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BIOLOGICAL RESEARCH AT MACQUARIE ISLAND

This issue and the next issue is devoted to the biology of Macquarie Island, a sub-Antarctic island in the Southern Ocean southeast of Tasmania, of which the island is a dependency. A map of Macquarie Island, showing place names mentioned in this issue, appears on p. 2.

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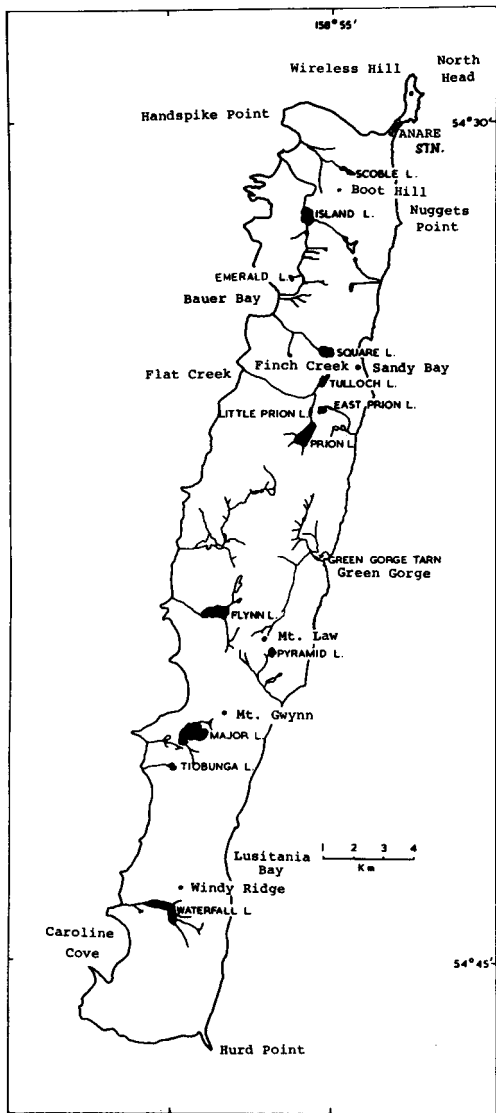
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Map of Macquarie Island showing place names mentioned in this issue.

A HISTORY OF MACQUARIE ISLAND BIOLOGICAL RESEARCH UP TO 1971

S.E. Ingham

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(Editor's note: Susan Ingham wrote this article largely from memory and a few meagre notes. Gavin Johnstone checked many of the details, made some alterations, and supplied some additional material.)

Early Years — 1948 - 55 (The Arthur Gwynn Era)

During the first few years, although biologists were included in ANARE parties, few of them were very successful. This was because they were young graduates whose supervisors had not visited the island and had no idea of the working conditions, and could not supervise adequately from a distance. Only the very well organised and highly motivated Bill Taylor (botany) (Taylor 1955a,b) and John Bunt (marine) (Bunt 1955a,c; 1965) succeeded in overcoming the difficulties.

By contrast, Arthur Gwynn (Gwynn 1953), who was Officer-in-Charge and Medical Officer in 1949, also managed to lay the foundations of all subsequent bird and seal work — but then he had a biological as well as a medical degree, and was (and still is!) a dedicated birdwatcher of many years' experience. He remained on the ANARE staff until 1955 and briefed several of the bird-and-seal-watchers (e.g. medicos Frank Soucek 1952 and Stefan Csordas 1955). He organised the elephant seal banding from 1951, when it became clear that Heard Island was not going to be occupied long enough to give decent results, and arranged for bird-banding, with a job lot of bands from New Zealand, from Dom Serventy and improvisations, in 1952. When the Australian Bird-Banding Scheme started up (1954), ANARE was a founder member; but even the 1952 and '53 expeditions produced results: some giant petrel recoveries (Downes *et al.* 1954), and some nesting albatrosses were banded so that their known breeding life became two years longer than it might have been. (Arthur also had the effect of making Phil Law, the then Director of the Antarctic Division, think that all Medical Officers could 'do biology' which was not always the case!)

The Late Fifties — Birds and Seals

During most of the 50's there were no full-time biologists, but some of the part-time bird-banders and seal-watchers made up in enthusiasm and regularity. Stefan Csordas, Medical Officer in 1955, '57 and '59 is the outstanding example: he not only organised the mass banding of giant petrels which produced some spectacular recoveries (Ingham 1959), but was out counting seals and looking for banded ones in all weathers except actual blizzards (Csordas 1962; 1963a,b; Csordas and Ingham 1965). On the morning after a ding, he'd leave the aspirin and alka-seltzer on the surgery bench with a notice 'Help Yourself', and be off down the Isthmus before anyone else was up. (I've also heard, though I can't vouch for it, that when Mike Taylor was Cook in 1954, he baked bread only once a week, and kept it locked up, to give himself more time for seal brand-hunting). The results of this are our elephant seal papers (Carrick and Ingham 1960; 1962a,b,c; Carrick *et al.* 1962a,b; Ingham 1967).

Robert Carrick took over the supervision of the general biological work in 1955 when Arthur Gwynn left the Antarctic Division (they visited Macquarie together in December 1954, which was Arthur's last visit and Robert's first).

1. He arranged for Technical Officers from the CSIRO Wildlife Survey Section (as it then was) to go to Macquarie while remaining on CSIRO payroll, i.e. the Antarctic Division paid their hard-lying allowance, keep and kit but did not have to find a position or salary. These were Kent Keith in 1956 and Mike Hines in 1957, and their job was primarily bird survey, especially collections (Keith and Hines 1958). Kent and

Mike also weighed Wandering Albatrosses chicks, proving that they must be fed throughout the winter, weighed elephant seal pups, and numerous other chores.

2. He arranged for two or more senior biologists to visit Macquarie on each changeover trip. Sometimes these were supervisors: sometimes they made collections and instructed party members, e.g. Durno Murray and George Dunnet not only collected ectoparasites but had Mike Hines and Stefan Csordas do some simple experiments during the year. Sometimes they were simply good publicity, e.g. the well known American bird-book-writer Roger Tory Peterson.
3. He arranged supervision for some of the graduate biologists who were appointed from 1960 on, e.g. Keith Watson (entomology) (Watson 1967), and Tony Evans (limnology of plateau lakes) (Evans 1970) both in 1960.

John Warham (1959-60) was another of the self-propelled birdwatchers, a Yorkshire terrier with inexhaustible energy. (Unqualified then, he used his Macquarie Island salary to return to England and go to Durham University, got his BSc and PhD, and is now a senior member of the Zoology Department at Canterbury University, New Zealand). Apart from his penguin studies (Warham 1963; 1971), he also worked with petrels, publishing on the white-headed petrel (Warham 1967) and on the giant petrel (Warham 1962) and with Bill Bourne's collaboration unravelling the mystery of the solitary and colonial nesting Nellyies (Bourne and Warham 1966).

My own modest claim to fame is that, while Biological Secretary to the Antarctic Division (1956 - 61), I walked into Phil Law's office one day in 1959, asked to go to Macquarie, and caught him at exactly the right moment. We easily made up a cabin of 4 women for the December 1959 changeover: Isobel Bennett and Hope Mackenzie (littoral ecologists) and Mary Gillham (cryptogamic botanist from England) and me. We were lucky with the weather and had a very successful trip. I fondly remember a day spent walking to Bauer Bay and back, with John Warham, in brilliant sunshine! After that women went on nearly all changeovers to Macquarie (a toe in the Antarctic door, if not a foot).

The Sixties

At the beginning of 1961 I left the Antarctic Division and joined CSIRO Division of Wildlife Research. I was no longer whole-time on Antarctic work; in particular, I had little to do with organization. Perhaps for this reason my memory for names and dates is not so good as for the earlier years — some I'm sure I've forgotten completely.

For us, the major work was the Royal Penguin Banding Study at Bauer Bay. Wim Vestjens (1962), Dave Purchase, Ken Simpson and Duncan Mackenzie are the names here, the first two being CSIRO personnel and the other two Antarctic Division appointees. Unfortunately, continuing problems with band wear and loss plagued us, and the birds became increasingly sensitive to the presence of observers, so that although we got some good results they were not as good as we'd hoped, and only a small selection has ever been written up (Carrick and Ingham 1970; Carrick 1972). At its peak, a large number of birds in the two small colonies at Bauer Bay were banded, and the colonies were staked in a grid for easy(!) location. We found considerable faithfulness to site and mate, and that chicks tended to return to breed in the part of the colony where they were banded. We also worked out how a pair divides the incubation and brooding: the male not only comes ashore first in spring and reclaims the site (sometimes 3 weeks before the female turns up) but also takes the first long stint of incubation, which is not what one would expect. Accommodation at Bauer Bay started with a tiny aluminium cabin (Wim's Inn; this was so unhealthy that Wim became physically ill, and had to be carried back to the ANARE station by stretcher party), then progressed to a small timber one-room shack (the Rex at Bauer, named after a Canberra hotel and Rex Filson, then carpenter and amateur botanist, now professional botanist at the Melbourne Herbarium), and then a two room palace (the Parker Royal, Alan Parker being the carpenter).

All (well, most) Wandering Albatrosses adults and chicks were banded in the population explosion of those years, and nests/nest sites monitored annually. We found a very high survival of chicks to the pre-breeding years, and that they tended to return to the general area where they were bred: Caroline Cove chicks to Caroline Cove, Flat Creek to Flat Creek area, Handspike-Bauer area to that same area.

Other more or less independent studies were undertaken through the 1960's. John Ling (Ling 1965, 1966, 1968; Ling and Thomas 1967) and Mike Bryden (Bryden 1968a,b,c; 1969a,b; 1971; Bryden and Lim 1969) had their own programmes on seals, building on what had gone before, and John Jenkin started his long-term studies of the island's vegetation (Jenkin and Ashton 1970).

Latterly, Antarctic Division appointees worked in the Royal Penguin study but also conducted their own studies, normally towards higher degrees. Peter Shaughnessy conducted a series of projects on population genetics of birds (Shaughnessy 1970a,b,c,d) and seals (Shaughnessy 1969), and Rod Simpson worked in the littoral and sub-littoral zones (Simpson 1976a,b).

In early 1967 Robert Carrick and I were seconded to the Mawson Institute for Antarctic Research at the University of Adelaide. I left to come to my present job in CSIRO Publications at the end of 1969; Robert stayed until his retirement to the north of Scotland in autumn 1971. Sadly, perhaps, biological science did not retain its footing in the Mawson Institute, but reverted to the Antarctic Division. Knowles Kerry and Gavin Johnstone were the last biologists to winter on Macquarie Island under the Carrick regime, in 1970, working mainly on albatrosses and giant-petrels. Upon Carrick's retirement, they were retained to form the nucleus of the Division's new Biology Section. At the same time, it was decided to phase down the Division's program of biological research at Macquarie and to develop a new program on the Antarctic continent. Fortunately this coincided with the establishment of the Tasmanian National Parks and Wildlife Service which has continued to conduct an active biological program at Macquarie Island since then.

And that's where my memory gives out, though I know there should be more!

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- (Editor's note: All references, other than those listed below, are cited in the paper "A review of biological research by Australian National Antarctic Research Expeditions, 1947 - 71" by G.W. Johnstone, 1972, *Polar Record* 16, 519 - 532).
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SUMMARY OF BIOLOGICAL RESEARCH ON MACQUARIE ISLAND 1972 - 1982

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Johnstone (1972) prepared a comprehensive review of earlier biological research on Macquarie Island from 1947 to 1971. The following brief summary (see Table 1) deals with subsequent work by Australian National Antarctic Research Expeditions to the island. In these eleven years biologists from the Antarctic Division (Department of Science and Technology), the Tasmanian National Parks and Wildlife Service, eight Australian universities and several overseas universities, the Australian Museum (Sydney), the National Museum of Victoria, and a variety of other organisations, occupied a total of 83 berths on the ANARE relief ships up to the end of the 1982-83 summer. Most of them (56) spent "changeover", a period of less than one week working on the island but the remainder (27) spent about 3 months during summer or a whole year. Space allows mention of only some of the major projects undertaken but a wide variety of shorter projects involving surveys and sampling for taxonomic, genetic, anatomical and physiological studies have taken place. Giant Petrels and Albatrosses (with the exception of the Light-mantled Sooty Albatross) continue to be banded to determine population trends over long time periods. The present longterm projects generally concern management of the island and processes which formed its biota. The largest programme is operated by the Tasmanian National Parks and Wildlife Service for the eradication or control of introduced animals; rabbits, cats and others. Rabbit ecology has been fully studied and control implemented with the result that the whole island has been transformed (Brothers *et al.* 1982). Out of this also came work on the status of all seabirds breeding on the island and an atlas of vascular plants (Copson 1984). Melbourne University projects have measured the productivity of tussock grasslands (Jenkin 1975) and studied the fungal (Kerry and Weste 1984) and algal flora of the island. The Australian Museum completed a large scale survey of the littoral habitat, including a diving programme (Lowry *et al.* 1978). Related programmes in palynology, glaciology and erosion have looked at present and past processes that formed the island and its biota. The Antarctic Division and the Tasmanian National Parks and Wildlife Service are currently censussing penguin populations and their diet. Many interesting and important papers produced in biological sciences during this period of research on Macquarie Island are contained in a bibliography of biological publications (Betts 1981). An example of one area of study not receiving much attention, however, is the terrestrial invertebrates and soil fauna. Given continued access to the island, though, such deficiencies will be made up in future years.

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TABLE 1. Biological projects undertaken on Macquarie Island 1972-1982.

Tussock grassland productivity 72-73, 75-77	
Rabbit ecology/control and work on vertebrates/vascular plants 72-82	
Litter decomposition 73, 75-78	Diatoms 78
Trace elements in tissue 73	Palynology/erosion 79
Cormorant breeding 73	Peat/cryophytes 79
Cryptogamic flora 75	Marine invertebrates 79
Marine algae 75, 80	Algal productivity 79
Planarian survey 75	Algae sampling 80
Seal ecology/anatomy 75-77	Littoral communities 80
Virology 76,82	Penguin taxonomy 80
Freshwater limnology 76, 78	Peat palynology 81
Marine littoral survey 77	Erosion 81
Flora conservation 77	House mouse ecology 81
Penguin ecology 78	Penguin anatomy/physiology 82
Algal taxonomy 78	

VASCULAR FLORA AND VEGETATION OF MACQUARIE ISLAND

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The subantarctic flora, both vascular and nonvascular, is characterised by few species (Greene and Greene 1963; Greene and Walton 1975) which are widely distributed. The number of species which inhabit an island is determined by its geological history together with its size, diversity of habitats, geographical isolation and climate. An early comprehensive review of the biogeography of subantarctic floras is given in a series of papers on the southern cold temperate zone published in the Proceedings of the Royal Society of London Series B in 1960. (Scottsberg 1960; Godley 1960; Wace 1960; Couper 1960; Du Rietz 1960; Troll 1960). This symposium is an invaluable reference source for the reader interested in the phytogeography of the subantarctic.

Forty five species are represented in the vascular flora of Macquarie Island. The first collections were made by sealers and sent by J.H. Fraser,

Superintendent of the Sydney Botanic Gardens, to W.J. Hooker at Kew in 1824. J.H. Scott undertook a short survey of the vegetation in 1880 (Scott 1882) and noted the affinity of the vegetation with the New Zealand flora. In 1884, A. Hamilton visited the island and made collections of nearly the entire vascular flora. The first long-term scientific study of the island was undertaken during the Australasian Antarctic Expedition of 1911-14 when H. Hamilton was stationed on the island as biologist. Cheeseman (1919) described at length the 36 vascular plants collected. Ecological notes accompanied by illustrations of the island's vegetation and flora were published later (Hamilton 1926).

In the first few years following the establishment of the Australian National Antarctic Research Expedition station in 1948, extensive collections of the flora were made by N. Laird (in 1948) and B.W. Taylor (in 1950). Taylor (1955) published a detailed account of the flora, vegetation and soils.

Recent additions to the checklist of vascular plants have included a filmy fern (*Hymenophyllum peltatum*) from fellfield outcrops (Hnatiuk 1972), an orchid (*Corybas macranthus*) originally from the boggy raised beach terraces (Brown *et al.* 1978), and *Rumex crispus* from a single locality on a boggy raised beach terrace on the west coast (Copson and Leaman 1981). Additional species now recognised in the flora include *Anthoxanthum odoratum*, *Poa litorosa*, *Uncinia meridensis* and *Galium antarcticum* (Seppelt and Copson, unpublished data). Altogether there are five introduced vascular plants on the island. Jenkin *et al.* (1981) documented many other introductions which have been made at times since European discovery of the island, but which do not appear to have become established.

The vegetation may be classified into a number of formations based largely on the dominant vascular plants. Taylor (1955) recognised five major formations: wet tussock grassland, herbfield, fen, bog and fellfield. This classification needs modification in the light of studies we have made over a number of years and we here have in part modified the classification derived by Taylor to include some of the results of our studies.

Tall tussock grassland, dominated by *Poa foliosa*, occurs on beach terraces, steep coastal slopes, in sheltered stream gullies and in isolated localities, of which some are quite exposed to the strong prevailing winds, in upland situations to about 300m. Ashton (1965) studied the regeneration dynamics of the dominant *Poa foliosa* in tall tussock grasslands. He found that there is a pattern of cyclic development of tussocks through pioneer, building, mature and degenerate phases, with a gap phase involving small herbs, grasses and bryophytes and the large, herbaceous *Stilbocarpa polaris*.

The broad-leaved *Stilbocarpa polaris* is often associated with *P. foliosa* on beach terraces, coastal slopes and along gullies. Both may occur as pure stands. Because of the often closed canopy few plants grow as an understorey, but *Cardamine corymbosa*, *Epilobium linnaeoides* and the bryophytes *Brachythecium salebrosum*, *Lophocolea bidentata* and *Metzgeria* species are found. In open spaces *Agrostis magellanica*, *Poa annua* and *Acaena* species are aggressive opportunists. The introduced meadow grass *Poa annua* is annual in its native Europe, but is perennial on Macquarie Island (Ellis *et al.* 1971).

Short tussock grassland occurs on the upper coastal slopes and plateau uplands and is dominated by *Agrostis magellanica*, *Luzula crinita* and *Uncinia*

species with *Festuca contracta* and *Deschampsia chapmanii* common locally. Often *Acaena* species invade the short tussock grassland, particularly in response to grazing pressure by rabbits, which were introduced to the island about 1880. Short tussock grassland is a favoured habitat for burrow-nesting sea birds, mice, rabbits and probably rats.

Herbfield on Macquarie Island has been generally considered a closed community with the large rosette-forming *Pleurophyllum hookeri* the dominant species, occurring in areas with a relatively high ground water table and moderate wind exposures at altitudes up to about 330m. However, *Pleurophyllum* occurs in a perplexing array of habitats and association. It may occur in wet mires, as on the raised beach terraces with a water table just below the surface and poor drainage and where it is a codominant with bryophytes. On better drained elevated beach terraces, coastal slopes and sheltered uplands it occurs abundantly as a significant associate in the short tussock grassland. It may also occur as a codominant in areas of *Azorella selago* on well drained sheltered slopes on the high plateau.

On Macquarie Island herbfield must be taken to include areas dominated by *Acaena* species as well as some *Pleurophyllum* dominated habitats but *Pleurophyllum* is not necessarily an indicator species as has been presumed in the past. The herbfields dominated by *Pleurophyllum* are usually strongly patterned, the distribution of *Pleurophyllum* plants within them being regular, random or clumped (Jenkin and Ashton 1979). The types of pattern are determined by the interaction between the morphology and performance of the dominant (in competition with other species) and such environmental factors as drainage, exposure to wind and altitudinally related temperature effects. The pattern is also strongly influenced by the balance between the seedling and vegetative reproduction of *Pleurophyllum*.

The productivity of Macquarie Island grasslands and herbfields have been studied by Jenkin (1972, 1975) and Jenkin and Ashton (1970). These authors found that both communities have a large standing crop and high annual production, in comparison with lowland grassland and montane herbfield in Victoria and with montane grassland in New Guinea. The high annual production on Macquarie Island is related to the extended growing season (eight to ten months of the year) and to the plants' ability to make efficient use of low levels of radiation at low, but uniform, temperatures.

Juncus scheuchzerioides was considered by Taylor (1955) to be a characteristic dominant species of the fen formation. *Juncus* dominated vegetation is confined to the margins of streams running through mires and the boggy margins of some tarns. It has a wide habitat range and is often encountered on well drained lowland slopes in short tussock grassland and in herbfield.

The bog formation is dominated by bryophytes, particularly *Breutelia pendula* and hepatics. Many bryophyte species are found associated in bogs. *Sphagnum falcatulum* dominated areas are small and scattered. Bog areas grade rather confusedly into mires, with a slightly lower water table. A number of vascular plant species, particularly *Acaena magellanica*, *Festuca contracta* and *Agrostis magellanica*, are associated with mires. The orchid *Corybas* typically occurs in mire communities. A fernbrake community occurs along the steep slopes of some gullies and on steep well drained sheltered lowland slopes. *Polystichum vestitum* and *Blechnum penna-marina* are the characteristic species.

Fellfield or feldmark is found on all areas subject to high wind velocities at all altitudes above about 170m. Nearly half the plateau is typically fellfield. The vegetation is commonly found in stripes or terraces interspersed with bare gravels. The vegetation cover is generally less than 50%. A few localities have a higher vegetation cover dominated by the cushion forming mosses *Ditrichum strictum* and *Rhacomitrium crispulum*. *Azorella selago* is the main vascular plant and forms low dense cushions.

Wind is a major factor governing the occurrence, distribution and orientation of plants in the fellfield where the vegetation may be easily disturbed (Ashton and Gill 1965). Scratching by rabbits and disturbance of the surface by man provides an opportunity for wind to erode the slow growing and delicately balanced vegetation.

The maritime communities, confined to the coastal fringe, are a complex of different habitats. *Cotula plumosa* and *Colobanthus muscoides* are colonisers of stabilised sands and gravels. The grass *Puccinellia macquariensis* is found only a coastal rock stacks, often with *Colobanthus*. *Crassula moschata* is found on rock outcrops and rock stacks along the coastal fringe. Many other vascular species are found in maritime communities but *Colobanthus*, *Cotula* and *Puccinellia* are perhaps characteristic.

Gillham (1961) published an account of the effects of sea birds and animals on the vegetation of the island. Modification of the vegetation is most marked in the vicinity of penguin colonies and elephant seal haul-out and wallow sites. Paddling and defaecating by King and Royal Penguins has stripped both vegetation and soil from areas these species use for breeding. King Penguins breed on the beach terrace but Royal Penguins occupy sites on both beach terraces and sites which may be up to 1 km from the sea and nearly 200m altitude. *Poa hamiltonii* is best developed in the vicinity of Royal and Rockhopper Penguin breeding colonies.

Gentoo Penguins move their breeding sites about on the raised beaches and lower coastal slopes each year. Trampling and defaecation together with stripping of vegetation for nest material all but destroys the vegetation in the vicinity of the colonies each year. Regeneration is comparatively rapid with *Agrostis*, *Poa annua* and *Epilobium* species being vigorous invaders.

Elephant seal pups, following weaning, lie about amongst the *Poa foliosa* tussocks and may flatten and destroy the growing tillers. Subadult and adult seals cause far more physical damage to tussocks by their weight. Tussock stools and the intervening peat are colonised by *Callitriche antarctica* and *Poa foliosa* together with algae and occasional bryophyte species. Adult seals may haul out to wallow areas up to 400m from the sea on the raised beach terraces on the northwest coast of the island and lesser distances elsewhere. Old wallows are revegetated by algae, *Callitriche*, *Poa annua*, *Ranunculus* and a few other species. *Stilbocarpa* is particularly susceptible to physical damage but regenerates from the hard rhizome.

J.R. Burton, writing in the *Australasian* on 23 June 1980, described the island as "dreadfully dreary to the ordinary observer, but to the naturalist it is full of fascinating interest." The island still retains its immense interest to the naturalist, both professional and amateur. Largely at the instigation of Douglas Mawson the island was declared a sanctuary on 17 May 1933, ending any exploitation of its wildlife. Sealers have left behind a legacy of cats, rabbits, mice, rats and wekas, and the tangle relics of rusting

digesters, boilers, tripots and decaying oil barrels. Further details of the ecological effects of man on the biota of Macquarie Island are given by Holdgate and Wace (1961) and Jenkin *et al.* (1981).

The single most devastating introduced vertebrate pest on the island has been the rabbit. Commencing with Taylor (1955) there have been ongoing studies of the effects of rabbits on the island's flora. Costin and Moore (1960) postulated that rabbits were largely responsible for the degradation of *Poa foliosa* grassland and implicated them also in the induction of subsequent soil erosion. Since then there has been a continuing debate about the relative roles of rabbits and geomorphological processes in the initiation of soil erosion (Griffin 1980, Selkirk *et al.* 1983, Scott 1983).

There is however, little doubt that the rabbit has markedly affected the distribution of *Pleurophyllum* (Jenkin and Ashton 1979) and probably also had a significant effect on the distribution of *Poa foliosa*, *Stilbocarpa polaris*, *Lycopodium sp.* and the spread of plants such as *Acaena* spp. and *Poa annua*. The distributions of the vascular plants on the island are mapped in Copson (1984). The distributions given there report the situation in 1978, prior to the introduction of the myxoma virus to control rabbit populations. These data will form a useful baseline for monitoring vegetation change following any reduction in rabbit numbers.

Biological studies are continuing; those of the Tasmanian National Parks and Wildlife Service (who administer the island) concern the overall management of the island, including monitoring the population status of vertebrates, eradicating introducing pests and monitoring the effects of these pests on the island's native biota.

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BRYOFLORA OF MACQUARIE ISLAND

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The earliest published record of Macquarie Island bryophytes (mosses and hepatics) was that of Scott (1882) reporting the presence of 8 mosses and one hepatic. An additional 8 bryophytes were found amongst a small vascular plant collection sent to Kew Gardens and reported anonymously in the Kew Bulletin of Miscellaneous Information in 1894 (Bull. 95, p. 401).

Although there were two early and significant collections of vascular plants, those of Scott (Scott 1882) and A. Hamilton (Hamilton 1894), no further bryophyte collections were made until the Australasian Antarctic Expedition of 1911 - 14. No determinations have been published and the collections have not been located.

In 1930 the British, Australian and New Zealand Antarctic Research Expedition (B.A.N.Z.A.R.E. 1929 - 31) collected 11 additional moss species. Following the establishment of a scientific and meteorological station at the northern end of the island in 1948, further collections of bryophytes as well as vascular plants were made by N. Laird (in 1948), B.W. Taylor (in 1950) and J. Bunt (in 1951). Clifford (1953) provided a key to the moss flora as it was then known and illustrations of typical leaves of the species.

The hepatic flora has not been studied in detail. A few species have been listed in ecological studies. Gillham (1961) included *Metzgeria* as a coloniser of revegetating elephant seal wallows. Ashton (1965) listed 3 hepatics as associates in vegetational succession in *Poa foliosa* grasslands. Four hepatic species were included as components of fellfield vegetation by Ashton and Gill (1965). Additional hepatic species were added to the checklist by Grolle (1967) and Inoue and Schuster (1971).

A checklist of mosses and hepatics was given by Seppelt (1977) and an updated moss checklist published later (Seppelt 1981). Following additional studies I have made the moss flora is now known to include at least 77 species. The hepatic flora is currently being revised. There are at least 40 species. Many new records, including *Plagiochila ratkowskiana* which was described recently from Tasmania, are included (Inoue and Seppelt *in press*), and at least one new species, a lobate *Symphogyna*, have yet to be described.

Despite the recent studies I have made the number of bryophyte species is well below the numbers recorded for the Auckland Islands and Campbell Island to the north east. Although these islands are often referred to as subantarctic they cannot be classified as such and should be referred to as cold temperate in climate. From the Auckland Islands Fineran (1971) listed 63 hepatics and 43 mosses. Later, Vitt (1979) included 145 species of moss from these islands. The moss flora of Campbell Island consists of 119 species (Vitt 1974). Hodgson (1962) had reported 152 species of hepatics from the Auckland Islands and Campbell Island.

Bryophytes are important components of the vegetation formations on Macquarie Island. The halophytic moss *Muelleriella crassifolia* is unique in that it is often inundated by waves where it occurs with lichens such as *Verrucaria* and *Xanthoria* species on rocks at the water's edge. Together with *Muelleriella* several other mosses such as *Pottia heimii* and *Ulota phyllantha* with the hepatics *Metzgeria* and *Lepidozia* are abundant in coastal communities. *Bryum argenteum*, *B. dichotomum* and *Pottia heimii* are important colonisers of stabilised sand. Mires and bogs on the waterlogged raised beach terraces are dominated by a variety of hepatic species and some mosses, the most abundant of which is *Breutelia pendula*. Species of the hepatics *Clasmatocolea*, *Lophocolea*, *Megaceros* and *Riccardia* with the mosses *Breutelia*, *Ptychomnion*, *Drepanocladus* and *Brachythecium* are important components of the wetter herbfield associations. *Sphagnum*

falcatulum occurs in small scattered patches in some of the acidic bogs and mires. Many bryophyte species are present in the short tussock grasslands which cover much of the lower uplands and sheltered highlands above the coastal slope associations of the tall tussock *Poa foliosa* and the broad-leaved *Stilbocarpa polaris*, beneath which few bryophytes or vascular plants are found. Nearly half of the island's plateau is typically fellfield, with cushion plants of *Azorella selago* and the cushion-forming mosses *Ditrichum strictum* and *Rhacomitrium crispulum* predominating. Vegetation cover in the fellfield rarely exceeds 50% and may be much less in the more exposed and windswept sites. *Jamesoniella colorata* is the most common hepatic of the fellfield areas with *Frullania rostrata* being widespread on rock outcrops.

Although the climate of the island is rigorous and uniformly cold, wet and windy, there is a marked seasonality in the vegetation. Spring and summer growth of the vascular plants and bryophytes is most marked. Nearly half of the moss species have been found with sporophytes. Only about one third of the hepatic species have been collected with sporophytes. Many of the mosses and hepatics have asexual propagules and many have been shown to be capable of reproducing from stem fragments, whole leaves or even parts of leaves.

Geologically the island is young and was subjected to at least local glaciation during the last ice age. Some of the bryophyte species may have arrived on the island via birds but long distance wind dispersal of spores or propagules must account for the greater proportion of the species.

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LICHENS OF MACQUARIE ISLAND

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The earliest reference to lichens on Macquarie Island is that of Scott (1882). In the report of his visit to the island in 1880 he noted that the compact and stable surface of *Azorella selago* cushions sometimes supported lichens and even other vascular plants. Seven lichens were listed in Scott's report of what was the first scientific collection of the flora.

A few years later, in 1894, A. Hamilton visited the island to make further botanical collections. The lichens and mosses he collected were too badly damaged by moisture by the time they reached New Zealand to be of any value.

During the Australasian Antarctic Expedition of 1911 - 14, H. Hamilton remained with the Macquarie Island party as biologist. Dodge (1948) published a short list of 5 lichens from this collection in the reports of the British, Australian and New Zealand Antarctic Expedition of 1929 - 31. The bulk of the A.A.E. collection was sent to the British Museum and the specimens were subsequently destroyed during the Second World War. The B.A.N.Z.A.R.E. collections included 37 lichen species (Dodge 1948).

Since the Australian National Antarctic Research Expedition established a permanently occupied station on the island in 1948 lichen collections have been made by N. Laird (in 1948), N. Haysom (in 1949) and D. Brown (in 1956). These collections, together with the early A.N.A.R.E. collections from Antarctica, were all forwarded to C.W. Dodge for determination. Twenty four new species and five new records were added to the checklist (Dodge and Rudolph 1955; Dodge 1968, 1970).

Collections of lichens on Macquarie Island since 1963 have been summarised by Filson (1981). During several visits since 1980 I have collected further lichen specimens and a number of additional species records are included. These collections are being systematically studied at the present time in conjunction with collections from Heard Island.

Saxicolous (rock inhabiting) lichens are abundant along the coastal fringe of the island. *Verrucaria* species and *Mastodia tessellata* are common together with *Microthelia*, *Xanthoria*, *Lecanora* and *Lecidea* species. Species of *Parmelia*, *Menegazzia*, *Pseudocyphellaria*, *Ramalina* and *Graphis* occur commonly on rock stacks on elevated beach terraces about the island. On the coastal cliffs *Usnea*, *Stereocaulon*, *Parmelia*, *Menegazzia*, *Microthelia* and other crustose genera are common. These genera, together with *Placopsis* and *Lecidea* and others, are widespread on plateau outcrops.

Lichens, together with bryophytes, comprise a significant component of the vegetation of the raised beach terrace herbfields and short-tussock grasslands of the plateau uplands. *Cladonia*, *Cladia*, *Peltigera*, *Pseudocyphellaria*, *Hypogymnia* and *Sphaerophorus* species are abundant in these habitats.

In the plateau short-tussock grassland/fellfield ecotonal areas and on fellfield terrace slopes *Hypogymnia*, *Usnea*, *Sphaerophorus* and *Pseudocyphellaria* species are common amongst the bryophytes and low vascular plants. *Lecidea* species and other crustose genera are found on gravel stones and on rocky outcrops. *Pertusaria* commonly grows over moribund moss and *Azorella*. *Baeomyces* also occurs on *Azorella* cushions. Species of *Stereocaulon*, *Lecanora*, *Lecidea* and *Placopsis* are abundant on rocky outcrops throughout the plateau.

The taxonomy of the lichen flora is confused. Many of the species were described by Dodge and considerable synonymy is now apparent. Despite these difficulties, approximately 100 species are represented in the flora. The revision of the lichen flora of New Zealand and associated islands by David Galloway, soon to be published, will greatly assist the study of the Macquarie Island lichens in addition to those of Tasmania. The number of lichen species in the Macquarie Island flora is comparable to that of the

Auckland Islands, where Fineran (1971) reported 116 lichens. This number is, however, an underestimate. Many of the species originally described from Macquarie Island are also known from the Auckland Islands.

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THE FUNGAL FLORA OF MACQUARIE ISLAND

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Introduction

Macquarie Island is characterised by constantly low temperatures (averaging 4.7°C), high precipitation (926mm annually) and high humidity (averaging 90%). Only 45 species of vascular plants have been recorded, and species diversity in lower plants is similarly restricted. This results in a limited range of plants available as host or substrate for fungi. Plants are the major food source of many fungi, their living tissues acting as host to many parasites and dead tissues providing substrate for a range of saprophytes.

This paper reviews current knowledge of the fungal flora of Macquarie Island, lists the species recorded to date, and relates their occurrence to the composition of fungal flora in other parts of the world. Processes likely to have been involved in the development of the fungal flora are explored, with particular reference to the microfungi which grow on leaves and litter.

Fungi Recorded

All major fungal taxa are represented in the Macquarie Island flora, that is, the Basidiomycetes, Ascomycetes, Imperfect Fungi and Lower Fungi.

A total of 27 genera and 19 species of Basidiomycetes have been recorded (Table 1), mostly by Bunt (1955, 1965) and Kerry *et al.* (1984), with single species by Scott (1883) and Kerry (1982). Taxa recorded before 1980 are reviewed in a survey of the higher fungi of Antarctica, the subantarctic zone and Falkland Islands (Pegler *et al.* 1980). Many Basidiomycetes grow in organic matter in the soil and produce fruiting bodies at or above ground level, which in most cases are visible to the naked eye. Most Basidiomycetes listed from Macquarie Island are in this category, although two genera of plant parasites, *Puccinia* and *Uredo*, are included.

Among the Basidiomycetes recorded are species reported only from Macquarie island (?endemics), others thought to occur only in Antarctic and

subantarctic regions (circum-Antarctic species), or to be restricted to north and south polar regions (species of bi-polar disjunction), and species which are common worldwide (cosmopolitan species).

Ascomycetes, Imperfect Fungi and Lower Fungi occur mostly as small or microscopic leaf spots or lesions, or in microscopic colonies in the soil. They are often called the 'microfungi'. A total of 57 genera and 48 species have been identified (Table 1), mostly by Bunt (1955, 1965), Kerry (1982) and Kerry and Weste (1984). Single species have also been reported (Scott 1983, Dennis 1958 and Pegler *et al.* 1980).

The species list is likely to be incomplete with respect to both Basidiomycetes and the microfungi. The Basidiomycete records come from collections made over much of the island and from a range of habitats, but no comprehensive collection has been made. Of the two main studies of microfungi, one was a detailed investigation of the fungi which colonize leaves and litter (Kerry 1982, Kerry and Weste 1984), and the other involved studies of ten common soil types (Bunt 1955, 1965).

Fungi on Leaves and Litter

The studies on leaves and litter were concentrated on the three most common plant species, *Poa foliosa*, *Stilbocarpa polaris* and *Pleurophyllum hookeri*, and were concerned with the numbers and types of fungi which occur on leaves as they grow, age and die, and as litter decomposes.

Fungal colonization of leaves has been investigated for many plant species from temperate and tropical regions, but until recently there has been no information from polar regions. The studies on Macquarie Island have extended knowledge of the subject to include these regions. They have also given an insight into some of the factors involved in the development of the fungal flora on Macquarie Island.

The fungal flora of leaves change as leaves develop and later decompose. In most cases the greatest changes occur after leaf death or 'senescence', when saprophytes with different nutritional requirements occur in sequence and systematically decompose different components of the leaves. The leaves gradually fragment and fall to the ground as litter. Later the remains occur as organic matter in the soil. The same nutritional types of fungi occur in the same order on the leaves of many plant species throughout the world, including the leaves of the Macquarie Island plants studied. There is also in most cases a characteristic order of appearance of the different fungal taxa because preference for certain substrates is often a characteristic of particular fungal taxa. A typical sequence, in its simplest form, begins with the establishment of cellulytic fungi, often Ascomycetes and Imperfect Fungi, as the leaf tissues die. Cellulose is a major component of plant cell walls and its breakdown results in the release of sugar-rich cell contents. This in turn results in the establishment and dominance of sugar decomposing fungi including many Lower Fungi and species of *Penicillium*. Once the sugar has been utilized a number of resistant compounds including lignin remain, and these are decomposed by a further group of specialized fungi including many Basidiomycetes.

Despite similarities as to general patterns of leaf colonization, the fungal flora of the Macquarie Island leaves differ from those of leaves from other parts of the world. In particular the types of fungal species which are the major colonizers of senescent and dead leaves are different. These species

are marked in Table 1. Most are uncommon, or in some cases previously unknown species, many of which are thought to be host-specific, or at least restricted to colonizing only a few plant species. In addition, many of these fungi, which are primarily saprophytes, are able to become established on the living tissues, that is, as parasites. In contrast, senescent and dead leaves of most plant species growing elsewhere in the world are colonized mainly by cosmopolitan fungi of wide host range, which only become established at or after the death of the leaf tissues.

Effects of Temperature

Like the Basidiomycetes, the fungi colonizing leaves on Macquarie Island include species which may be endemic, and others which are more widespread but appear to favour cold climates. These characteristics suggest that temperature may be an important factor controlling species composition. This possibility was investigated for leaf colonizing fungi by growing as many as possible of the most common species in incubators at 4, 10, 15, 20 and 25°C, and measuring growth rates of the colonies (Kerry 1982).

The experiments showed that many of the leaf-colonizing fungi on Macquarie Island can grow faster at 4°C than other fungi. In addition, their highest growth rates are at 15 or 20°C and they show little or no growth at or above 25°C. These results suggest that the development of the Macquarie Island leaf microflora involved selection for species which can grow better than others at low temperatures, or adaptation of existing species to grow better at low temperatures. Selection for 'cold-tolerance' as it is called has been demonstrated for soil fungi on Signy Island in the Maritime Antarctic (60°43'S. 45°38'W.). The air spora over the island contain spores of a wide range of fungal species which are common in soils in temperate regions, but few of these colonize Signy Island soils (Latter and Heal 1971).

Although the Macquarie Island fungi can grow better at low temperatures than most fungi, at 4°C they still only grow at between 10 and 20% of their maximum rates. Therefore the low temperatures still inhibit fungal growth, and presumably also decomposition.

Other Effects on the Leaf Microflora

High humidity favours the growth of fungi, and in particular those growing on exposed surfaces. The constantly high humidity on Macquarie Island is probably an important factor involved in the establishment of saprophytes on living leaves.

The types of plants available as hosts and providing substrate must also have played an important part in determining species composition in the leaf microflora, in view of the host-restricted nature of many of the fungi.

Conclusion

There are still many gaps in the knowledge of the Macquarie Island fungal flora. Detailed studies over the entire island and representing all habitats are required to provide a more complete species list and to indicate associations between species present and habitat types. There is still much to be learnt of the occurrence of fungi in the entire Antarctic-subantarctic region, and until further information is available no definite conclusions can be reached about the degree of host-specificity or of geographical limitations of fungi in the region.

TABLE 1. Fungi recorded from Macquarie Island. The major colonizers of *Poa foliosa*, *Stilbocarpa polaris* and *Pleurophyllum hookeri* leaves are marked Pf, Sp and Ph respectively, with these initials underlined for major colonizers of senescent and dead leaves. Species recorded only from Macquarie Island (?endemics) are marked (+), also those thought to be new species (*).

Basidiomycetes

	<i>?Camarophyllum</i> sp.		<i>Hygrophorus conicus</i> Scop. ex Fr.
	<i>Cantharellus</i> sp.		<i>Lepista fibrosissima</i> Singer
	<i>Clavaria</i> sp.		<i>Mycena metata</i> (Fr. ex Fr.) Kummer
	<i>Clavinolopsis</i> sp.		<i>Mycena</i> sp.
	<i>Clitocybe</i> sp.		<i>Naucoria</i> sp.
	<i>Coprinus disseminatus</i> (Pers. ex Fr.) S.F. Gray		<i>Nolanea</i> sp(p).
	<i>Cystoderma amianthinum</i> ([Scop.] Fr.) Fayod		<i>Omphalina</i> sp.
	<i>C. carcharis</i> (Pers. ex Secr.) Fayod		<i>Panaeolus moellerianus</i> Singer
	<i>Eccilia</i> sp.		<i>P. papilionaceus</i> (Bull. ex Fr.) Quél.
	<i>Galera</i> sp.		<i>Panaeolus</i> sp.
	<i>Galerina longinqua</i> Smith and Singer		<i>Phaeogalera stagnina</i> (Fr.) Pegler and Young
+	<i>G. macquariensis</i> Smith and Singer		<i>Pholiota myosotis</i> (Fr. ex Fr.) Singer
	<i>G. vittiformis</i> (Fr.) Singer	+	<i>Pholiota</i> sp.
	<i>G. vittiformis</i> var. <i>pachyspora</i>		<i>Psathyrella maquariensis</i> Singer
	<i>Galerina</i> sp(p).		<i>Psathyrella</i> sp.
	<i>Gerronema schusteri</i> Singer	+	<i>Psilocybe longinqua</i> Singer
	<i>Hygrocybe conica</i> (Scop. ex Fr.) Kummer, Führ		<i>Puccinia</i> sp.
	<i>H. nigrescens</i> (Quél.) Kühn.		<i>Rhodophyllum sericeus</i> (Bull. ex Mérat) Quél. s.sp. <i>antarcticus</i> (Singer) Singer
	<i>Hygrocybe</i> aff. <i>ceracea</i> (Wulf. ex Fr.) Kummer		<i>?Tricholoma</i> sp.
	<i>Hygrocybe</i> spp.		<i>Tubaria</i> sp.
			<i>Uredo</i> sp.

Ascomycetes

	<i>Ceratospaeria</i> sp.		<i>Leptosphaeria eustoma</i> (Fuckel) Sacc. [Pf]
	<i>Chaetomium</i> sp.		<i>L. doliolum</i> (Pers. ex Fr.) Ces. and de Not.
+	<i>Dasyscyphus</i> cf. <i>enzenspergerianus</i> (P. Henn.) Dennis [Pf]		<i>Leptosphaeria</i> sp.
	<i>Didymella proximella</i> (Karst.) Sacc.		<i>Mycosphaerella tassiana</i> (de Not) Joh. [Pf]
	<i>Dothidea spilomea</i>	+	<i>Mycosphaerella</i> sp. 1 [Sp]
	<i>?Fabraea</i> sp. [Sp]		<i>Mycosphaerella</i> spp. [Pf]
	<i>Hendersonia microstricta</i>		<i>Lachnea</i> sp.
	<i>?Hymenoscyphus</i> sp. [Sp]		<i>Niesslia exosporioides</i> (Desm.) Wint.
	<i>Hypodermella</i> sp.		

Ascomycetes (cont.)

- Pleospora graminearum* Wehm.
P. heleocharidis Karst.
P. lutea Wehm.
P. vagans Neissl.
Pleospora sp.
Sarcoscypha sp.
+ *Schizothyrioma stilbocarpae*
 Spooner
Sphaeria depressa
S. herbarum (*Pleospora herbarum*)
S. phaeosticta

Imperfect Fungi (Coelomycetes)

- Ascochyta stilbocarpae* Syd.
 [Pf, Sp, Ph]
Camarosporium metableticum
 Trial. [Pf]
Camarosporium sp.
Colletotrichum gloeosporioides
 Penz.
Diploidia sp.
Phoma exigua Desm. [Ph]
Phoma ?herbarum Westend
+ * *Phoma* sp. 1 [Pf, Ph]
+ * *Phoma* sp. 2 [Pf]
+ * *Phoma* sp. 3 [Ph]
Phyllosticta sp.
?Rhodesiopsis gelatinosa [Ph]
Septoria sp.
Stagonospora ischmaemi Sacc.
 [Pf]
Tunicago sp.

Imperfect Fungi (Hyphomycetes)

- Acremonium kiliense* Grütz.
A. strictum W. Gams [Sp]
A. terricola (Miller *et al.*) W. Gams
A. ?zonatum (Sawada) W. Gams [Sp]
Acremonium spp. [Sp]
Alternaria alternata (Fr.) Keissler
Aspergillus sydowi (Bain and Sartory) Thom and Church
Aureobasidium pullulans (de Bary) Arnaud [Pf]

- Botrytis cinerea* (Pers. ex Fr.) Rabenh. [Ph]
Cephalosporium sp.
Chalara sp.
Chrysosporium pannorum (Link) Hughes
Cladosporium cladosporoides (Fresen.) de Vries
C. herbarum (Pers.) Link
Cladosporium spp.
Curvularia trifolii (Kauffm.) Boedjn
Cylindrophora sp.
?Diplospora sp.
Epicoccum purpurascens Ehrenb. ex Schlecht.
Fusidium sp.
Gliocladium sp.
Graphium sp.
Hyalopus sp.
Monosporium sp.
Paecilomyces sp.
Penicillium brevi-compactum Dierckx [Pf, Ph]
P. corylophilum Dierckx
P. cyclopium Westling [Pf, Ph]
P. decumbens Thom.
P. frequentans Westling
P. granulatum Bain.
P. restrictum Gilman and Abbot
Penicillium spp.
Polyscytalum sp.
Spicaria sp.
Sporotrichum sp.
Stemphyllium botryosum Wallr.
Trichoderma harzianum Rifae
Trichoderma sp.
Verticillium lecanii (Zimm.) Viégas
Volucrispora graminea Ingold McDougall and Dann

Lower Fungi (Zygomycetes)

- Mortierella gamsii* Mil'ko [Sp]
Mortierella spp.
Mucor hiemalis Wehmer f *hiemalis*
Mucor mucedo (L.) Fresenius
Mucor sp.
Rhizopus nigricans Ehrenb.

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HOLOCENE VEGETATION HISTORY OF MACQUARIE ISLAND

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The present climate of Macquarie Island is cool, windy and constantly wet (mean temperature 4.5°C, mean windspeed 8.3m sec⁻¹, mean annual rainfall 926mm).

The island's flora consists of about 40 vascular plant species and about 110 bryophyte species, growing in tussock grasslands, mires and fellfield (Taylor 1955, Seppelt 1984, Seppelt and Brown 1984). Fossil evidence of past vegetation in the form of pollen grains, spores, diatom frustules, seeds, leaf and stem-fragments is preserved in peat and lake deposits.

Although snow may fall at any time of year, Macquarie Island now has no permanent ice or snow. During the last glacial period, ice and snow cover on all the subantarctic islands was more extensive than at present. The extent of former glaciation on Macquarie Island is uncertain but it seems clear that only limited glaciation occurred. Colhoun and Goede (1974) estimated that approximately 40% of the island had been glaciated; Löffler and Sullivan (1980) considered a somewhat larger area was involved. By either estimate, there would have been sufficient area on the island free of permanent ice and snow to allow persistence of some vegetation.

Radiocarbon dating and pollen analysis of peat samples from several sites shows that vegetation was established, and plant remains had begun accumulating at these sites by 8,000 to 10,000 years ago (Table 1). Many species in the island's present flora have been present throughout the Holocene (Table 2). A small number of pollen grains from exotic species, representing long-distance transport from other land masses, are preserved in peat and lake deposits (Salas 1983, Selkirk, Selkirk and Griffin 1983). There is no evidence for a flora substantially different from that on the island today during the Holocene period, the last 10,000 years. As on Marion Island (Hall 1980) and Iles Kerguelen (Young and Schofield 1973), it is likely that at least some vegetation persisted in ice-free refugia throughout the last glacial period, then spread to other parts of the island as the climate ameliorated about 10,000 B.P.

Permission to visit Macquarie Island, granted by Macquarie Island Advisory Committee, and logistic support from Antarctic Division for visits in 1979-80, 1981 (PMS) and 1983 (DMB) are gratefully acknowledged. An ARGS grant to PMS and DRS financed radiocarbon dating.

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TABLE 1. Radiocarbon dates from Macquarie Island, showing start of vegetation accumulation at various sites.

Site	Depth (cm below surface)	Lab. No.	Conventional radiocarbon age (yrs. B.P. \pm std. dev.)	Calibrated* radiocarbon age (yrs. B.P. \pm 95% confidence interval)	Deposit
Ridge near Green Gorge	130	SUA 2164	7200 \pm 130	8000 \pm 525	peat
Nuggets Point	440	SUA 1894	9400 \pm 220	10200 \pm 400	lake exposure
Scoble Lake**	more than 200	WK 349		8700 \pm 200	lake sediment

* Calibrated following method of Klein *et al.* (1982) for ages less than 8000 radiocarbon years. Dates of 8000-10000 radiocarbon years calibrated by adding 800 yrs. to the conventional date and doubling the standard deviation (M. Barbetti 1980 and pers. comm.)

** from Salas, 1983.

TABLE 2. Plant remains present in Holocene deposits on Macquarie Island.

Site	Depth (cm below surface)	Lab. No.	Conventional radiocarbon age (yrs. B.P. \pm std. dev.)	Calibrated* radiocarbon age (yrs. B.P. \pm 95% confidence interval)	Fossils** present include:
Wireless Hill	206-210	SUA1459	1600 \pm 130	1600 \pm 350	Po, St, Ca, Pl.
Wireless Hill	313-315	SUA1682	3490 \pm 210	3820 \pm 450	Po, St, Ca, Co, Pl.
Wireless Hill	384-394	SUA1527	4880 \pm 90	5580 \pm 260	Po, St, Ca, Co, Pl, Ac.
Ridge near Green Gorge	88	SUA1462	5140 \pm 140	5960 \pm 350	Po, St.
Ridge near Finch Creek	190	SUA1845X	5930 \pm 240	6790 \pm 410	Po, St, Pl, Az.
Ridge near Green Gorge	130	SUA2164	7200 \pm 130	8000 \pm 525	Po, Pl, Ac.
Nuggets Point	147	SUA1467	8560 \pm 200	9360 \pm 400	My, Fr, Da, Po, St, Pl, Ac, Az.
Nuggets Point	440	SUA1894	9400 \pm 220	10200 \pm 400	Po, Pl.

* Calibrated as for Table 1.

** Pollen grains: Po = Poaceae, Ca = *Callitriche*, Co = *Cotula*, Pl = *Pleurophyllum*, St = *Stilbocarpa*, Ac = *Acaena*, Az = *Azorella*.
Leaves and stems: My = *Myriophyllum*, Fr = *Fissidens rigidulus*, Da = *Drepanocladus aduncus*.

FELDFIELD ON MACQUARIE ISLAND

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Fellfield, or feldmark (Fjaeldmark), is a high altitude or high latitude vegetation dominated by bryophytes and cushion-forming vascular plants. Generally, vegetation cover is less than 50% and large expanses of bare ground are common.

Nearly half of the plateau of Macquarie Island is typically fellfield (Ashton and Gill 1965; Jenkin 1975). Leeward and, to a lesser extent, windward slopes of plateau hills and rises are often terraced (Taylor 1955a; Löffler 1983; Löffler *et al.* 1983).

Plateau climate is likely to be more severe than at the meteorological observatory at the A.N.A.R.E. Station where, at 6m altitude, mean monthly minimum temperature is 2.8°C; mean monthly maximum 6.2°C; mean annual precipitation 926mm; and mean wind velocity 8.6m sec⁻¹. Taylor (1955a, b) estimated that plateau temperatures are likely to be 2-4°C lower and wind speeds at least 25% greater than at sea level. Precipitation is also likely to be higher on the plateau as the upper levels of the island are often shrouded in cloud.

Although fellfield on the island is considerably variable, both in species dominance and vegetation cover, Ashton and Gill (1965) regarded it as a single vegetation unit manifested in a variety of forms. We agree with this interpretation and illustrate the variability with selections from our data collected at 21 fellfield sites about the island.

Over all sites we have recorded a total of 63 species: 18 vascular plants, 29 bryophytes, and 16 lichens.

At some sites (A and B, Table 1) there is extensive bare, stoney ground. At other sites vegetation cover is more extensive with the vegetation sometimes forming stripes (Site C) or dominating terrace slopes with the terrace flats being largely bare gravelly ground (Site D). At some sites the vegetation cover may be almost continuous (Site E).

The bare gravels of many of the exposed slopes show extensive development of sorted stone stripes (Bunt 1954; Löffler *et al.* 1983; Peterson *et al.* 1983).

Polsters of *Ditrichum strictum* and tufts or turves of *Rhacomitrium crispulum* are the dominant species and life forms of mosses. Both may contribute significantly to biomass and productivity in the fellfield (Seppelt and Ashton 1978). Other mosses - *Andreaea* spp., *Rhacocarpus purpurascens*, *Rhacomitrium lanuginosum*, hepatics - *Jamesoniella colorata*, lichens - *Perusaria*, *Stereocaulon*, and small vascular plants - *Agrostis magellanica*, *Ranunculus biternatus*, *Azorella selago*, are generally only minor components of the total vegetation cover. The cushion-forming vascular plant *Azorella selago* may occur as discrete cushions (Site A), as continuous stripes (Site D), or form extensive patches (Site E). Percentage cover varies considerably (Table 1). Bryophytes and vascular plants are often found growing amongst the dense *Azorella* stems or at the edges of the cushions or swards.

Periglacial processes ensure gradual movement of the substrate on leeward and windward slopes. This movement, together with wind effects (probably the dominant factor) ensures continual but gradual change in vegetation patterns in the fellfield (Ashton and Gill 1965).

There are many ecotonal associations between fellfield and short-tussock grassland (characterised by *Agrostis magellanica*, *Festuca contracta*, *Luzula crinita*, *Uncinia* spp., with many other vascular plants, bryophytes and lichens) or wet herbfield (with the rosette-forming *Pleurophyllum hookeri* and bryophytes predominating). All of the vascular plant species, bryophytes, and most of the lichen species of the short-tussock grassland formation and the plateau wet herbfield formation are found as minor components of the fellfield.

The form which fellfield assumes at a particular site is determined by many contributing factors. Cryoturbation of the surface layers of the soil, and wind, are important. The predominant wind direction is west to north west, but surface topography has a direct influence on local wind direction and velocity. Aspect, altitude and land-form at a site, wind exposure, soil depth, moisture availability and frost frequency, all contribute to fellfield composition and character in a way which is as yet not understood.

TABLE 1. Percentage occurrence at 2000 points of first contact along 20m line transect.

Site	A	B	C	D	E
Location of site	near Boot Hill 225m a.s.l.	North of Prion Lake 175m a.s.l.	Windy Ridge 325m a.s.l.	S.E. of Mt. Gwynne 300m a.s.l.	East side of Mt. Law 300m a.s.l.
Vascular plants	7	1	9	33	65
Bryophytes	16	23	69	16	24
Lichens	0	2	7	5	1
Total vegetation	23	26	85	54	90
Selected species:					
<i>Azorella selago</i>	5	1	8	30	50
<i>Ditrichum strictum</i>	15	17	14	1	0
<i>Racomitrium crispulum</i>	0	1	18	11	13
<i>Andreaea acuminata</i>	0	0	23	0	0
Total no. of species	8	14	20	25	23
Number of transects	3	2	2	2	1

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LIMNOLOGICAL STUDIES ON MACQUARIE ISLAND

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The freshwaters of Macquarie Island, and the organisms which inhabit them, have yet to receive the attention they deserve. However, a few detailed investigations have been made, particularly of the lakes: Tyler (1972) and Buckney and Tyler (1974) carried out surveys of the water chemistry of most of the lakes, and Evans (1970) investigated in detail the ecology of the copepod *Pseudoboeckella brevicaudata* Brady 1875 on the island, and presented a list of the flora and fauna of two lakes and three ponds. Other researchers have measured light penetration in the lakes, and collected samples of freshwater algae for identification. This article summarises the most pertinent aspects of these surveys, and draws heavily in particular on the papers of Tyler (1972), Buckney and Tyler (1974), and Evans (1970).

The lakes are all located on the plateau area of the island, and total 203 ha in area. The largest are Major, Waterfall, Flynn, Prion and Island Lakes, but there are many more smaller lakes and tarns. They are very clear, as their waters contain very little humic colouration. Green Gorge Tarn, which receives water from an extensive, low-lying area, is the only water to show appreciable colour. On a world scale the lake waters are soft, with Total Dissolved Solids (TDS) values not exceeding 180 mg/l and Ca^{2+} not greater than 0.85 meq/l. The waters are of relatively uniform composition, the highest TDS being little more than twice that of the lowest, and seasonal variation seems to be slight. The year-round high humidity and low temperatures prevent concentration by evaporation even in summer. Most waters are near neutral but Square Lake is slightly alkaline (up to 7.8 pH units) because of its higher HCO_3^- content (see below). Levels of silica, required for cell wall development in diatoms, are low: rainfall could well supply all the silica found in the plateau lakes.

Atmospheric precipitation is the major supplier of ions to the waters of Macquarie Island. As the proportions of sodium and chloride in the lakes are almost the same as those of seawater, and the cationic dominance order is usually $\text{Na} > \text{Mg} > \text{Ca} > \text{K}$ (as in seawater), and salinities decrease across the island from west to east, it is clear that sea spray borne on prevailing westerlies is the major supplier of ions. However, there are two significant exceptions: Square Lake and Waterfall Lake have considerably higher calcium

concentrations than most other lakes, sufficient to change the cationic dominance order from that of seawater to $\text{Na} > \text{Ca} > \text{Mg} > \text{K}$. Skua Lake also has this dominance order though calcium does not greatly exceed magnesium in this case. The reason for this enrichment in calcium is not clear, but geochemical addition of Ca^{2+} and HCO_3^- is suggested, either from local outcrops of weatherable rocks or groundwater circulation. Square Lake is also different in other respects: It has a higher phosphate content than the other plateau lakes, the macrophyte *Myriophyllum elatinoides* is present, and it has relatively high chlorophyll levels. It seems certain that the differences result from geochemical processes but present knowledge of geology and soil chemistry does not allow complete explanation. Some geological influence is indicated in other lakes by the anionic dominance order: the order $\text{Cl} > \text{HCO}_3^- > \text{SO}_4$ is observed instead of the seawater order of $\text{Cl} > \text{SO}_4 > \text{HCO}_3^-$ in Square, Waterfall, Scoble, Flynn and several other lakes and tarns.

Evans (1970) looked at the flora and fauna of five water bodies: Square Lake, Prion Lake and a small pool on the plateau, and two small ponds on the coastal terrace. His faunal records were few: he recorded 2 copepods, *Pseudoboeckella brevicaudata* and *Thalassidra sp. ?*, 5 cladocerans, *Daphnia carinata*, *Alona diaphana*, *Alona quadrangularis*, *Macrothrix hirsuticornis* and *Chydorus poppei-barroisi*, 1 ostracod, 1 acarine, several turbellarians, and noted that tardigrades, nematodes, rotifers and dipteran larvae were also present in his collections. On the floral side, he identified 3 vascular plants, *Myriophyllum elatinoides*, *Callitriche antarctica* and *Ranunculus biternatus*, some 90 diatoms, and 5 other species of algae. Of the diatoms, only about 20 were reported as being of more than occasional occurrence, and only 5 as being abundant in any of the sampling locations: *Acanthodes biasolettiana*, *Cocconeis placentula*, *Fragilaria virescens*, *Melosira decipiens* and *Surirella angustata*. He found only 5 other species of algae, the Chlorophyceae *Rhizoclonium*, *Spirogyra* and *Staurastrum*, and the Cyanophyceae *Nostoc* and *Nodularia* (?). *Rhizoclonium* is particularly significant in that it forms almost continuous surface mats on Square Lake.

More recent collections of freshwater algae have shown that many more members of the Chlorophyceae are present (Blackburn, pers. comm.). Desmids in particular are prevalent: 5 species of *Closterium* have been observed, 3 of *Cosmarium*, and specimens of *Staurodesmus*, *Sphaerzosma*, *Tetmemorus*, *Netium*, *Pleurotaenium*, *Cylindrocystis* and *Euastrum* have also been seen. The organisms *Zygnema*, *Oedogonium*, *Tribonema*, *Stigeoclonium* and *Pediastrum* have also been observed.

With a few important exceptions, the results to date show the water bodies of the island to be clear and oligotrophic, with few species. It is to be hoped that more detailed studies will be conducted on them, as the damp maritime climate affords an excellent opportunity to study the role of cyclic salts in the nutrient regime of the lakes, and an absence of fish allows the study of primary production and energy flows in communities with few tertiary consumers. The waters of Macquarie Island also have a role to play in investigations of circum-antarctic affinities of flora and fauna, and the routes by which post-glacial transoceanic colonisation occurred.

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THE SHORE ECOLOGY OF MACQUARIE ISLAND

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Collections from the shores of Macquarie Island were first made at the end of the 19th century and extensive collecting was undertaken during the Australasian Antarctic Expedition of 1911 - 1913. Since the establishment of a base on Macquarie Island by ANARE, a number of further collections of marine littoral flora and fauna have been made (Kenny and Haysom, 1962; Bennett, 1971; Simpson, 1976a) including subtidal collections using SCUBA equipment (Simpson, 1976a; Lowry *et al.* 1978). From these studies, the zonation of dominant plants and/or animals down Macquarie Island rocky shores has been described. Further studies on the reproductive and physiological strategies of some littoral invertebrates in relation to their distribution and abundance on the shore have been undertaken (Simpson 1976b, 1977, 1982a).

Shore zonation provides a framework of ecologically similar areas within and across which the distribution of littoral flora and fauna can be compared. In turn, the zonation pattern of a region can be compared to other patterns around the world — that is, how does the local scheme fit in with any concept of a universal scheme of ecologically equivalent areas on all shores?

Figure 1 shows the zonation pattern of Macquarie Island rocky shores in relation to a universal shore zonation scheme — that of Lewis (1964). In the littoral zone (that region receiving alternating exposure to air and wetting by submersion, splash or spray), the uppermost region is characterized by lichens and is known as the littoral fringe. The lowermost part of the littoral zone is the eulittoral zone and on Macquarie Island, four distinct sub-zones were recognizable within the eulittoral zone. These were, in descending order down the shore, a zone dominated by the alga, *Porphyra umbilicus* (*Porphyra* Zone), a zone dominated by a siphonariid limpet, *Kerguelenella lateralis* (Bare Zone — because of the scarcity of algal cover here), a zone dominated by a red alga *Rhododymeria* sp. (Upper Red Zone) and a zone occupied by the holdfasts of the giant bull kelp (*Durvillea antarctica*). Below the *Durvillea* holdfasts, encrusting pink coralline algae (Lower Red Zone) marked the commencement of the sub-littoral zone — a region occupied primarily by fully marine organisms. On some parts of the shore there may be localized differences to the general pattern. For instance, a zone dominated by the algae *Ulva* sp. and *Chaetangium fastigiatum* often encroached upon, or in some instances replaced, the Bare Zone. One notable feature on Macquarie shores was that, despite the prevailing westerly weather conditions, the same zones existed on both the eastern and western sides of the island — differing only in degree or in relation to local topography.

The zonation pattern describes the shore but what factors bring about the actual distribution abundance of the various algae and animals? Some relationships can be discerned by casual observation, such as that between the location of the *Durvillea* holdfasts and the surge of the sea. Extremely turbulent, stormy seas obscure any such observations but in the more prevailing conditions, waves would sweep around rocks carving out fleeting water-line patterns which would be indelibly marked by the *Durvillea* holdfasts.

Simpson (1976b) recorded some features, both physical and biotic, which influence the distribution and abundance of some molluscs on the rocky shores. A small chiton, *Hemiarthrum setulosum*, takes refuge on the rocks among the *Durvillea* holdfasts under the canopy of the proximal stipes and fronds. In experiments when *Durvillea* was removed from areas of the shore, the numbers of *H. setulosum* drastically decreased and the limpet, *Nacella* (*P.*) *macquariensis* "moved in". Also, other truly marine invertebrates, such as tube-worms, starfish and small holothuroids, either died in or disappeared

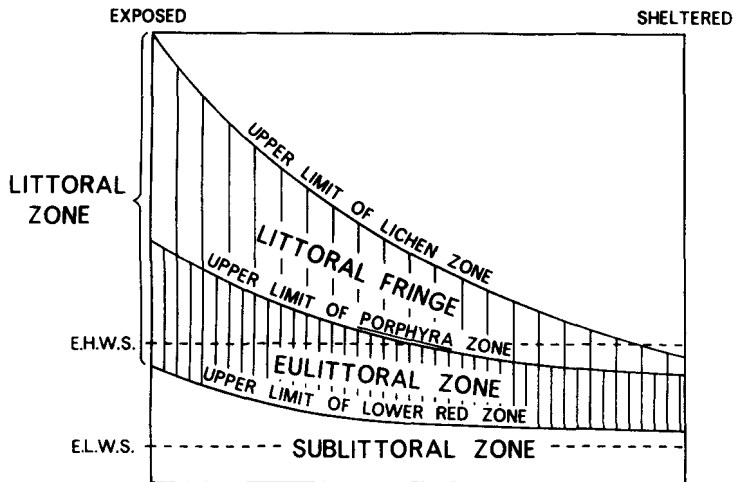


Figure 1

Zonation of Macquarie Island rocky shores, in relation to a universal zonation scheme. EHWS: extreme high-water spring tidal mark; ELWS: extreme low-water spring tidal mark.

from areas of *Durvillea* removal. *H. setulosum* broods its young to a fully formed juvenile stage before the young leave the parent and this reproductive strategy suits its cryptic habitat. However, despite this seemingly restrictive mode of dispersal, this small chiton is widely distributed throughout the cold temperate/sub-Antarctic regions of the Southern Hemisphere. The explanation lies in the fact that *H. setulosum* invades *Durvillea* holdfasts which are often dislodged, attached to the fronds, to float around the ocean thus aiding wide distribution of the chiton. The limpet, *Nacella* (*P.*) *macquariensis*, can be found from the eulittoral zone to ten metres depth and beyond. It provided a very good study subject. Its distribution and abundance was shown to be influenced by algal cover and by a combination of high temperatures (high for Macquarie Island, that is) and predation. The shape of the shell varies throughout its range with the degree of water turbulence being strongly correlated with the limpets' having relatively higher shells. Other features, such as predation by Dominican gulls on the large chiton *Plaxiphora aurata*, desiccation tolerance by the siphonariid limpet *Kerguelenella lateralis*, occupation of rock pools by the littorinid *Laevittorina caliginosa*, the physiological and morphological limitations for the trochid *Cantharidus* (*P.*) *coruscans* to occupy areas high in the littoral zone — contributed to an understanding of the ecology of the shore molluscs of Macquarie Island. Many of the molluscs and echinoderms studied also had some form of protection for their developing larvae until they were fully formed juveniles — by brooding or by depositing egg-cases attached to the substrate (Simpson 1977, 1982a). The holothuroid, *Pseudopsolus macquariensis*, released its brooded juveniles to a markedly synchronized degree and had the apparent option of being male or female from year to year. Although some species have pelagic larval development, such as the limpet *Nacella* (*P.*) *macquariensis* (Simpson, 1982b), the predominance of a protected, non-pelagic mode of development in the molluscs and echinoderms is part of the phenomenon

of increasing frequency of such a mode with increasing latitude. There have been a number of hypotheses to explain this phenomenon—the more plausible of which include the very restricted seasonal nature of food for pelagic larvae in cold waters, rigours for survival for larvae in cold waters, and the reduced chances of returning to land in areas of large ocean—which would also apply to island fauna in warmer regions as well.

The intertidal regions provide a mosaic of studies in ecology with the interface of land, air and sea acting as the basic ingredient for the setting of differing conditions for flora and fauna to adopt different biological and ecological strategies for interaction and survival. The seemingly inhospitable shores of Macquarie Island are no exception. The relatively even, low temperatures and persistent cloudy, wet weather combined with the location of Macquarie Island in the sub-Antarctic Ocean—north of the Antarctic convergence and at the southerly end of ice-free littoral shores—provides a very different shore habitat to most other regions in the world. This allows important and interesting comparisons with the structure and ecology of shore communities elsewhere.

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INSHORE FISHES OF MACQUARIE ISLAND

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Isolated islands such as Macquarie Island are frequently rich sources of unique or rare species of animals and plants, or have unusual faunal assemblages, but as far as fish are concerned, Macquarie Island is rather disappointing. Apart from a dubious record of a large shark and occasional beach strandings of small fish which usually inhabit the upper waters of the open oceans, the island can only boast six fish species from nearshore waters. This figure could well increase with more intensive sampling, but experience from other more thoroughly studied islands in similar situations in the sub-Antarctic indicates that the figure would not rise dramatically.

Of the five common species, four (*Notothenia magellanica*, *N. rossii rossii*, *N. microlepidota* and *Harpagifer georgianus georgianus*) belong to the peculiarly Antarctic group, the Notothenioidae or Antarctic cods, while *Zanclorhynchus spinifer* belongs

to the small family Congiopodidae or pig fishes, so called because of their rather produced snout with thick rubbery lips. The sixth nearshore species is *Neophrynichthys magnicirrus*, a small scorpaenid only known from four specimens trawled from 2km off the east coast of Macquarie Island.

Although Macquarie Island lies just north of the Antarctic Convergence, its ichthyofauna resembles that of the Antarctic more than those from more northerly locations. Based on fish distribution, it is included in the same zoogeographic zone as the Kerguelen Islands 2000 miles southwest of Western Australia rather than New Zealand or Tasmania, to which it is closest geographically. The paucity of the fish fauna can be explained on two counts. Firstly and most obviously the great expanses of deep ocean separating it from neighbouring land masses (New Zealand is closest, 585 nautical miles to the northeast) have restricted the ability of shallow water bottom living fishes to reach the island. The generally eastward flowing currents of the region under the influence of the prevailing westerly winds do not aid the spread of pelagic young stages of fish from the Australia-New Zealand region either, and in fact those fish which do have pelagic young stages (*Notothenia magellanica*, *N. rossii rossii* and *Zanclorhynchus spinifer*) are all derived from sub-Antarctic areas to the west of Macquarie Island. The only species with distinct affinities with the Australasian region are the scorpaenid *Neophrynichthys magnicirrus* with related species in the southern Pacific area, and one of the more northerly of the antarctic cods, *Notothenia microlepidota*, which is also found in southern New Zealand and its islands to the south. The other four species all have Antarctic affinities, with *Notothenia magellanica*, *N. rossii* and *Harpagifer* spp. having wide sub-Antarctic distributions, while *Z. spinifer* is only known elsewhere from Kerguelen Islands. Having its fish fauna derived largely from Antarctic areas provides the second reason for the limited number of species because the Antarctic fish fauna itself is very limited, comprising less than 200 species of the 20,000 or so known worldwide. The original centre of radiation of this fauna appears to have been in the South Atlantic/Patagonian area, which puts Macquarie Island at the farthest point from the centre of dispersal.

Not a lot is known about the biology of even the common species, as we have not yet had an opportunity to study them. Observations by divers have confirmed reports from elsewhere that the fish are very sluggish, and some are easily caught by hand! The small *Harpagifer georgianus georgianus* overcomes this shortcoming by being cryptically marked and hiding under stones or kelp holdfasts, while the excessively spiny *Z. spinifer* presumably relies on its armour for protection, as it has most often been encountered on almost bare sandy bottoms. Of the Antarctic cods, *Notothenia magellanica* is the commonest fish at the island. The silvery young stages are pelagic and presumably account for this species being one of the most widespread in the Antarctic region, but the older stages (> 7cm long) have a generally brown colouration and are usually found in the kelp zone, although some of the larger adults seem to revert to a pelagic habit and become blue and silver again. *N. rossii rossii* is in many ways similar in having a pelagic young stage and a more or less benthic habit when adult, but is much less common than *N. magellanica* at Macquarie Island. The *Notothenia* species, as elsewhere appear to feed mainly on benthic and some pelagic crustaceans such as amphipods, euphausiids and isopods. Fish in turn form almost the entire diet of the Macquarie Island shags (mostly *H.g.georgianus* and small *N.magellanica*), and an important component in gentoo and royal penguins.

ON A MASS MORTALITY OF LANTERN FISH AT MACQUARIE ISLAND

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Reports of mass mortalities of fish are common, if not of near daily occurrence somewhere in the world. Generally these mass die-offs appear to be the result of local pollution and environmental contaminants. The information presented here is interesting in two respects: firstly, it took place more than 960 kilometers from the nearest population center, and secondly, because it involves two species of fish, *Electrona subaspera* and *Gymnoscopelus braueri*, both lantern fish, associated with deep water.

Macquarie Island is in the belt of strong prevailing winds commonly referred to as the Roaring Forties. At Macquarie these winds average nearly 20 knots and predominate from the north west. Conditions are seldom calm.

On the evening of May 13, 1967 a great many of these lantern fish were washed ashore. On the 14th I wrote a brief report on this event, in part as follows: "Last night a great many lantern fish were washed ashore along the east coast of the Isthmus. The number of fish is in the thousands. In a count of three hundred individuals, twenty were *G. braueri* and this ratio appear uniform." Also collected were two squid (later identified as *Nototodarus sloanii*) and one small fish, probably *Notothenia macrocephala*.

The first indication I had that such numbers of fish were present was during my regular Dominican Gull census from Sandy Bay to the Base. Normally about 60 birds were present for this 7km stretch of coast. On the 12th, 288 gulls were present.

At Nuggets Point I disturbed a gull which disgorged a large wad of fish which I thought could be lantern fish. Though I had never encountered this group of fishes previously the dark photophores were distinctive. This observation was confirmed a short while later when I found three very bruised specimens on the beach near the Base.

Previous to these observations the weather had been unusually still, the weather cold. What winds that were recorded were from the South. Snow had fallen on most days. The sea water temperature had dropped suddenly 2°F. It is believed that these conditions, primarily the drop in sea water temperature, was responsible for the die-off. A similar situation was believed the cause of another lantern fish mortality in California (Aughtry 1953).

Usually Macquarie Island lies just north of the Antarctic Convergence. What appears to have happened was that this body of colder water pushed northward to engulf the island and that those species and/or individuals that could not tolerate this change in temperature conditions perished. Some were washed ashore which permitted the observations recorded here.

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NEXT ISSUE: Eleven papers on the animals of Macquarie Island.