexistent and even breeding colony data are highly approximate. It is well known, for instance, that estimates of the world population of emperor penguin have increased as more and more complete exploration has discovered further colonies, and Korotkevitch (1962) reporting a known world population of this species of 350000 birds, went on to estimate that the real total might approach 1500000 birds, when all breeding sites had been discovered. On a more restricted scale Prévost (1963) computed that at Pointe Geologie, Terre Adelie, there was a biomass of 3000 kg of birds and Weddell seals at peak per 100 m of coast. Penguins made up over 90% of this total, while petrels, though numerous, because of their small size, accounted for a negligible part of the total. If we accept that this population must be sea-feeding, even if the animals only migrated due north for distances of not more than 1000 km, thus retaining the 3000 kg of Prévost's estimate within an area of 100 m × 1000 km the result would be to spread the standing crop of birds and Weddell seal at a density of only 0·03 g/m^2 of ocean. But Prévost's computations apply to an extremely unusual section of the mainland coast of Antarctica—an archipelago of small rock islands in an area largely made up of ice-cliff, and only a small percentage of the total perimeter of the continent offers similar opportunities for breeding birds. It would probably be within an order of magnitude to say that Prévost's data were applicable to only 1% of the Antarctic coastline, including the islands. The aggregation of Antarctic birds at their breeding grounds is a familiar feature of the natural history of the zone, succinctly summarized by Murphy (1964) in the statement that such species 'can feed where they wish, but must breed where they can'. It would seem reasonable to suggest that despite the overwhelming numbers in which such breeding birds appear they yet represent a very small actual biomass per square metre of ocean surface. Of this biomass perhaps 60% depends on plankton as a food source, while the remainder take fish and squids or are predatory on other birds or are scavengers.

Hart (1942) includes fishes as a group feeding in part upon krill and other plankton, although Marshall (1964) confirms that some 90 species of Antarctic fishes are benthic as compared to 60 pelagic species (Andriayshev 1965). Even nototheniid species, ordinarily benthic, can however become secondarily pelagic and take krill during the summer. Unfortunately there are no figures of any kind for fish biomass in Antarctic waters, and such information as does exist suggests that the abundance and species composition of the stock will vary widely from one area to another. Cephalopods are also undoubtedly of very great importance as consumers of the plankton and also of some higher levels in the food chain but there are no estimates of their standing crop. They form a staple diet of the toothed whales and also of certain seals and birds. Tickell (1964), for example, found squid remains consistently in 80 to 95% of samples from *Diomedia chrysostoma* and *D. melanophris*: a substantially higher level than was averaged by euphausians.

The extremely rough figures given here suggest a total for all open sea higher trophic levels except fish and squids of about 14·5 mg/m^3. This is in the ratio 1:7·2 to the total of the zooplankton and is of a plausible order, allowing a significant figure for fish and squids. It is apparent that the open ocean food chains are fairly complex and with a probably steady flow of organic material to successively higher trophic levels. The high standing crop of whales represents (or represented) a rather striking accumulation of living material not immediately returnable via other consumers to the system, but apart from that there are few or no 'dead ends' or static elements. One other interesting generalization can be drawn from the analysis at this stage. Sladen (1964) has pointed out that the annual crop of whales taken by man from the southern ocean over recent decades amounted to 15×10^8 kg. This is equivalent to 64 mg/m^2 of surface, or to 10% of the standing crop. The stock has been unable to withstand harvesting at this level. Sladen (1964) points out that the quantity of whale removed is equivalent in biomass to about 300 million pygoscelid penguins and that in view of the probable similarity in food requirements of certain birds, crabeater seals, and whalebone whales, the reduction in stocks of the latter may be expected to be paralleled by a compensating increase in the former, assuming food to be involved in the mechanism of population control. This is a topic to which discussion will return when the terrestrial ecosystem is considered.

The marine benthos

The total biomass of living matter in the open ocean is about 440 mg/m^3 averaged over the top 50 m. In contrast the benthic biomass in shallow waters is a great deal more, at least in the most productive areas. Belyaev (1958) and Ushakov (1962) indicate standing crops in the 200 to 300 m range off Sabrina Coast of 183 to 1383 g/m^2, and average values over the 100 to 500 m levels of 400 to 500 g/m^2—a standing crop greater by 10^3 than that per cubic metre of open ocean. At 2000 m the standing crop of benthos falls to 2·8 g/m^2 and at 3500 m to 1·4 g/m^2 (figure 73). The figures for great depths are comparable with those from the Sub-Antarctic Indian Ocean or the boreal Pacific, but the shallow water values are substantially greater than those, for example, in Bering Strait where the biomass at 100 to 200 m averages 165 g/m^2 and at 200 to 500 is 113/g m^2.

Similarly, dense benthic communities have been photographed and sampled in the Ross Sea (Bullivant 1959) and off McMurdo (Tressler 1964). It is not at present possible to assess how typical they are of the Antarctic shelf area as a whole, but it seems likely that the sea floor communities do vary a good deal from place to place.

Tressler (1964) comments, for example, on the lower apparent productivity of the benthos at Wilkes station as compared with McMurdo, perhaps to be correlated with the presences of granitic rather than volcanic rocks, and refers to Lisitsin (1959) for confirmatory evidence that the volcanic regions of the Antarctic are especially productive of benthic organisms. Even under the ice shelves, however, some considerable benthos is often present: the area studied in detail by Tressler had only recently been made available for examination by the break off of a large area of shelf, while Littlepage & Pearse, working through a tidal crack several miles from the edge of the Ross Ice Shelf, reported a rich benthic fauna. As Tressler (1964) points out, such under-shelf areas are only marginally darker than normal sea floor regions at 400 to 500 m depth: there can be negligible primary production and provided there is sufficient current circulation to bring in detritus, there is no reason why a substantial fauna should not develop. It is none the less likely that biomasses under the inner parts of these shelves will be rather less than in open waters. Similarly, in coastal waters, ice scour becomes an ecological factor of major importance and restricts algal communities (often dominated by *Desmarestia* spp.) to recesses and crevices. Bearing all these factors in mind, one might none the less expect that the figures cited above will be correct within an order of magnitude for the Antarctic shelf area, and even if the standing crop over the area as a whole is only 10% of the average off the Sabrina Coast, it will approximate in biomass to the standing crop in the entire water column above it.

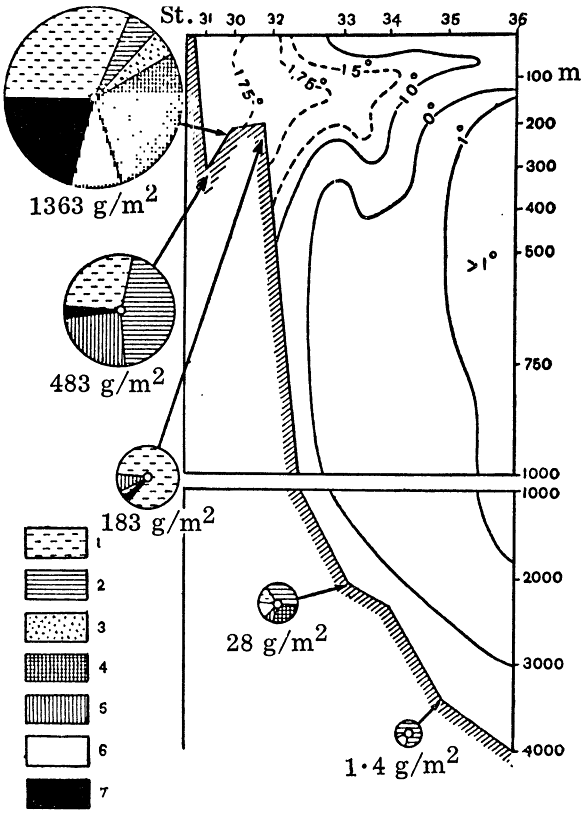

FIGURE 73. Benthic biomass off Sabrina Coast. (From Ushakov 1962.) Note that the scale for Stations 33 and 35 is magnified 25 times as compared with the other sites. 1 = Porifera; 2 = Vermes; 3 = Mollusca; 4 = Bryozoa; 5 = Echinodermata; 6 = Crustacea; 7 = other groups.

The benthos in Antarctic waters differs from the plankton and nekton in that a very high proportion of it is made up of slow-growing, sessile or sluggish organisms such as sponges, bryozoa, echinoderms, gorgonians and tunicates. Belyaev (1958) estimates that as much as 60% of the standing crop of benthos may not be directly available as food for other organisms, and Holme (1964) has referred to the sponges in particular as a 'dead end in the food-chain'. However, Fry (1964) points out that pycnogonida of the genus *Collossendeis*, which are abundant in the Antarctic, feed largely on sponges there and reports that dissection of sponges at McMurdo Sound revealed the presence within them of numerous animals; some nudibranchs may also utilize this food source. Even so, it seems likely that the production rate of benthos is likely to prove low, and the energy flow within the system will also be generally slow. Many organisms may return to the cycle only through the decomposers. Tressler (1964) reports that there is little accumulation of organic material below the benthic communities of McMurdo Sound, although, off Wilkes, microbial degradation was more evident in the sediments.

Of the 40% of benthos available to higher trophic levels, much will be made up of Polychaeta, Amphipoda and other Crustacea which are locally abundant. These animals presumably form the staple diet of nototheniid fishes which are predominantly bottom feeding and which may in turn be taken by Weddell seals and penguins, and so be brought into the main food chain of the ocean as a whole. Among the sublittoral/littoral benthos in the shallowest water the limpet, *Patinigera polaris* is an important element in the diet of gulls, *Larus dominicanus*.

The terrestrial ecosystem

1. *Interflow between marine and terrestrial ecosystems*

The complex food chains and high standing crops of the oceanic ecosystem in the Antarctic contribute to the land via four main pathways. These are:

Wind deposited spray.
Excreta of seals and seabirds.
Food sources for one land-based bird (the sheathbill).
Energy sources for an invertebrate community at the supralittoral fringe level.

Wind-borne sea-spray is, as Allen & Northover (this Discussion), Holdgate, Allen & Chambers (1967) and Allen, Grimshaw & Holdgate (1967) have demonstrated, an important nutrient source for the cryptogamic vegetation of the land, and in Maritime Antarctic localities, such as Signy Island, it may reach unusually high levels. Allen and his collaborators have also demonstrated that the high nitrate and phosphate levels found on Signy Island can be correlated with the large populations of breeding seabirds on that island, although there is some doubt as to mechanism of dispersal of these nutrients.

The density of seabirds over the Southern Ocean has already been demonstrated to be very low. Conversely, the breeding aggregations represent a very high biomass per unit area of the breeding grounds. Taking Prévost's data (1963), supported by an independant check for Signy Island, the peak breeding biomass of birds on the latter island would if averaged over the whole land surface amount to from 15 to 40 g/m^2 in summer, falling to no more than 0·1% of this figure at winter minimum. Locally, as in penguin colonies, the mass of birds present is far greater, reaching the order of 10 kg/m^2 at the height of the breeding season. Under these circumstances it is evident that the mass of faecal matter deposited is likely to amount to many g/m^2 day in the breeding colonies, and to a appreciable amount even over the general surface of the land. The influence is intensified by the common co-existence of the main bird colonies and of the chief vegetation carpets in the snow free lowlands, but the general over-flying of the island by birds undoubtedly result in contamination even of the central snowfields, which in turn increases the nutrient level of meltwater. The influence of seals is of course concentrated in the coastal lowlands, but even these animals influence some vegetation directly, and the prevailing strong winds can be expected further to distribute nutrients from their wallow grounds as well as from the bird colonies.

The nutrient input from birds and mammals is the major pathway for energy from the marine to terrestrial ecosystem in the Antarctic, and it appears to result in the land areas in the maritime zone paralleling the sea in having abundant nutrients at all seasons for plant growth. The littoral fringe also supports one bird, the sheathbill (*Chionis alba*), which is a shore feeder in winter and a scavenger about penguin colonies in summer (Jones 1963). This species is the nearest approach to a true land-bird in the Antarctic Zone, although it depends indirectly or directly upon marine sources for all its food and makes long trans-oceanic migrations. In a similar way marine birds such as the skua, *Catharacta skua lönnbergi*, and giant petrel *Macronectes giganteus*, although predominantly predators and scavengers feeding both on land and water, depend upon marine food sources in both situations. The final, small, energy pathway from sea to land in the Antarctic occurs through the medium of beach debris. Cast up algae are to be found locally within the supralittoral fringe, although never in the quantities characteristic of temperate zones with a much greater littoral and sublittoral vegetation. Within this debris there are a few characteristic mites, and enchytraeid worms on Signy Island also appear restricted to such submaritime habitats. In other localities along the Antarctic Peninsula the two Diptera *Belgica antarctica* and *Parochlus steineni* appears largely confined to the coastal zone, breeding in brackish pools or among wet debris.

In general, therefore, it may be said that the land and sea ecosystems in the Antarctic interact only in one major way—through the flow of nutrients from sea to land via wind-deposited spray and excreta. There is no doubt that proportionately this nutrient source is of much greater significance in the Antarctic Zone than in temperate and tropical regions, because purely terrestrial nutrient sources are reduced. The dependence of land vegetation on nutrient input from sea birds reaches its climax, however, in continental localities where the richest vegetation (and in Dronning Maud Land, the only moss) is restricted to the immediate vicinity of snow petrel (*Pagodroma nivea*) colonies (Siple 1938; Dalenius & Wilson 1958; Bowra, Holdgate & Tilbrook 1966; Llano 1965).

In an earlier section mention was made of the food resources released for other consumers, by the human harvest of whales. This crop was said to be equivalent to 300 million penguins per annum. The present world population of pygoscelid penguins is not known but is probably of the same order as this. Inspection of the coastal area in the Maritime Antarctic suggests that the limiting factor in population increase is likely to lie in the availability of breeding grounds accessible to feeding areas during the nesting season. Granted a parallel restriction of crabeater seals in the pack ice zone, one might suggest that the krill unconsumed by whales may either remain unconsumed or be taken by a genuinely pelagic animal which can parallel the whale's ecology more closely than either penguin or seal.

2. *Vegetation*

In the summer of 1963/64 a series of cores from the main bryophyte communities on Signy Island were weighed fresh and after drying. Dry weights were rather constant and crude measurements suggested that the potential air space in the vegetation was also rather uniform, the mean value being near to 70%, but actual air space varied a great deal, inversely with water content. Gimingham (this Discussion) confirms this result. Rough computations based on the field data suggest that if the living moss layer is 3 cm deep, the standing crop per m^2 should be of the order of 5000 to 10000 g. Further figures, kindly made available by Mr P. J. Tilbrook confirm this suggestion. Even if this result is substantially in error the conclusion cannot be avoided that in terms of living biomass the terrestrial vegetation in the richest parts of the maritime Antarctic must exceed or be at least comparable to that of the richest areas of the ocean floor. Equally the standing crop even of these rich areas is minute compared to that in temperate regions where the ground carpet has super-imposed upon it, field, scrub and canopy layers of a complex vegetation.

There are three important comments to be added. First there is as yet negligible information on the rates of production by Antarctic bryophytes. Gross extrapolation based on a radiocarbon date of near 1900 years for the base of a frozen moss bank 180 cm high on Signy Island might suggest a minimal increment of 1 mm per annum, but this growth is the result of a balance between elongation of shoots and decomposition of dead material below the surface crust. There is also evidence of some compaction in the deeper layers of the frozen peat. Longton (this Discussion) suggests that 3 mm is an approximate annual increment in one bryophyte species at South Georgia: extrapolation from this result to Signy Island is obviously a doubtful procedure. It is probably not worth saying more than that a 1 mm increment would imply a production of the order of 300 g live weight/m^2 y or 100 g dry weight/m^2 y. Critical direct measurements of these parameters are urgently needed.

The second qualifying comment is this. Bryophyte vegetation covers only a small proportion of the most favourable areas within the Maritime Antarctic. On Signy Island half the surface is permanent snow and ice, and of the remainder probably only 10% supports substantial plant communities. A 5% cover over the whole area would give an average biomass down to 250 to 500 g/m^2. Signy Island is substantially better vegetated than many maritime Antarctic localities: Coronation Island, for example, has at least 90% of its surface covered in permanent snow. Such areas may support the snow algae described by Fogg (this Discussion) and have a slow rate of primary production, adding some nutrients to the terrestrial ecosystem, but the contribution from this source is evidently slight. The continental area is a whole order of magnitude poorer again in the proportion of vegetated land and the richness of the vegetation it supports. Hence the figures for standing crop can be reduced to an infinitesimal level by averaging over the whole continent. The only procedure at the present time to retain any meaning is to analyse one area at a time and that is why for the remainder of the present paper Signy Island alone will be considered.

Thirdly, on Signy Island, there is a marked local variation in decomposer activity. Allen & Northover (this Discussion p. 179) have pointed out that in many vegetation types there is only a thin layer of organic material below the living crust of vegetation and that this in turn does not intergrade into the mineral material beneath. They conclude therefore that decomposer activities are rapid and that dead moss stems are destroyed as fast as they are produced. Elsewhere substantial peat banks up to 2 m deep underly a turf of *Polytrichum* and *Dicranum* and this frozen material represents a capital of organic production temporarily withdrawn from the circulation but locally brought into it again by erosion which allows surface thawing and decomposition.

Taking all these elements together, one may conclude first that there is intense local variation in the mosaic of terrestrial habitats and vegetation types in the Maritime Antarctic; secondly, that this variation applies equally to distribution of standing crop, production and decomposition; and thirdly, that despite the need for qualification, at its richest Antarctic vegetation can provide as high a production and a higher standing crop than any maritime area in the adjoining ocean. The seas are distinguished by their uniform habitat conditions and more general high level of production, not by actually surpassing the land in gross biological capacity. Equally, while the seas compare with temperate waters in these respects, the land is poor on any such comparison with other climatic zones.

3. *Secondary production*

A further paradox of the terrestrial ecosystem in the Maritime Antarctic is that, so far as is known the large standing crop of mosses and hepatics which covers substantial lowland areas is scarcely grazed by herbivorous invertebrates; Dodge (1964) commented similarly that apparent damage to lichens by invertebrates was rare or non-existent. It is known (Gressitt 1964) that a substantial microarthropod fauna inhabits areas of Antarctic land where bryophytes and indeed all macroscopic vegetation cannot be found.

The arthropod and nematode fauna of the Maritime Antarctic probably feeds largely on fungi and perhaps small soil algae. They thus depend on the larger primary producers only through an intermediary. Microfungi are certainly abundant both in Maritime (Heal, Bailey & Latter, this Discussion) and Continental Antarctic soils (Gressitt 1964), and Janetschek (1963) has stated that they form the main food of Collembola and are the start of numerous food chains. Other arthropods and nematodes may take plant debris as well as living material. Tardigrades and nematodes may feed directly upon green plants, the latter piercing cell walls with stylets. The whole question of food requirements by the Antarctic land fauna is still almost unexamined but it seems likely that critical studies will confirm that the terrestrial higher vegetation, like the marine benthos, represents an accumulation of organic matter which is grossly underutilised by the fauna.

Heal (1965) has demonstrated that the biomass of testate amoebae in the soils of Signy Island is comparable with that in northern British temperate areas. The richest soils have a biomass of 2·03 g/m^2 of these organisms, while the poorer areas may support only about one tenth this figure. In terms of numbers of individual organisms, the Maritime Antarctic soils are comparable with those of temperate regions, while in terms of numbers of species they are significantly poorer: a startingly high proportion of the total testate amoebal fauna is provided by one animal, *Corythion dubium* (Heal 1965; Heal, Bailey & Latter, this Discussion, p. 191).

It seems likely that the remaining protozoan fauna of the Signy Island soils will have a biomass approximately equal to that of the Testacea. Thus the Protozoa alone will account for some 4·0 g/m^2 .Tilbrook (this Discussion) has provided information about Nematoda, mites and Collembola which resemble the Testacea in having small species diversity but great abundance of those organisms that do occur, with a biomass comparable to that in the same British soils to which Heal referred. Taking this result as a guide, the biomass of Nematoda in the most favourable Antarctic habitats is likely to be about 0·5 g/m^2, of Collembola 0·4 g/m^2 and of Acarina 0·2 g/m^2. A small fraction of the latter biomass, under 0·05 g/m^2 will consist of predatory species representing a higher trophic level. No estimates for Tardigrada and Rotifera have been made, but it is unlikely that these together total more than 0·1 g/m^2. Taking all these results together, the result is to indicate a land faunal biomass not exceeding 5·2 g/m^2. In many areas far less favourable than those sampled it will be much less, and over the vast expanses of snow and bare rock, it may be taken as nil.

Summarizing the land ecosystem, it is therefore apparent that the biomass of plant material vastly exceeds that of the fauna dependent upon it (by a factor of 10^2 or 10^3). In this assessment no allowance has been made for the biomass of fungi and bacteria which might be expected significantly to exceed that of the land fauna, which substantially depends upon these groups. It is clear that the groups that are represented in the area occur with an abundance comparable to that in temperate regions, but that in species and groups the Antarctic biota is impoverished and disharmonic. Heal, Bailey & Latter (this Discussion, p. 195) and Stanley & Rose (this Discussion, p. 205) point out that a substantial measure of temperature tolerance characterizes the microflora and that temperature adaptation has also occurred. Even so the optimum for microfloral growth in the Maritime Antarctic is around 10 to 15 °C (the same as the marine phytoplankton, according to Bunt 1964). These temperatures are reached in summer as a result of radiation warming (Longton & Holdgate, this Discussion, p. 238), but only for brief spells. Processes of decomposition on Signy Island are about three times slower than in upland Britain (Heal, Bailey & Latter, this Discussion, p. 195). The activity of the fauna may also be dependent upon brief periods of thermal amelioration and some Antarctic Collembola are known to be virtually quiescent around 0 °C (Pryor 1962: Tilbrook, this Discussion, p. 274). Consequently it may prove that biological processes at all trophic levels proceed relatively slowly and spasmodically and that the habitat mosaic on the island in respect to microclimate (especially temperature) and water availability is of paramount significance.

Finally, it is noteworthy that the 'distributed biomass' of breeding birds in summer over Signy Island and probably over many other Maritime Antarctic localities is a factor 10 times greater than the standing crop of truly terrestrial animals. This, too, is likely to be a feature characteristic of the whole polar region. In a temperate zone, even in coastal areas where a large breeding avifauna exists, the biomass of soil animals, might on the other hand, be expected to reach from 50 to 200 g/m^2, the Lumbricidae (absent from the Antarctic) making up a large proportion of the total (Cragg 1961).

The freshwater ecosystem

The freshwater lakes of Signy Island and comparable Maritime Antarctic localities derive nutrients from rocks and land drainage, and the latter is materially affected by input from marine sources. Furthermore, the breeding bird populations undoubtedly contribute nitrate and phosphate directly, and wallowing elephant seals play a major part in determining the characteristics of some pools (Heywood, this Discussion, p. 353).

For the greater part, the freshwater ecosystem in the Antarctic is in other respects a rather closed web of interactions, and little can be added to the account by Heywood. In contrast to the land areas, there is a substantial fauna probably depending fairly directly on the primary producers among the plankton and the benthic felt of Cyanophyceae. Higher trophic levels are also more in balance with the herbivores, while a small amount of vertebrate predation probably occurs from terns (*Sterna vittata*) taking Anostraca (*Branchinecta gaini*). Losses from the system also occur via the outflow drainage. The freshwater ecosystem on Signy Island as a whole would certainly appear to be a more complete microcosm, and in this respect closer to the marine situation, than that on the land. No measurements of biomass, production, or of the rates of processes are available for a Maritime Antarctic locality.

Discussions and conclusions

This speculative review, which incorporates many figures of dubious reliability presents for the purposes of future discussion some tentative conclusions concerning the energy flow within marine and terrestrial ecological systems in the Antarctic, and more especially in the Maritime Antarctic. It is summarized diagrammatically in figure 74. The first conclusion that must be drawn is that vastly more quantitative work is required upon standing crops, production rates, and rates of energy flow between higher trophic levels. The following conclusions, based on work already done, are suggested as hypotheses for testing:

(1) The marine ecosystem in the Antarctic is a fairly completely surveyed system of interactions, with standing crops and rates of primary and secondary production at least comparable with those in temperate waters, or in some respects (especially biomass) above them. Nutrients do not limit plant production, but the seasonal light and ice regimes are of prime importance.

(2) The benthos in the Antarctic with its large standing crop of slow-growing organisms, is only partly available as a food resource for higher trophic levels and to a large degree returns to the system via the decomposers.

(3) The whale biomass in the Antarctic at peak greatly exceeded that of any other plankton consumer, and its recent reduction by man may therefore be expected to have major ecological consequences. Breeding space competition may limit any compensating increase by seabirds, while the restriction of crabeater seals to the pack ice zone may prevent their exploitation of the surplus. A pelagic consumer (or man), may ultimately remove this surplus.

(4) The marine organisms in the Antarctic are adapted to varying degrees to the low ambient temperatures. The primary producers have thermal optima above ambient, but krill and fishes are more closely adapted and have optima near to 0 °C and upper limits around 4 to 5 °C (MacWhinnie 1965; Wohlschlag 1964).

(5) There is very substantial spatial and seasonal variation in biomass and production in the marine ecosystem. The variability is even more extreme in the terrestrial system. Spatially, the biomass of the terrestrial cryptogamic vegetation ranges from zero to a level exceeding that of even the dense marine benthos. Seasonally, terrestrial life proceeds by

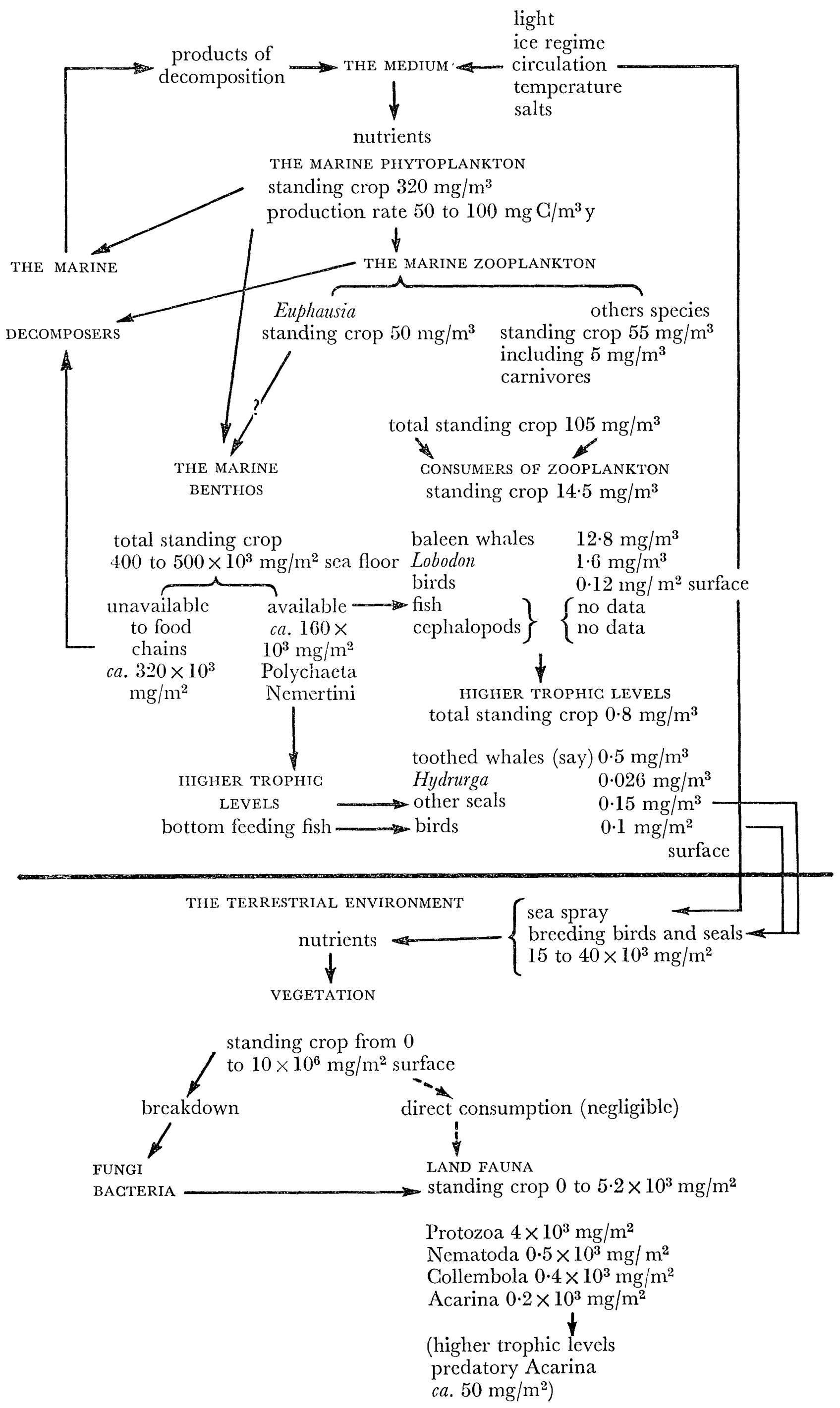

FIGURE 74. Food chain diagram for the more important interrelationships in the Antarctic seas.

brief periods of high activity during short spells of temperature amelioration and water availability.

(6) The terrestrial vegetation in the Maritime Antarctic, like the marine benthos, is only consumed to a small extent by herbivores and is largely made available by decomposers, and especially by fungi.

(7) The heavy seabird aggregations over small land areas in summer exceed in distributed biomass (and still more in actual concentrated biomass) that of all other animal matter and have a profound ecological impact, especially in providing nutrients of marine origin for the flora. As in the sea, it is unlikely that nutrients are limiting to plant growth in terrestrial maritime environments, but they can reach toxicity levels locally.

(8) The terrestrial flora and fauna is impoverished and disharmonic. Few species occur, but those that do exist are locally abundant, and the main groups compare in biomass with their populations in upland temperate areas. The species poverty and disharmony may, in some groups at least, arise from biogeographical causes and reflect the isolation of Antarctica by sea barriers over the 10000 years for which the present habitats in the coastal zone have probably been available.

(9) The terrestrial biota contains many organisms with tolerance of low temperatures, but few so closely adapted to the polar habitat as to be active in subzero conditions. In most cases optima are probably in the range of 10 to 15 °C, reached only locally in summer in areas open to radiation warming. For such organisms, life probably involves short spells of rapid activity and long periods of semi-quiescence. Tolerance of extremely rapid temperature fluctuations is essential.

(10) The freshwater ecosystem is relatively closed and complete with several trophic levels represented among the few species present, these species being relatively temperature tolerant, but not adapted to extreme cold.

(11) A very high proportion, at least of the Antarctic land biota, can be regarded as cool-temperate zone species with substantial temperature tolerance and efficient dispersal capacity, rather than highly specialized polar organisms operating only—or most efficiently —at low temperatures.

This paper comes at the conclusion of five years close involvement with Antarctic biology. I would like here to express my warmest thanks to those with whom I have been associated in this period. I am especially indebted to Sir Vivian Fuchs and others in the British Antarctic Survey, particularly P. J. Tilbrook, R. B. Heywood, and R. E. Longton and to Dr S. W. Greene of the Department of Botany, University of Birmingham. The support and encouragement of Dr G. de Q. Robin and other colleagues in the Scott Polar Research Institute has been a continued stimulus. Finally I am most grateful to Dr J. E. Smith, F.R.S., who as Professor of Zoology at Queen Mary College, London, watched over the growth of the British Antarctic Survey Biological Unit.

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