RESEARCH PAPERS

NO. 39

SHORT-TERM CHANGES IN THE AQUATIC MACROPHYTE FLORA OF LOCH FLEET, S.W. SCOTLAND, FOLLOWING CATCHMENT LIMING, WITH PARTICULAR REFERENCE TO SUBLITTORAL *SPHAGNUM*.

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SUMMARY

Loch Fleet, a remote upland lake in S. W. Scotland, rapidly acidified in the 1970's and became fishless. A major five-year research project (1985-89) was undertaken to investigate and improve the water quality of the loch in order to re-establish a sustainable brown trout fishery. As part of the biological investigations, aquatic macrophytes were surveyed annually, during September, before (1985) and after (1986-88) catchment liming, by taking Ekman grab samples both throughout the loch and along transects.

Prior to limimg, the species-poor macrophyte flora was restricted to water ≤5m deep. There was a distinct depth zonation with *Littorella uniflora*, *Lobelia dortmanna*, *Isoetes lacustris* and *Sphagnum auriculatum* dominant in progressively deeper water. *Sphagnum* was the dominant macrophyte in the sublittoral.

After catchment liming, loch water pH increased from 4.5 to >6, and the most profound changes were:

1 A 99% decline in *Sphagnum* biomass within 30 months.

2 Colonisation of deeper water by *Utricularia* and two previously unrecorded mosses, *Amblystegium serpens* and *Drepanocladus fluitans*.

3 Evidence for increased abundance of *Isoetes lacustris* and decreased abundance of *Lobelia dortmanna* despite little change in both their distributions.

4 A proliferation of filamentous green algae in 1988, which, due to smothering of foliage, adversely affected growth of *Lobelia*, *Juncus fluitans* and most particularly, the liverwort *Solenostoma triste*.

5 A reduction in the maximum depth of macrophyte growth to 4m.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

INTRODUCTION

There is irrefutable scientific evidence that lakes and streams in catchments with particularly sensitive geologies, and soils with a low buffering capacity, are susceptible to water acidification from human activity. Anthropogenic 'acid rain' is primarily a consequence of burning fossil fuels, but the production of nitrogen oxides by motor vehicle engines may also be an important contributory factor. Other factors, most notably afforestation of catchments with coniferous trees, can exacerbate the problem of water acidification (United Kingdom Acid Waters Review Group, 1989).

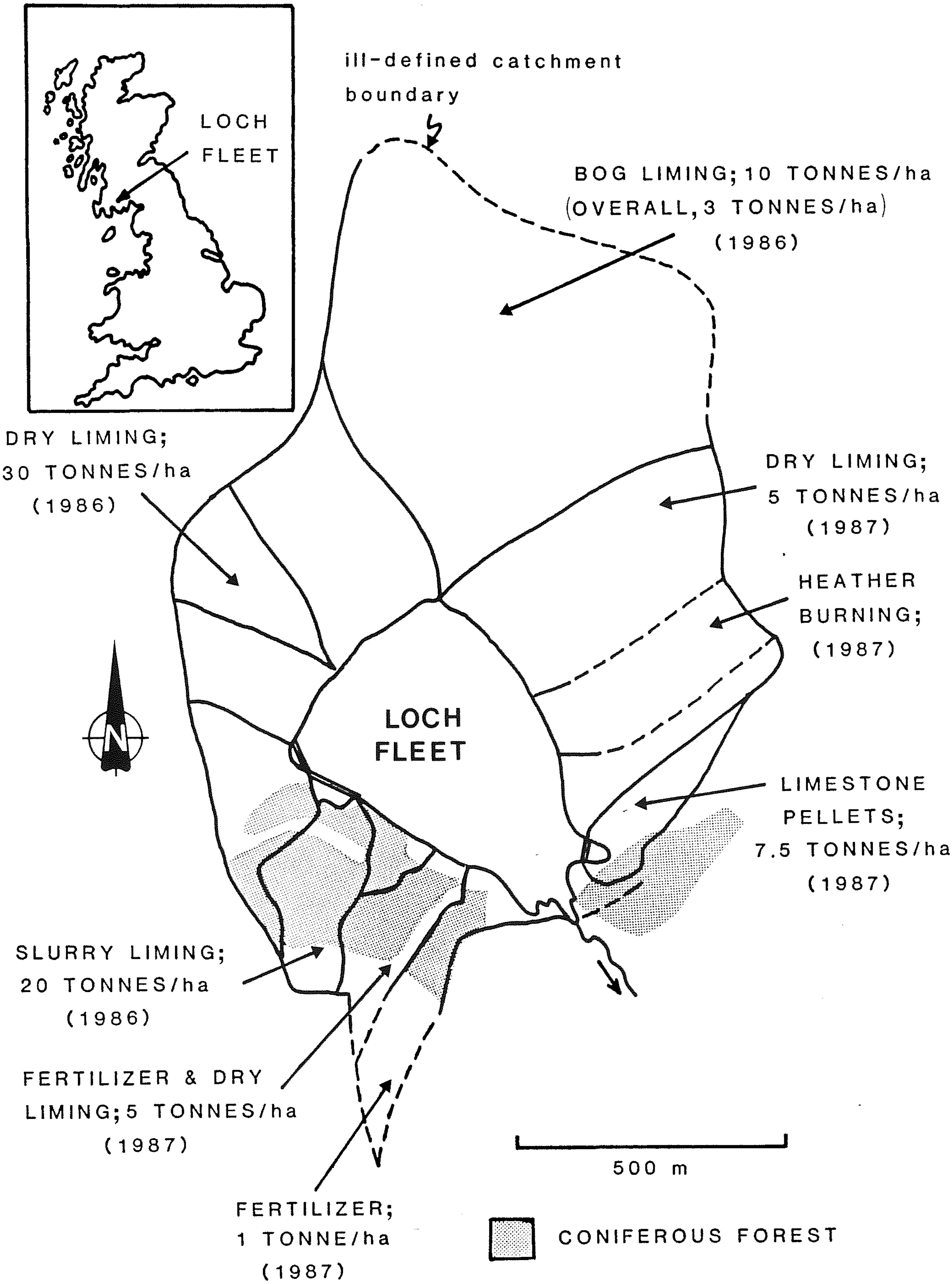
The biological consequences of acidification are profound, producing significant changes in aquatic plant and animal communities. The loss of trout (*Salmo spp.*) from acidified lakes is a well known phenomenon (eg Overrein *et al.*, 1981), but changes in aquatic macrophyte communities have received less attention. However, comparison of historical macrophyte records with recent botanical survey data has indicated significant floristic change in some recently acidified soft-water lakes in Sweden (Grähn *et al.*, 1974; Grähn, 1977), a number of heathland ponds in the Netherlands (van Dam and Kooyman-van-Blokland, 1978; Roelofs, 1983) and Lake Avalanche in the U.S.A. (Hendrey and Vertucci, 1980). In these sites, previously dominant isoetid communities, comprising shoreweed, *Littorella uniflora*, water lobelia, *Lobelia dortmanna* and quillwort, *Isoetes lacustris*, have declined in relative abundance and been partially or, in some cases, totally replaced by *Sphagnum* moss and/or bulbous rush, *Juncus bulbosus* var *fluitans* which both thrive in acid water. *Sphagnum* has also become established in the sublittoral of a number of acidified lakes in parts of Scotland and Wales (Raven, 1988 and unpublished data).

Attempts to remedy the effects of water acidification have largely been confined to Scandinavia and North America where a large number of acidified lakes have been limed (eg Erikson *et al.*, 1983; Krester & Colquhoun, 1984). However, due to different prevailing hydrological conditions, notably much more rapid turnover times in smaller lakes, direct lime application to lakes is inappropriate in Britain (Underwood *et al.*, 1987). Experiments involving catchment liming and other treatments have been undertaken in Scotland and Wales to identify the most ecologically and economically satisfactory methods of restoring lakes to their pre-acidified state (Howells & Brown, 1987; Welsh & Burns, 1987; Underwood *et al.*, 1987). One of these studies, the 'Loch Fleet Project' was a major 5-year (1984-89) research programme sponsored by the Central Electricity Generating Board, the South of Scotland Electricity Board, the North of Scotland Hydro Electric Board and British Coal (Howells & Brown, 1987). The prime objective was to restore a self-sustaining trout fishery to a small upland acidified lake in Galloway, S. W. Scotland, by producing suitable water chemistry conditions through catchment liming and other treatments. This paper describes changes in the distribution and relative abundance of aquatic macrophytes in Loch Fleet during 1985-88 as a result of this restoration programme.

The Study Site

This section is a short summary of the Loch Fleet Project abstracted from Howells & Brown (1987) and Howells (1989).

Fig. 1 The Loch Fleet catchment, showing treatments applied to experimental sectors during 1986 and 1987.
Taken from CEGB (1989).



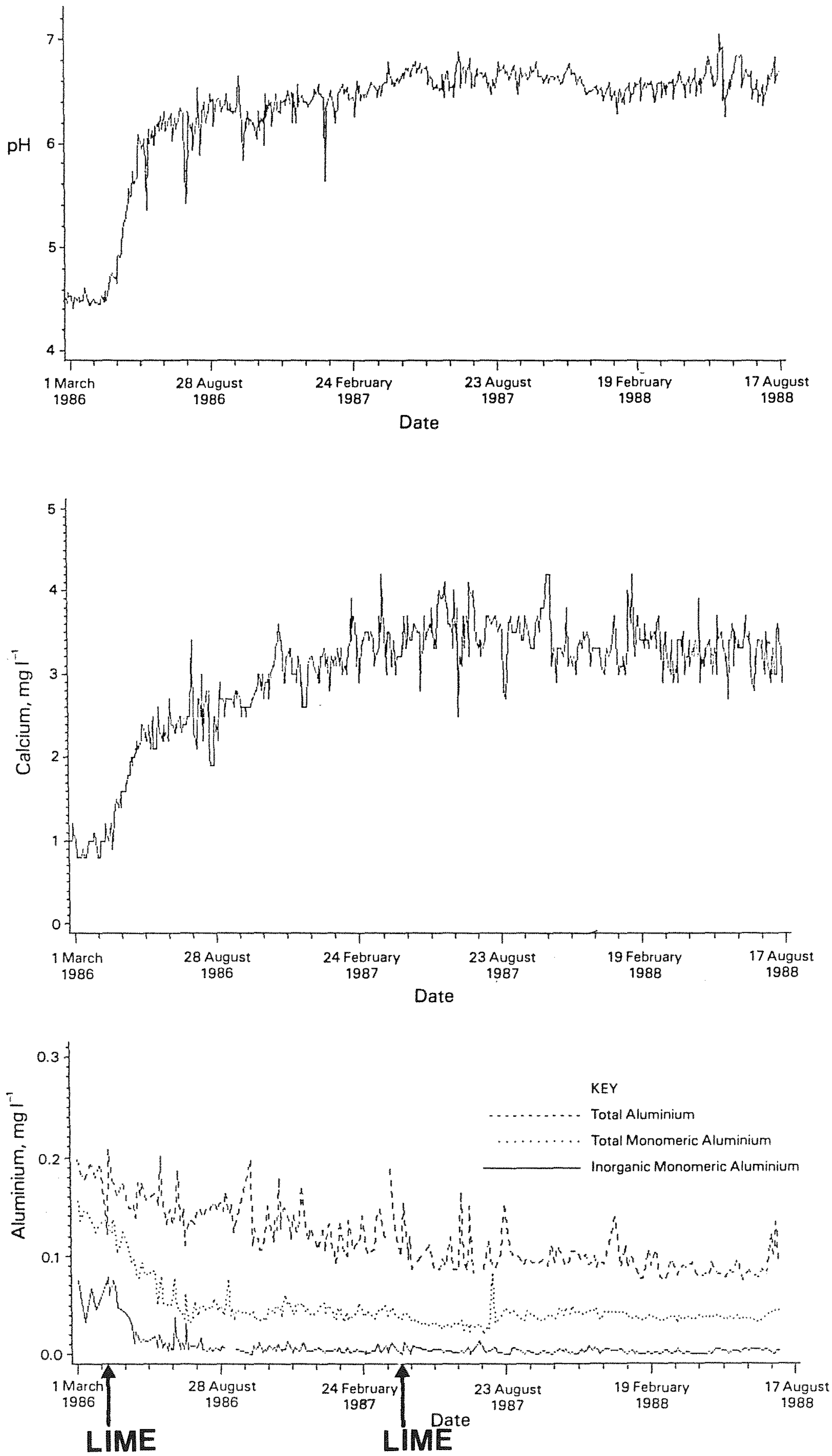
Loch Fleet is a small (17 ha) upland (altitude, 340m) lake in Galloway, S. W. Scotland (National Grid Reference, NX 560698). The catchment area of 111ha comprises granite bedrock overlain by thin layers of predominantly stony-sandy loam, peat and peaty gleys. Rough moorland comprising mainly heather, *Calluna vulgaris* and purple moor grass, *Molinia caerula* is the dominant vegetation but 10% of the lower catchment was planted with spruce *Picea spp.*, lodgepole pine *Pinus contorta* and larch *Larix spp.* in 1961/62.

The loch supported a healthy trout fishery until the 1950's, but rapid acidification after 1970 effectively rendered the water fishless. In 1984, the water was very acid (pH 4.2 - 4.5) and had high concentrations (ca. 0.2 mg l^{-1}) of aluminium.

Following extensive baseline studies of several environmental parameters, soil, vegetation and aquatic biota, the catchment was divided into experimental sectors, most of which were subjected to different types of treatment, (principally the application of limestone), in 1986-87 (Fig. 1). Water chemistry was closely monitored by taking samples from the sub-catchment sectors, four artificial embayments constructed within the loch, the main loch and the outflow. Changes in catchment soils, vegetation and aquatic biota were also monitored.

Water quality rapidly improved in lime treated sectors and the pH of the outflow increased from 5.5 to 6.3 over 2.5 months, an improvement (including significantly higher calcium and significantly lower aluminium concentrations) which was subsequently maintained (Fig. 2). Water in embayment 5 remained acidic (ca. pH 4.5 - 4.7), reflecting the non-treatment of sector V.

Fig. 2 Water chemistry changes at the Loch Fleet outflow in relation to liming of experimental sectors in the catchment. Taken from CEGB (1989).



The loch was restocked with brown trout *Salmo trutta* in May 1987 and July 1988. Successful spawning occurred in the autumn of both years and recaptured adult fish were found to be in good condition.

METHODS

Vascular plants, bryophytes (mosses and liverworts) and algae easily discernable with the naked eye (eg filamentous green algae, *Batrachospermum*) were all included as aquatic macrophytes. Where ever possible, plants were identified to species in the field. Bryophytes were retained and dried for subsequent examination with a compound microscope, and voucher specimens were kept as a reference collection. Identification of algae was not attempted beyond a rudimentary level.

Aquatic macrophyte distribution was assesed by three methods:

1) mapping littoral vegetation from the shore.
2) taking random Ekman grab samples in deeper (sublittoral) water, and
3) taking Ekman grab samples at regular intervals along four transects aligned perpendicular to the shore.

Littoral mapping

Littoral (nearshore) vegetation around the loch was mapped from the shore in July 1983 (Raven, 1985). This was repeated in September 1988 to identify major floristic changes within this habitat.

Random grab samples

A preliminary assessment of sublitoral macrophyte distribution was obtained by recording plant material recovered in 80 Ekman grab samples during a bathymetric survey in July 1984 (Anderson *et al.* 1986). Water depth, substrate and macrophyte taxa were recorded and each sampling site was accurately located using shore-based plane table planimetry. Comprehensive pre-liming distribution data were achieved by further survey of the whole loch in September 1985 when 5 grab samples (surface area 15 x 15 cm) were taken within a grid of 100 x 100 m squares delineated on the water surface by temporary buoys (Appendix 1).

The 1984-85 data indicated that living macrophytes were confined to water ≤ 5 m deep. Each of the three subsequent annual surveys (September 1986-88) therefore concentrated in these areas (Appendix 2). Compass bearings were taken onto known landmarks around the shore to locate and subsequently map the sample sites. Random grab samples were also taken in experimental embayments 4,5 and 9 (Fig. 3).

Transects

Four 30 m long transects were established in September 1985 and re-surveyed in 1986-88 (Fig. 3). Transects 'B' and 'D' were located on the sheltered, gently shelving southwestern shore and the steep, exposed northern shore respectively. Transects 'A' and 'C' were located to be within embayments 9 and 5 respectively, the latter representing an acid water control. Ekman grab samples were taken every two metres along each transect and water depth, substrate and macrophyte taxa recorded (Raven, 1986). As with the random samples, the amount of plant material recovered in each grab was visually estimated using a crude qualitative scale, comprising 'present', 'abundant' and 'very abundant'.

Estimating *Sphagnum* biomass and condition

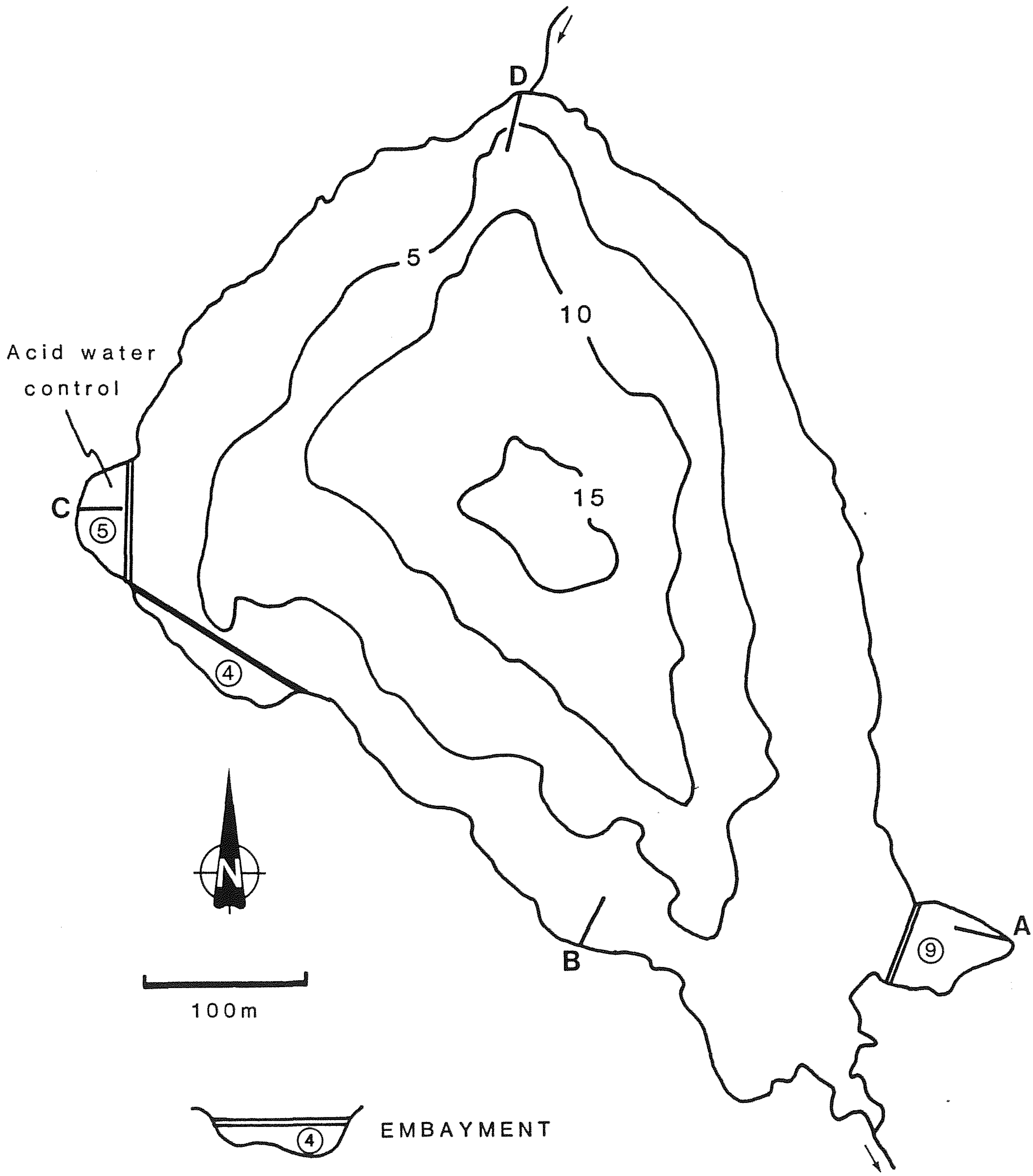
Changes in the status of *Sphagnum* in the loch before and after liming was the main focus for this study. Samples of *Sphagnum* were retained to estimate mean dry weight for each of the qualitative abundance categories described above. Total *Sphagnum* dry weight biomass in the loch was simply estimated by multiplying the relative percentage occurrence and abundance data presuming that the percentage occurrence data were a good overall indication of *Sphagnum* cover.

The length of the green (living) portion of *Sphagnum* shoots, which broadly indicates the amount of growth during the current growing season (Grähn, 1985), was measured to assess annual changes in condition. The occurrence of obvious die-back and *Sphagnum* debris were recorded in the field.

Data presentation

Water level was measured relative to a fixed shore-line mark on each

Fig. 3 The location of transects "A" - "D" and the experimental embayments in Loch Fleet. Bathymetric contours at 5 m intervals (Anderson <u>et al.</u> 1986).



sampling day. There was a range of 0.5m in water levels recorded during 1985-88, so all water depths were standardised to the September 1986 level. Floristic changes throughout the loch were assessed by comparing the percentage occurrence of individual taxa during 1985-88. Changes were evaluated further by considering each 1m depth interval. For simplicity, the random sublittoral and transect Ekman grab data other than those taken within the embayments were combined. The number of samples taken in embayments 4 and 9 were too small for meaningful annual comparisons to be made, but data from embayment 5 were used as an acid water control during 1986-88.

In addition to simply assessing changes in the percentage occurrence data for individual taxa, annual changes in relative abundance for selected macrophytes were estimated using an index system calculated by numerically weighting the abundance categories recorded in the field (see Table 1 for an example calculation). For each taxon, the pre-liming (1985) abundance status was represented by a baseline index value of 100. Abundance in subsequent years was expressed as a percentage of that value: for example, an index of 200 represented an abundance twice that in 1985. This index system could only be used for assessing relative changes in the abundance of individual taxa from year to year, not directly as a comparison between taxa. However, together with the percentage occurrence data, it provided a useful indicator of the response of macrophyte taxa following catchment liming.

A more accurate assessment of change in the abundance of *Sphagnum*, based on dry weight biomass, is described above.

TABLE 1. An example calculation of the relative abundance index for macrophytes in Loch Fleet, 1985-88.

e.g. *Isoetes lacustris* (1986)

Abundance category*	Numerial weighting (v)	Number of occurrences	Proportion of total observations (%) (p)	(pv)
Present	1	15	48	48
Abundant	2	12	37	74
Very Abundant	3	5	16	48
Σpv				169

Σpv multiplied by % occurrence in Ekman grab samples [36.8%]

169 x 36.8 = 62.2

1985 value, calculated the same way = 47.6; INDEX VALUE = 100

1986 index = 62.2 ÷ 47.6 x 100

= 131 and so on.

* amount of plant material recovered in Ekman grab.

RESULTS

Lake vegetation before catchment liming

Shortly before catchment liming, the species-poor aquatic flora was typical of an exposed upland oligotrophic lake with very acid water (Table 2). Emergent vegetation comprised two small stands of bottle sedge *Carex rostrata* growing in the sheltered N.W. bay (Appendix 1), although jointed rush *Juncus articulatus* was locally abundant on peaty substrate near the water's edge, particularly along the western shore.

The predominantly rocky and boulder-strewn shorline severely restricted the development of macrophytes inshore. Both *Littorella uniflora* and *Lobelia dortmanna* were patchily distributed and were abundant only in areas with sand or gravel substrate. Vascular plants were extremely scarce on the exposed rocky eastern shoreline where liverworts were predominant. Mosses, notably *Racomitrium aciculare* were abundant on boulders near the water's edge. Filamentous green algae, particularly *Mougeotia spp.* coated submerged liverworts and the underwater parts of *Lobelia* flowering stems. *In deeper water Isoetes lacustris* and *Sphagnum auriculatum* were locally abundant on organic sediment. Consequently, there was a distinct *Littorella - Lobelia - Isoetes - Sphagnum* depth zonation (Fig. 4).

Sphagnum auriculatum was the dominant macrophyte throughout the loch in water 2 - 5 m deep, and was particularly abundant on muddy sediments off the sheltered western shore, forming dense carpets more than 30cm deep in places. However, the tall, quill-like stems of *Isoetes lacustris* still

TABLE 2. The percentage occurrence of aquatic macrophytes in Loch Fleet before and after catchment liming. Figures represent occurrence in Ekman grab samples from water ≤ 5 m deep. Taxa arranged in order of initial relative frequency.

	BEFORE	AFTER LIMING		
Macrophyte	September 1985	September 1986	September 1987	September 1988
Sphagnum auriculatum	54.2	57.5	7.8[39.9]	7.6
Isoetes lacustris	34.5	36.8	34.6	38.2
Lobelia dortmanna	18.7	10.3	13.1	10.2
Solenostoma triste	12.1	20.7	24.8	–
Sphagnum cuspidatum	9.3	5.7	0.6	–
Littorella uniflora	8.4	2.3	11.1	10.8
Filamentous green algae	5.6[m]	4.6	11.1	58.6
Juncus bulbosus var *fluitans*	0.9	2.3	8.5	3.8
Utricularia sp.	0.9	4.6	13.7	20.4
Fontinalis antipyretica	–*	–	–	0.6
Isoetes echinospora	–*	–	2.0	1.9
Amblystegium serpens	–	2.3	2.6	11.5
Batrachospermum spp.	–	–	1.3	0.6
Bryum pallens	–	–	–	0.6
Calypogeia mulleriana	–	1.1	2.0	2.5
Cephalozia connivens	–	1.1	1.3	1.3
Drepanocladus fluitans	–	1.1	4.6	8.3
Lophozia sp.	–	1.1	–	–
Polytrichum commune	–	1.1	–	0.6
Scapania undulata	–	1.1	–	0.6
Number of Ekman grabs	107	87	153	157

[ ] includes *Sphagnum* showing signs of die-back

[m] mainly *Mougeotia sp.*

* recorded during littoral mapping survey.

penetrated through this blanket of mosses. In September 1985, the total dry weight biomass of *S. auriculatum* in the loch was estimated to be 508kg. Although *Sphagnum cuspidatum* was recovered in 9.3% of Ekman grab samples it was much less abundant than *S. auriculatum*, with an estimated total dry weight biomass of 2.6kg.

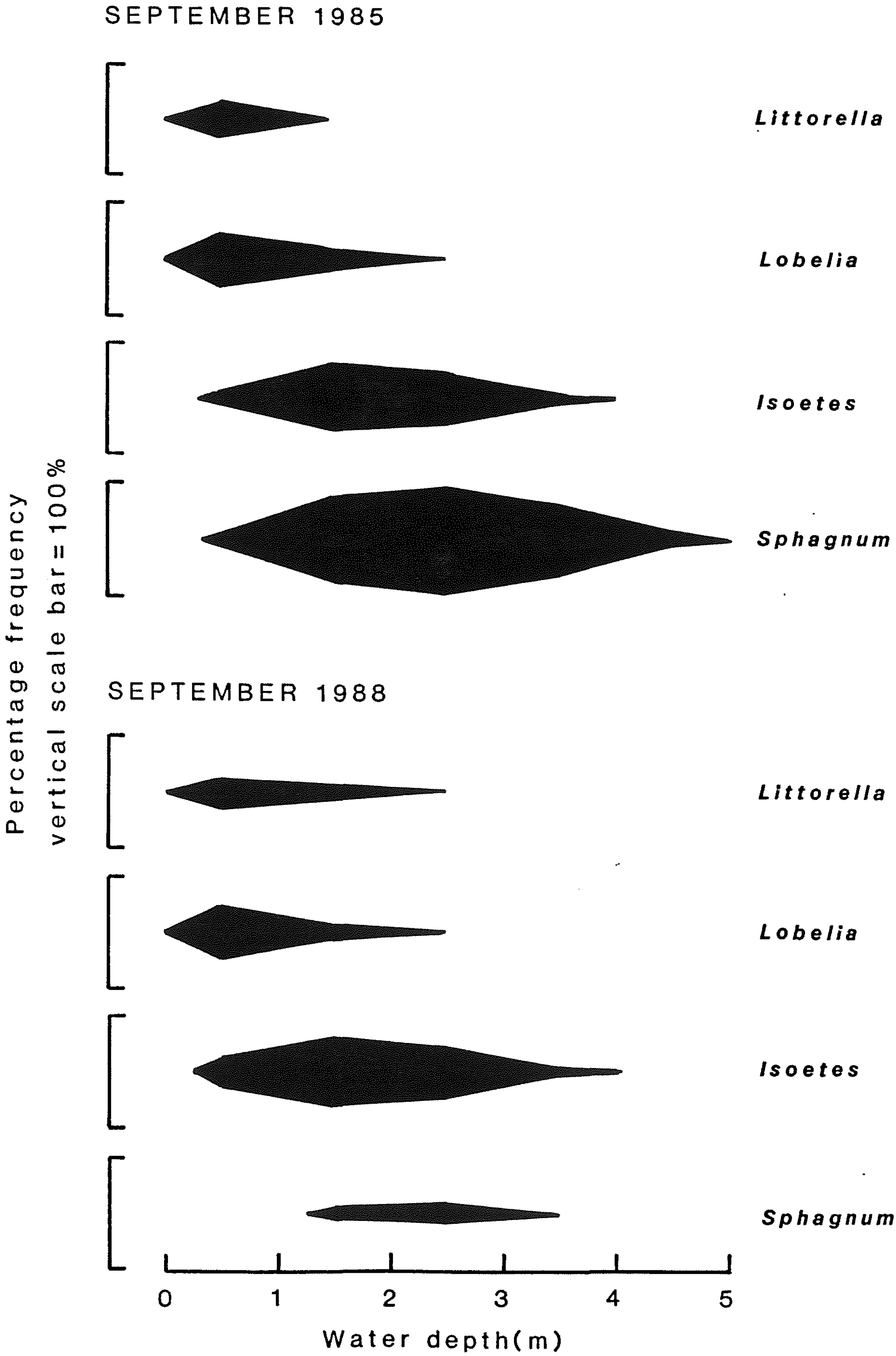
Since living macrophytes were restricted to water no more than 5m deep, only 45% of the total lake bed constituted the colonization zone (cf Grähn, 1985). Inblown *Molinia* grass debris had accumulated in a few shallow areas, but *Sphagnum* debris was largely confined to deeper water (Appendix 3).

Vegetation changes after catchment liming

There were no significant changes in the littoral vascular macrophyte community discernable by walking around the lochshore. However, a single small stand of various-leaved pondweed *Potamogeton polygonifolius* appeared by September 1986 and within 2 years several other sites, including embayments 4 and 9 had been colonized by this species. It was also evident that filamentous green algae were extremely abundant in shallow water in September 1988.

The total number of macrophyte taxa recorded from Ekman grab samples increased after liming, due mainly to the appearance of a number of bryophytes (Table 2). However, with few exceptions, these newly-established taxa remained a minor component of the macrophyte community. Twelve macrophytes will be considered in some detail; indeed, the most

Fig. 4 The depth distribution of Littorella uniflora, Lobelia dortmanna, Isoetes lacustris and Sphagnum auriculatum in Loch Fleet before (1985) and 30 months after catchment liming.



significant change in the aquatic plant community, namely the decline of *Sphagnum*, requires special attention in a separate section below.

Lobelia remained the most frequently recorded vascular plant in shallow water throughout 1985-88 although there was evidence for a decline in abundance during 1988 (Tables 3 and 4). *Littorella* became more widespread in water 1.1 - 2.0 m deep during 1987-88 and also became more abundant overall, with a relative abundance index more than twice that prior to liming. However, the large variations in percentage frequency occurrence of both *Lobelia* and *Littorella* may have reflected the patchy distribution of these macrophytes due to the extreme diversity of different substrate types in shallow water.

The previously widely distributed leafy liverwort, *Solenostoma triste* increased both in distribution and abundance during 1986 and 1987, particularly in water up to 3m deep, but was not recovered alive in Ekman grab samples taken in September 1988. There was an unusually large amount of dead liverwort material in 1988 and virtually all liverworts in shallow water were smothered by filamentous green algae, which had proliferated in water up to 3m deep that year (Tables 3 and 4). *Juncus fluitans* was another macrophyte which increased in distribution and abundance after liming but suffered a reversal in 1988 when a large proportion of plants were also thickly coated with filamentous green algae.

Bladderwort, *Utricularia sp.*, recovered in only one Ekman grab sample (in the north-west bay) prior to liming, rapidly spread and proliferated after liming, particularly in water 1 - 3 m deep. By 1988 it was the second most widespread vascular macrophyte (20.4% frequency), with a relative abundance

TABLE 3. Changes in the relative abundance index of 12 selected macrophyte taxa in Loch Fleet after catchment liming.
Figures represent an abundance index indicating percentage of the pre-liming (1985) value for each macrophyte*.
(See Table 1 for calculation of index).

	Abundance index Before 1985	 After liming 1986	 1987	 1988
(a) Taxa with >10% frequency in any one year.				
*Sphagnum auriculatum***	100	90	8	1
Isoetes lacustris	100	131	150	151
Lobelia dortmanna	100	118	101	50
Solenostoma triste	100	236	301	0
Littorella uniflora	100	41	240	236
Filamentous green algae	100	246	243	2217
Utricularia sp.	100	767	3250	4667
(b) Taxa with >10% frequency in at least one 1m depth interval in any year.				
*Sphagnum cuspidatum***	100	50	20	0
Juncus fluitans	100	225	944	422
Isoetes echinospora	-	-	100	95
Amblystegium serpens	-	100	113	720
Drepanocladus fluitans	-	100	418	1328

* index of 100 shown for first year each taxon recorded in Ekman grab samples.

** based on dry weight biomass.

Batrachospermum not included.

TABLE 4. The depth distribution frequency of selected macrophyte taxa in Loch Fleet before (1985) and after catchment liming. Figures represent frequency ≥ 10% to nearest integer; absence indicated by -

Depth(m)	Macrophyte	Before 1985	After liming 1986	1987	1988
	Lobelia dortmanna	42	57	53	45
	Littorella uniflora	29	14	47	25
	Filamentous green algae	19	29	37	75
	Isoetes lacustris	16	36	26	25
≤ 1.0m	*Solenostoma triste*	13	14	32	-
	Sphagnum auriculatum	13			
	Juncus fluitans	-	14	37	15
	Isoetes echinospora	-	-	11	15
	Batrachospermum sp(p).	-	-	11	
	Sphagnum auriculatum	74	77	12	
	Isoetes lacustris	62	59	61	60
	Lobelia dortmanna	18		18	14
	Solenostoma triste	13	32	31	-
1.1-2.0m	*Sphagnum cuspidatum*	10		-	-
	Littorella uniflora	-	-	16	14
	Utricularia sp.			27	35
	Juncus fluitans		-	12	
	Filamentous green algae	-	-	14	92
	Sphagnum auriculatum	94	82		15
	Isoetes lacustris	44	50	33	43
	Solenostoma triste	13	18	24	-
2.1-3.0m	*Sphagnum cuspidatum*		14	-	-
	Utricularia sp.	-	14	11	25
	Filamentous green algae	-	-		53
	Amblystegium serpens	-			17
	Drepanocladus fluitans	-	-		11
	Sphagnum auriculatum	64	70		-
	Sphagnum cuspidatum	29	-	-	-
3.1-4.0m	*Solenostoma triste*	14	15	13	-
	Isoetes lacustris		15	-	
	Amblystegium serpens	-	-		25
	Drepanocladus fluitans	-			13
	Sphagnum auriculatum	14		13	-
	Solenostoma triste	-	22	13	-
4.1-5.0m	*Sphagnum cuspidatum*	-	-	13	-
	Filamentous green algae	-	-	13	-
	Amblystegium serpens	-	-	13	-
	Drepanocladus fluitans	-	-	13	-

See Appendix 4 for full details of occurrence frequency data.

index almost 50 times that prior to liming (Tables 2,3 and 4).

The distribution of *Isoetes lacustris* in water 1 - 3 m deep was similar before and after liming, but its relative abundance index had increased 50% by 1987. Furthermore, it was noticeable that many of the plants recovered in Ekman grab samples were particularly large and vigorous during 1987-88. *Isoetes echinospora*, previously restricted to shallow water increased in distribution, and was recovered from Ekman grab samples in 1987 and 1988, but remained relatively scarce compared with *I. lacustris*.

Amblystegium serpens and *Drepanocladus fluitans*, two bryophyte species unrecorded prior to liming, increased significantly in distribution and abundance during 1987-88, particularly in deeper water (Tables 3 and 4). Indeed these mosses replaced *Sphagnum spp.* as the most frequent taxa in water 3.1 - 4.0 m deep.

The decline of *Sphagnum*

Although there was no decrease in the percentage occurrence frequency of *Sphagnum auriculatum* within 6 months of liming (Table 2), there was an apparent reduction in growth during the 1986 summer implied by shorter living shoots compared with the previous year (Fig. 5). Eighteen months after liming (September 1987), there was considerable *Sphagnum* die-back and most shoots were either dead or showed less than 10mm growth. The occurrence of healthy *S. auriculatum* in the main loch declined from 54% before liming to 7.8% and 7.6% after 18 and 30 months respectively. During the same period, the occurrence of *Sphagnum* debris in water < 5m deep increased from 0.9% to 16.6% of Ekman grab samples.

Changes in the estimated total dry weight biomass were even more pronounced (Table 5; Fig. 6). Before liming, the bulk of the estimated 508kg (d-w) *Sphagnum* occurred in water 1.1 - 4.0 m deep. Within 30 months of liming, only 1.1% (5.6kg) remained alive, the remnant plants confined to water 1.1 - 3.0 m deep. However, the surviving *Sphagnum* was apparently in good condition, with some living shoots exceeding 40mm in length (Fig. 5).

Sphagnum cuspidatum declined in distribution and abundance relatively quickly. It had disappeared fron deeper water (3.1 - 4.0 m) within 6 months and was not recorded at all from the main loch 30 months after liming (Tables 2.4 and 5).

Information gleaned from Ekman grab samples and general observations of the lake bed indicated that *Sphagnum* rapidly died in embayments 4 and 9 in which the pH of the water increased from ca. 4.5 to more than 6.

In direct contrast to the main loch, *S. auriculatum* and *S. cuspidatum* continued to flourish in embayment 5 where the water remained at an acid pH of ca. 4.5 - 4.7 throughout (Fig. 5). Indeed, the length distribution frequency of living shoots from embayment 5 in 1988 was similar to that for the entire loch before catchment liming, the modal class length being 41 - 50mm in each case. Moreover, the estimated dry weight biomass of *S. auriculatum* in the embayment increased from 6.0kg to 13.4kg during 1985-88.

Fig. 5 The length of living Sphagnum auriculatum shoots in Loch Fleet before (1985) and after catchment liming, compared with an acid water control.

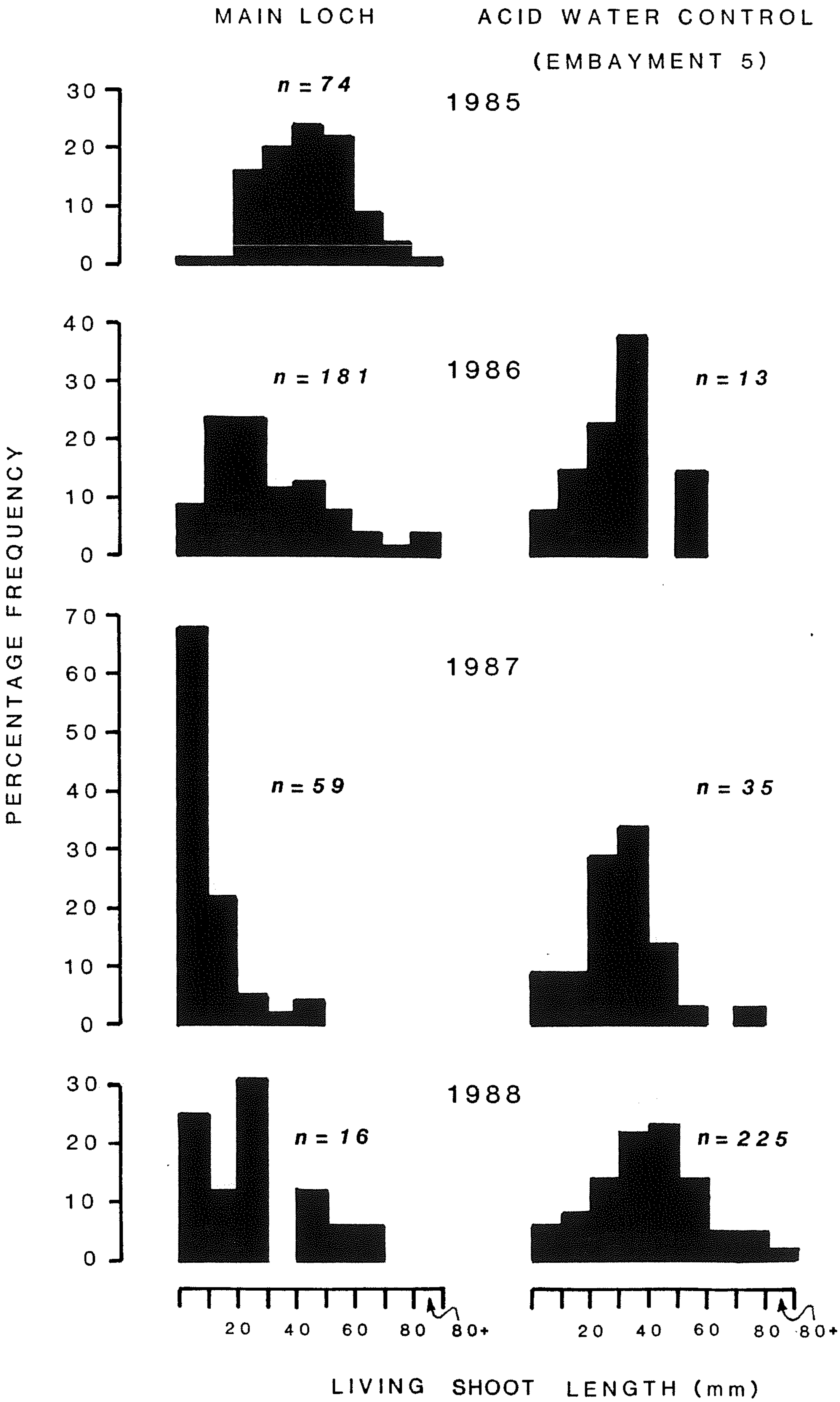


TABLE 5. The estimated dry weight biomass of *Sphagnum auriculatum* and *S. cuspidatum* in Loch Fleet before (1985) and after catchment liming.

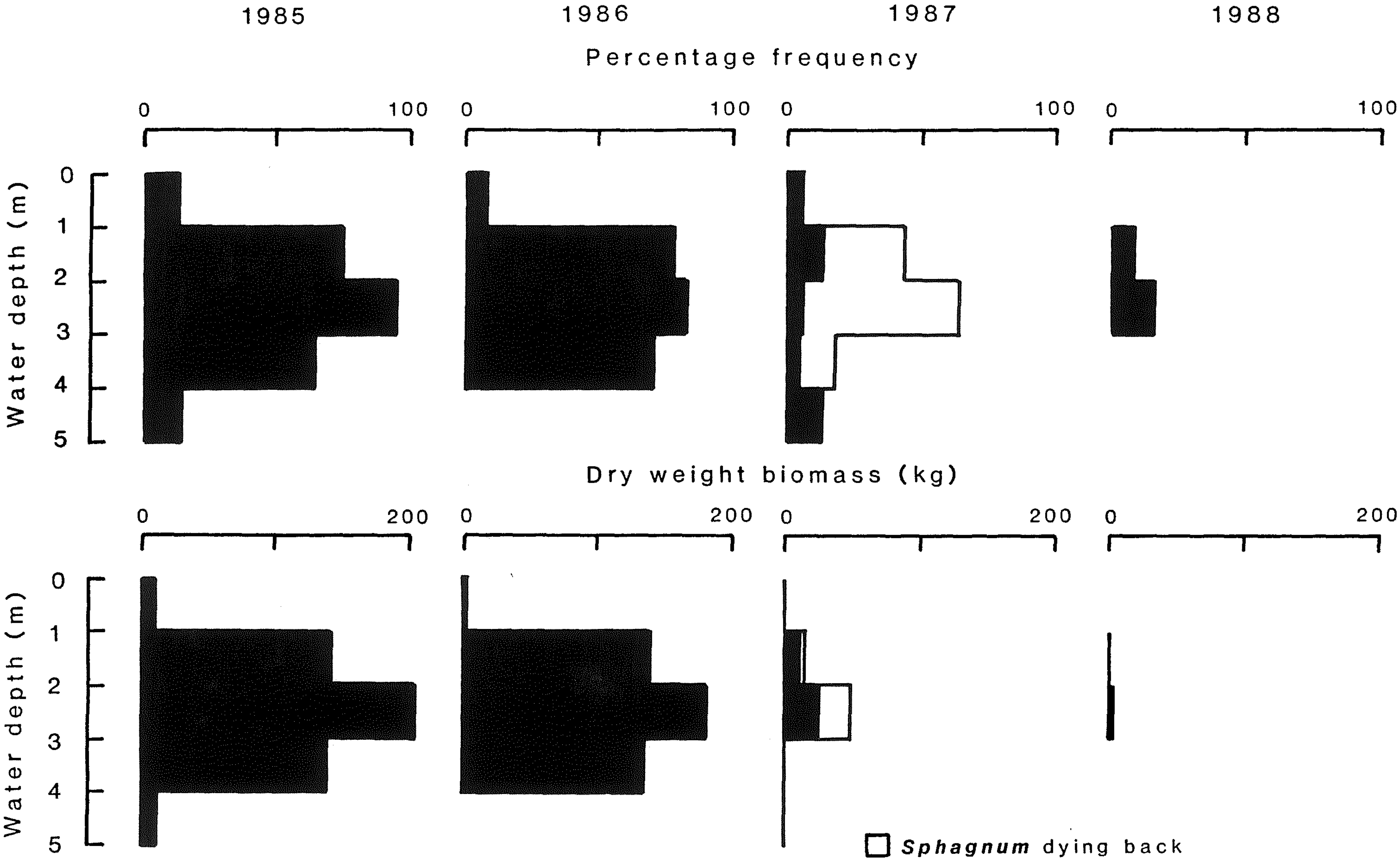
(a) *Sphagnum auriculatum*

Water depth (m)	Dry weight biomass (kg) 1985	1986	1987	1988
≤ 1.0	9.4	1.5	0.9	-
1.1-2.0	143.3	139.2	11.3	1.9
2.1-3.0	205.2	182.9	24.6	3.7
3.1-4.0	138.4	136.3	1.3	-
4.1-5.0	11.9	-	1.3	-
TOTAL	508.2	459.9	39.4	5.6

(b) *Sphagnum cuspidatum*

Water depth (m)	Dry weight biomass (kg) 1985	1986	1987	1988
≤ 1.0	0.23	-	-	-
1.1-2.0	0.59	0.52	-	-
2.1-3.0	0.37	0.79	-	-
3.1-4.0	1.42	-	-	-
4.1-5.0	-	-	0.53	-
TOTAL	2.61	1.31	0.53	-

Fig. 6 The depth distribution of Sphagnum auriculatum in Loch Fleet before (1985) and after catchment liming expressed as percentage occurrence and estimated dry-weight biomass.



A summary of the main vegetation changes

The most profound short-term vegetation changes in response to liming were:

i) a 99% decline in *Sphagnum* biomass within 30 months.

ii) colonisation of deeper water (2.1 - 4.0 m) by *Utricularia* and two previously unrecorded mosses *Amblystegium serpens* and *Drepanocladus fluitans*.

iii) despite evidence for more vigorous growth of *Isoetes lacustris*, no indication that it had started to colonise deeper water areas newly devoid of living *Sphagnum*.

iv) a proliferation of filamentous green algae, particularly in water up to 2m deep in the third summer after liming resulting in the smothering of liverworts (eg *Solenostoma triste* was effectively killed off) and the dense coating of *Lobelia* stems and *Juncus fluitans* foliage, with both these species declining in abundance during 1988.

v) a reduction in the maximum depth of macrophyte growth from ca. 5m in 1985-87, to 4m in 1988, and consequently a reduction in the proportion of lake-bed area constituting the colonisation zone from 45% to 38%.

DISCUSSION

The proliferation of *Sphagnum* in acidified oligotrophic lakes is by no means a universal phenomenon (Wile, 1983; Roberts *et al.*, 1985). However, there is little doubt that *Sphagnum* invaded and proliferated in Loch Fleet as the water rapidly acidified during the early 1970's (Raven, 1986; Anderson *et al.*, 1986). Indeed, the increase of *Sphagnum* from 6.0kg to 13.4kg dry-weight biomass in the acidic water control (embayment 5) during 1985-88 indicated that the moss would have continued to increase in the main loch after 1985 had the catchment not been limed. The abundance of *Sphagnum* in Loch Fleet prior to liming was similar to that in Lake Gårdsjön, Sweden before surface limimg, the estimated mean dry weight biomass within the vegetated lake bed being 12.6 gm^{-2} and 14.2 gm^{-2} respectively (cf. Grähn, 1985).

The decline in *Sphagnum* in Loch Fleet after liming was broadly consistent with, but relatively slower than, that reported for some surface-limed acid lakes in Sweden and upland Wales. For example, *Sphagnum* growth in Lake Trehörningen was greatly impaired very soon after liming, while in Lake V. Skälsjon, *Sphagnum* in contact with unslaked lime died almost immediately (Eriksson *et al.*, 1983). However, in Lake Lysevatten, where lime was applied to shallow areas, some depauperate *Sphagnum* survived in deeper (2 - 10 m) water (Hultberg and Andersson, 1982). In Llyn Berwyn, some *Sphagnum* survived in the vicininty of acid inflow streams (N. Stringer, Welsh Water Authority, *pers. comm.*). Because the lake water re-acidified relatively quickly (often within 2 - 5 years) at each of these example sites, *Sphagnum* was able to rapidly recolonise and proliferate once again. Frequent lime application to the water surface was therefore required to maintain the required pH, particularly in the two Welsh lakes which had short retention times (Underwood *et al.*, 1987). By comparison, liming the catchment of Loch Fleet produced a more gradual and sustainable increase in lake pH, together with a concomitant decline of *Sphagnum*. However, the continued vigorous growth of *Sphagnum* in the acidic control embayment, and apparently healthy vestigial remnant plants in the main loch indicate that recolonisation and proliferation by *Sphagnum* would probably occur if the water were to re-acidify in future.

Assessing changes of macrophytes other than *Sphagnum* is difficult because there are very few other studies for comparison. Furthermore, (i) no two lakes contained the same pre-liming flora, (ii) there is no consistent between-site trend shown by individual taxa (Table 6), and (iii) there is a lack of quantitative and experimental biomass data needed for detailed evaluation of the responses of the plants to changes in water chemistry, competition and grazing pressure etc. It is also self evident that since each catchment is unique, and the method of lime application was not standardised, directly comparable results are highly unlikely.

In Lake Bredvatten, for instance, both *Isoetes* and *Lobelia* recolonised areas vacated by *Sphagnum* after liming (Hultberg and Andersson, 1982), but in three other limed lakes in Sweden, no such response was reported (Eriksson *et al.*, 1983). Despite evidence that *Littorella* was extending into deeper water and that *Isoetes* growth was more vigorous after liming (Tables 3 and 4), isoetid species had clearly not colonised areas vacated by *Sphagnum* in Loch Fleet within 30 months of liming. However, given suitable conditions, this might occur in the longer term. Indeed, there is evidence in the sedimentary record, that *Isoetes* was much more abundant in Loch Fleet prior to acidification (Anderson *et al.*, 1986).

In the short term, it appears that *Utricularia, Amblystegium serpens*, and *Drepanocladus fluitans* responded quickly to liming by colonising deeper water (2 - 4 m) as *Sphagnum* died. *Utricularia* increased after liming in

TABLE 6. Changes in the distribution and abundance of selected macrophytes in Loch Fleet and four other lakes after liming.

Macrophyte taxa	L. Fleet (4.2-4.5)[c]	L. Trehörningen (4.0-5.3)[l]	L. Långsjön (4.6-5.5)[l]	Llyn Berwyn (4.2)[l]	Llyn Hir (4.8)[l]
	Site (pre-liming pH value)				
Mosses					
Sphagnum spp.	-	-	-	-	-
Drepanocladus fluitans	*(+)	0		-	
Isoetids					
Littorella uniflora	0(+)		0		-
Lobelia dortmanna	0(-)		0		+
Isoetes lacustris	0(+)		0		+
Nymphaeids					
Potamogeton natans	*[p]	*	*		
Sparganium angustifolium		+	+		+
Elodieds					
Myriophyllum alterniflorum			+		+
Juncus fluitans	+		0		
Utricularia sp.	+	+			

Data from Eriksson *et al.* 1983; N. Stringer, *pers. comm.*

[c] catchment limed; [l] lake-surface limed.

\+ increase after liming } symbols in brackets for Loch Fleet represent changes
\- decrease after liming } in abundance where distribution unchanged
* new species after liming
0 unchanged after liming
[p] *P. polygonifolius*

Lake Trehörningen, but the appearance and subsequent increase of *D. fluitans* in Loch Fleet after liming contrasts with its rapid decline in Llyn Berwyn (Table 6).

The relative scarcity of *Juncus fluitans* in Loch Fleet before liming and its increase after liming were unexpected in the light of evidence suggesting that this species usually proliferates in acid waters (eg. Roelofs, 1983) and declines rapidly when water is de-acidified (Alio, 1987).

Colonisation of limed lakes by *Potamogeton* has been reported elsewhere. For instance, *P. natans* colonised L. Gårdsjön (Lazarek, 1986), L. Trehörningen and L Långsjön (Eriksson *et al.*, 1983), while *P. polygonifolius* appeared in Loch Fleet after liming. Probably as a result of its exposed location, Loch Fleet contained no nymphaeid and only one helophyte species (*Carex rostrata*) prior to liming. In some lower altitude sites, species such as white water-lily *Nymphaea alba*, floating bur-reed *Sparganium angustifolium* and alternate-flowered water milfoil *Myriophyllum alterniflorum* have increased after liming (eg Eriksson *et al.*, 1983). *Myriophyllum alterniflorum* generally inhabits oligotrophic upland waters with a pH ≥ 5.5 but it is unlikely to naturally colonise Loch Fleet due to the remoteness of the site. Furthermore, it does not previously appear as a macro-fossil in the sedimentary record (Anderson *et al.*, 1986).

Algae can have a significant impact on the depth distribution of macrophytes through a shading effect (Sand-Jensen and Søndergaard, 1981). It is probable therefore, that shading by filamentous green algae in Loch Fleet helped to reduce the water transparency to 2.0m secchi disc depth in

1988 compared with 2.7m prior to liming. This may have been responsible for a reduction in the maximum depth of macrophyte growth from 5m to 4m that year. A reduction in water transparency resulting from phytoplankton changes in response to newly available nutrients (especially phosphorus) has been reported from limed lakes elsewhere (Hultberg and Andersson, 1982; Eriksson *et al.*, 1983). Direct smothering by filamentous algae probably caused the demise of the liverwort *Solenostoma triste* in Loch Fleet during 1988. Furthermore, the apparent decline in *Lobelia* abundance that year (Table 3) could also have been due to reduced photosynthetic activity caused by the shading effect of the algae because *Lobelia* growth is known to be particularly sensitive to the presence of epiphytic algae (Lazarek, 1986).

It is clear from the sudden proliferation of filamentous green algae in 1988, that the Loch Fleet ecosystem was still unstable 30 months after catchment liming. Longer-term floristic changes will depend upon numerous factors including water chemistry, nutrient availability, water transparency, competition and grazing pressure. This will depend to a large extent on the long term suitability of the loch to support a sustainable trout fishery and consequently any catchment management required to maintain suitable water quality. This study has provided a descriptive, semi-quantitative baseline suitable for assessing longer-term changes in the macrophyte community. It would be worthwhile to continue this study and relate future changes to water chemistry parameters which will be monitored as a long-term extension of the Loch Fleet project.

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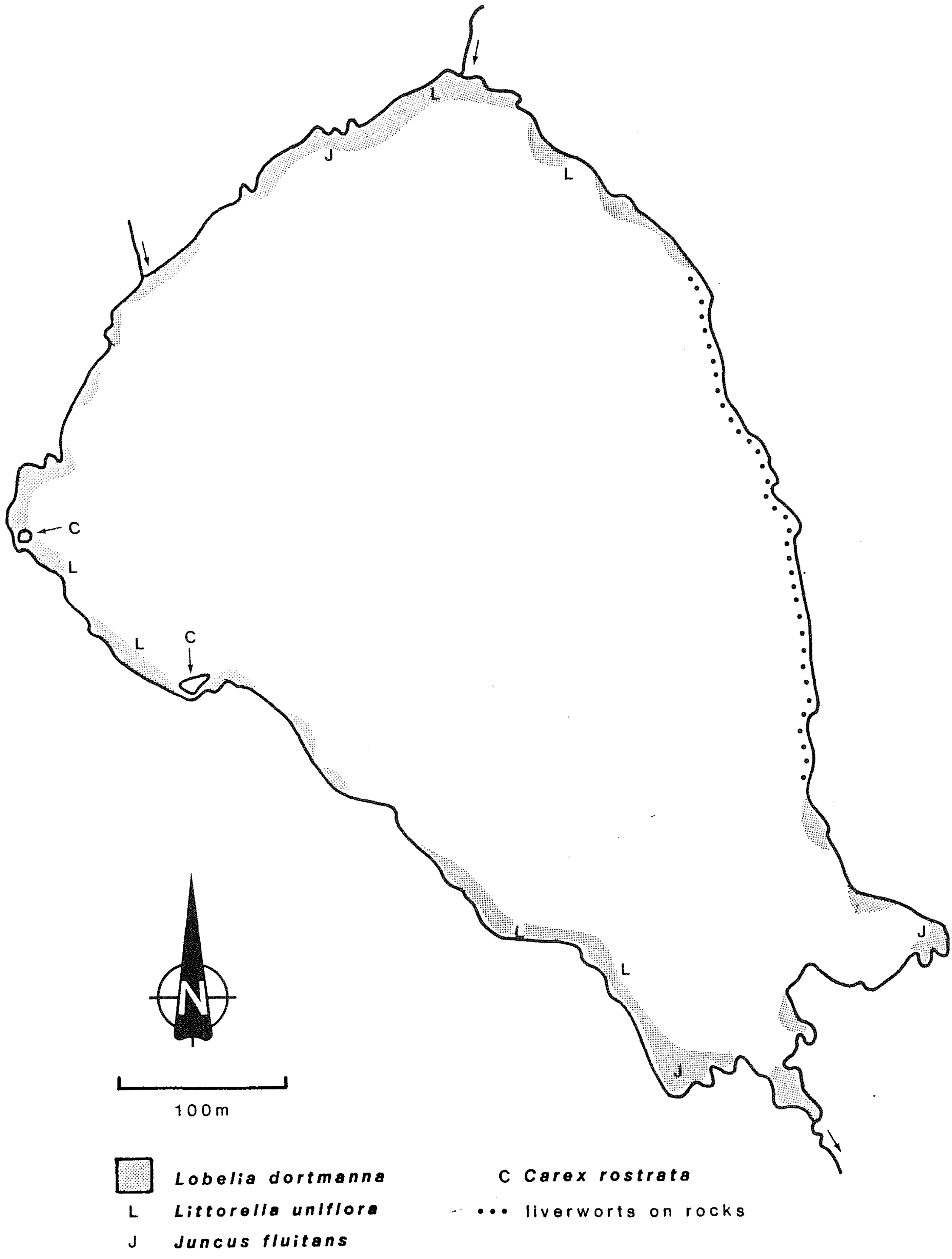
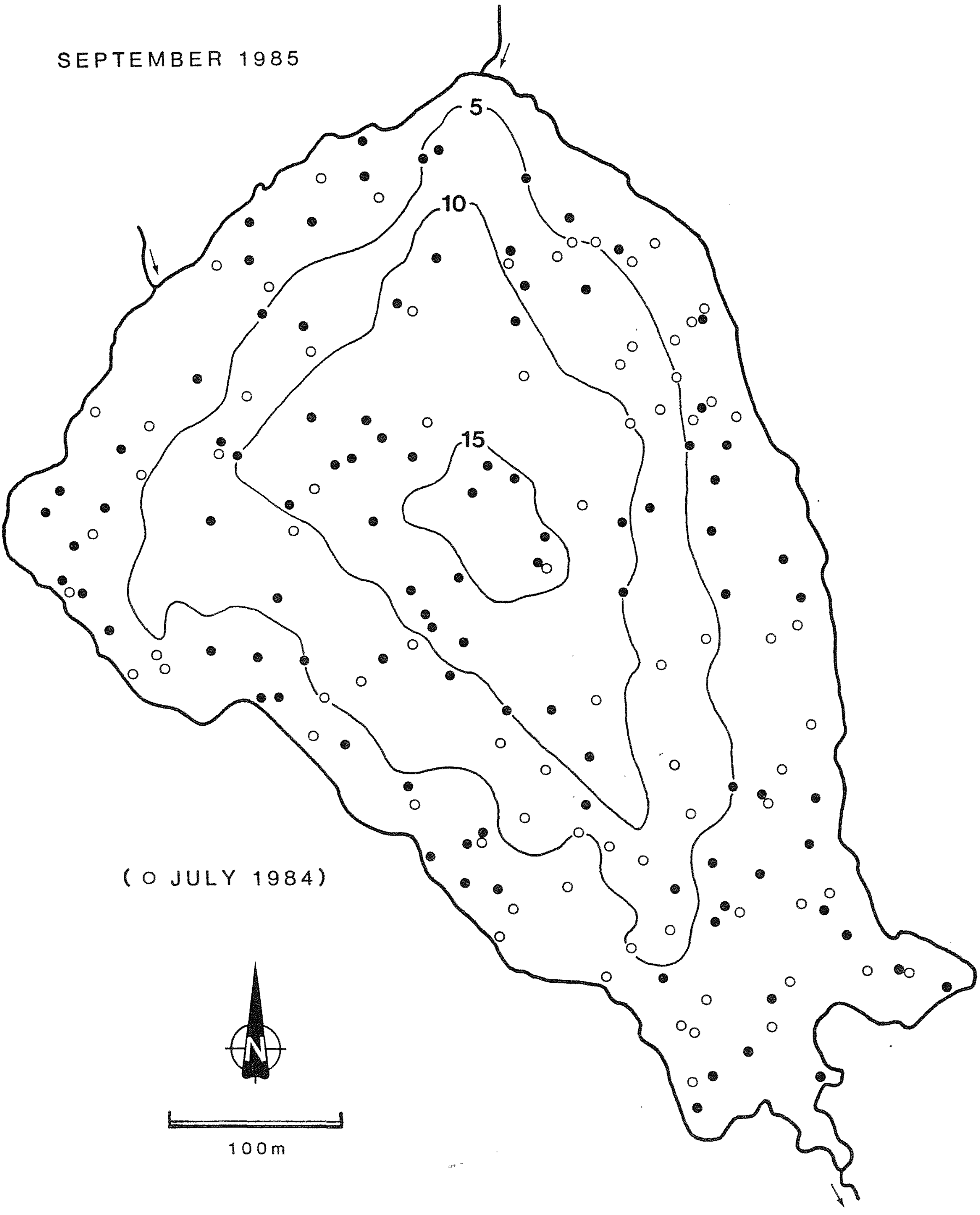
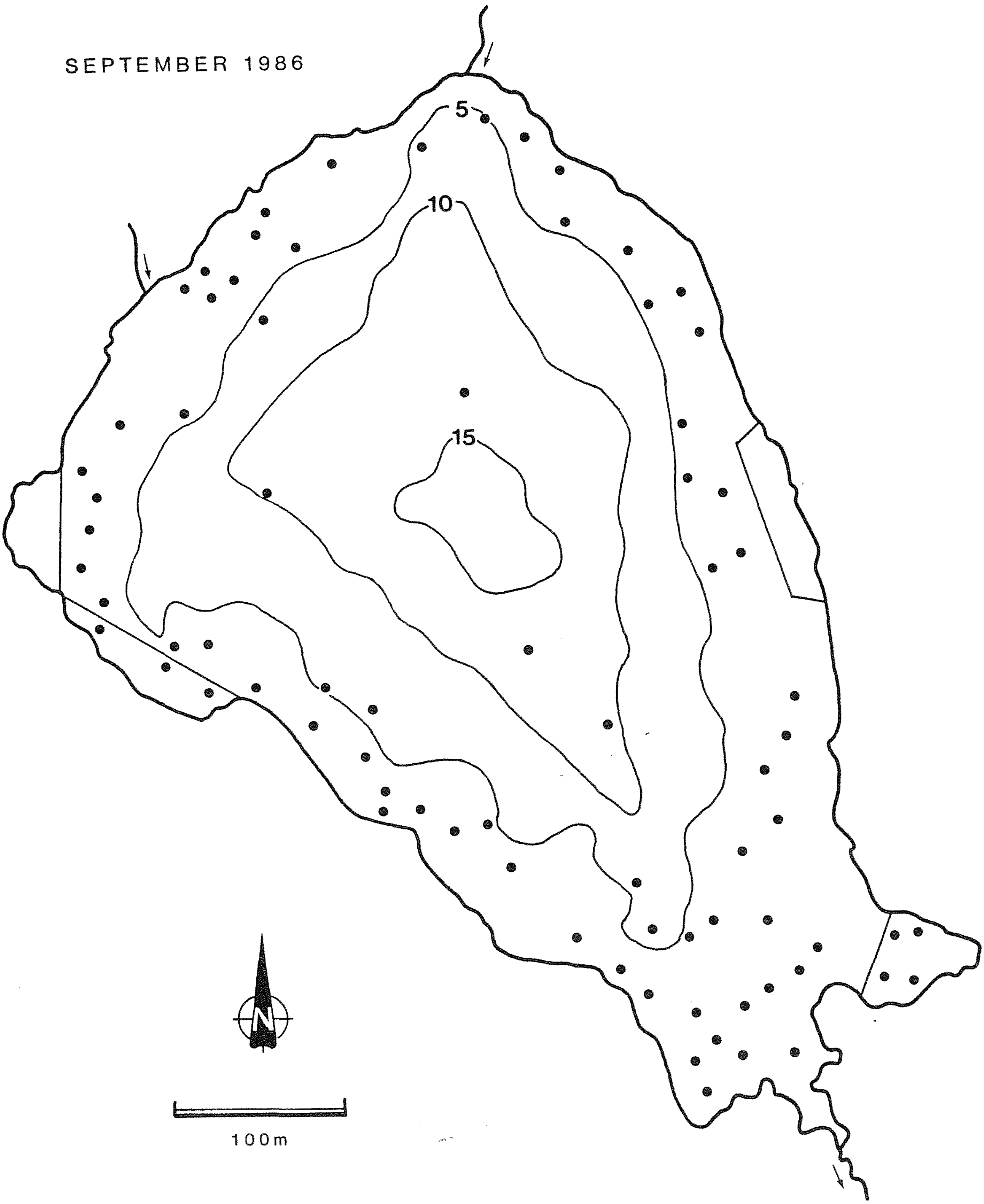
Appendix 1. The distribution of littoral macrophytes in Loch Fleet before catchment liming.



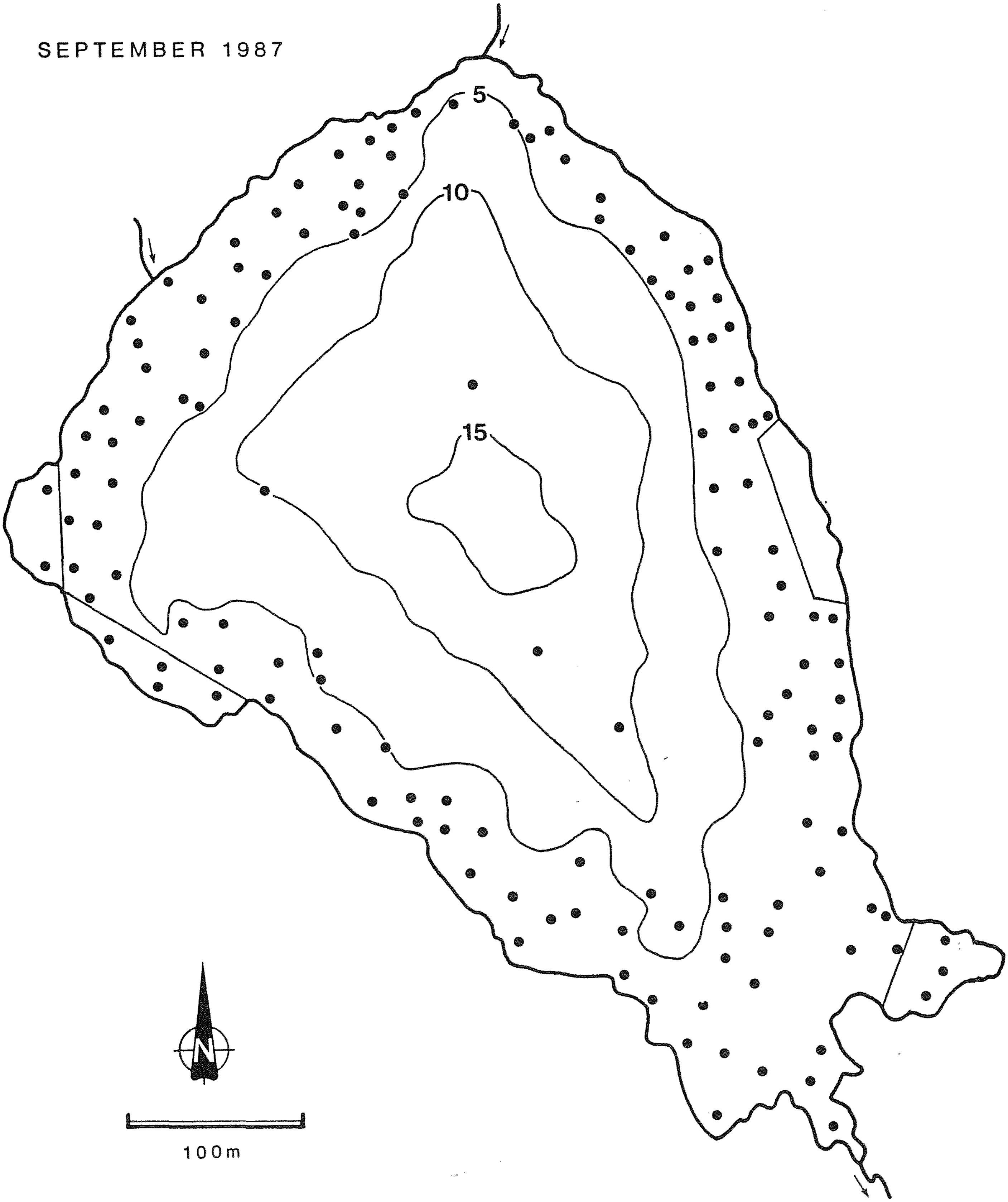
Appendix 2. The location of random Ekman grab samples taken in Loch Fleet, 1985 - 1988. [July 1984 Ekmans taken during previous study, (Anderson et al. 1986)]. Bathymetric contours at 5 m intervals.



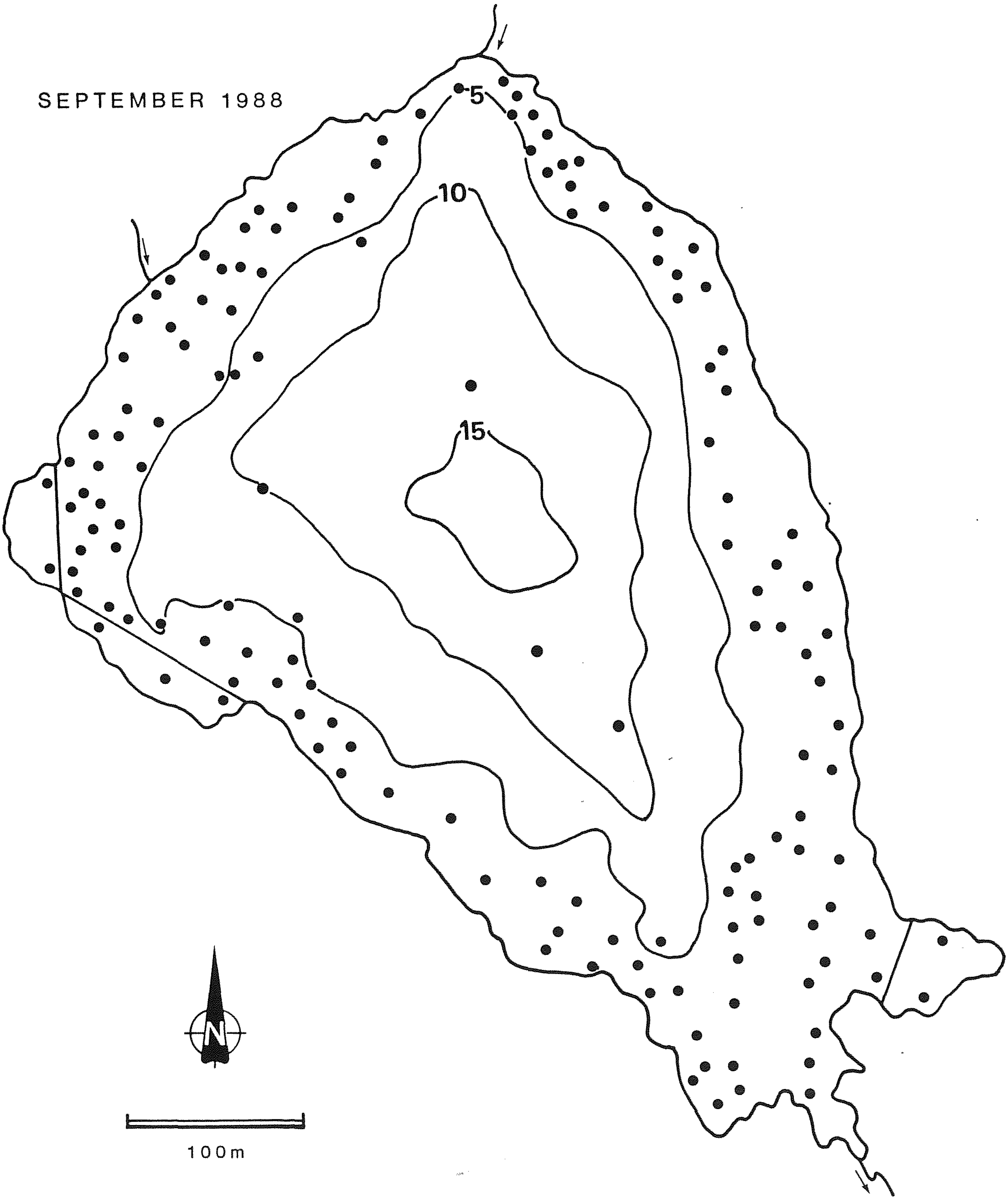
Appendix 2 (cont). The location of Ekman grab samples taken in Loch Fleet, 1985 - 1988.



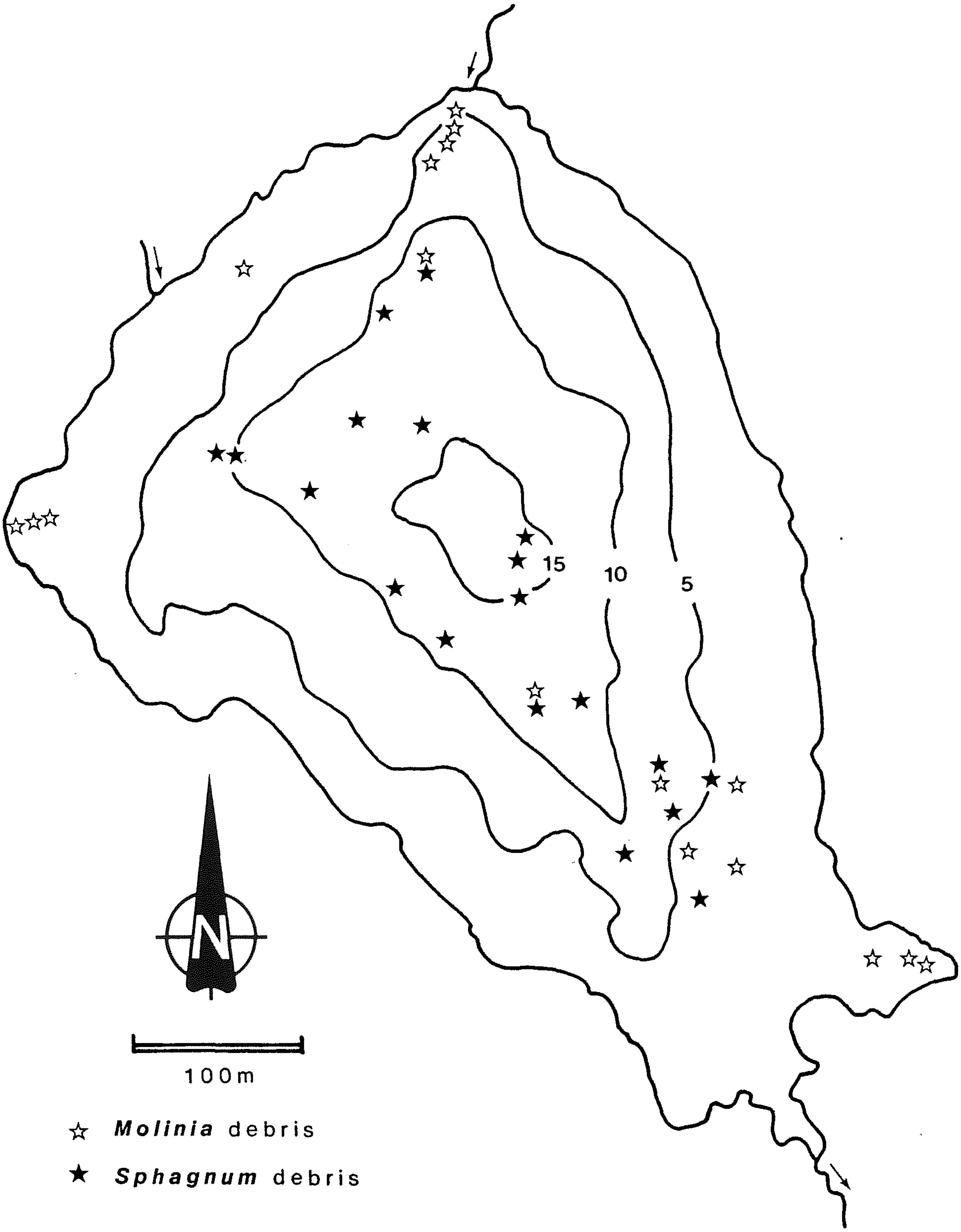
Appendix 2 (cont). The location of random Ekman grab samples taken in Loch Fleet, 1985 - 1988.



Appendix 2 (cont). The location of random Ekman grab samples taken in Loch Fleet, 1985 - 1988.



Appendix 3. The distribution of Molinia and Sphagnum debris recovered in Ekman grab samples from Loch Fleet before catchment liming. Bathymetric contours at 5 m intervals.



Appendix 4. The percentage occurrence of macrophytes recovered in Ekman grab samples from Loch Fleet before (1985) and after catchment liming.

Data from random sublittoral grabs and transects B and D in the main loch.

Macrophyte	Year	Water depth (m) 0.0-1.0	1.1-2.0	2.1-3.0	3.1-4.0	4.1-5.0	0.0-5.0m Total
ALGAE							
Batrachospermum sp(p).	1985	-	-	-	-	-	-
	1986	-	-	-	-	-	-
	1987	10.5	-	-	-	-	1.3
	1988	5.0	-	-	-	-	0.6
Filamentous green algae	1985	19.4	-	-	-	-	15.6
	1986	28.6	-	-	-	-	4.6
	1987	36.8	14.3	3.7	-	12.5	11.1
	1988	75.0	92.3	52.8	4.2	-	58.6
MOSSES							
Amblystegium serpens	1985	-	-	-	-	-	-
	1986	-	-	9.1	-	-	2.3
	1987	-	2.0	1.9	4.3	12.5	2.6
	1988	-	5.8	17.0	25.0	-	11.5
Bryum sp. (pallens?)	1985	-	-	-	-	-	-
	1986	-	-	-	-	-	-
	1987	-	-	-	-	-	-
	1988	-	(1.6)*	-	-	-	(0.6)*
Drepanocladus fluitans	1985	-	-	-	-	-	-
	1986	-	-	-	5.0	-	1.1
	1987	-	2.0	7.4	4.3	12.5	4.6
	1988	-	7.7	11.3	12.5	-	8.3
Fontinalis antipyretica	1985	-	-	-	-	-	-
	1986	-	-	-	-	-	-
	1987	-	-	-	-	-	-
	1988	-	-	1.9	-	-	0.6
Polytrichum sp. (commune?)	1985	-	-	-	-	-	-
	1986	-	-	4.5	-	-	1.1
	1987	-	-	-	-	-	-
	1988	-	1.9	-	-	-	0.6

Appendix 4 (cont.)

Macrophyte	Year	0.0–1.0	1.1–2.0	2.1–3.0	3.1–4.0	4.1–5.0	0.0–5.0m Total
		Water depth (m)					
Sphagnum auriculatum	1985	12.9	74.4	93.8	64.3	14.3	54.2
	1986	7.1	77.3	81.8	70.0	-	57.5
	1987	5.3	12.2	5.6	4.3	12.5	7.8
	1988	-	7.7	15.1	-	-	7.6
Sphagnum cuspidatum	1985	3.2	10.3	6.3	28.6	-	9.3
	1986	-	9.1	13.6	-	-	5.7
	1987	-	-	-	-	12.5	0.6
	1988	-	-	-	-	-	-
LIVERWORTS							
Calypogeia muelleriana	1985	-	-	-	-	-	-
	1986	-	-	4.5	-	-	1.1
	1987	-	2.0	3.7	-	-	2.0
	1988	-	3.8	1.9	4.2	-	2.5
Cephalozia connivens	1985	-	-	-	-	-	-
	1986	-	-	4.5	-	-	1.1
	1987	-	2.0	1.9	-	-	1.3
	1988	-	-	3.8	-	-	1.3
Lophozia sp.	1985	-	-	-	-	-	-
	1986	-	-	-	5.0	-	1.1
	1987	-	-	-	-	-	-
	1988	-	-	-	-	-	-
Scapania undulata	1985	-	-	-	-	-	-
	1986	-	4.5	-	-	-	1.1
	1987	-	-	-	-	-	-
	1988	-	1.9	-	-	-	0.6
Solenostoma triste	1985	12.9	12.8	12.5	14.3	-	12.1
	1986	14.3	31.8	18.2	15.0	22.2	20.7
	1987	31.6	30.6	24.1	13.0	12.5	24.8
	1988	-	-	-	-	-	-
VASCULAR CRYPTOGAMS							
Isoetes echinospora	1985	-	-	-	-	-	-
	1986	-	-	-	-	-	-
	1987	10.5	2.0	-	-	-	2.0
	1988	15.0	-	-	-	-	1.9

Appendix 4 (cont.)

Macrophyte	Year	0.0-1.0	1.1-2.0	2.1-3.0	3.1-4.0	4.1-5.0	0.0-5.0m Total
		Water depth (m)					
Isoetes lacustris	1985	16.1	61.5	43.8	7.1	-	34.5
	1986	35.7	59.1	50.0	15.0	-	36.8
	1987	26.3	61.2	33.3	-	-	34.6
	1988	25.0	59.6	43.4	4.2	-	38.2
DICOTYLEDONS							
Littorella uniflora	1985	29.0	-	-	-	-	8.4
	1986	14.3	-	-	-	-	2.3
	1987	47.4	16.3	-	-	-	11.1
	1988	25.0	13.5	-	-	-	10.8
Lobelia dortmanna	1985	41.9	17.9	-	-	-	18.7
	1986	57.1	4.6	-	-	-	10.3
	1987	52.6	18.4	1.9	-	-	13.1
	1988	45.0	13.5	-	-	-	10.2
Utricularia sp.	1985	-	2.6	-	-	-	0.9
	1986	-	4.5	13.6	-	-	4.6
	1987	5.3	26.5	11.1	4.3	-	13.7
	1988	5.0	34.6	24.5	-	-	20.4
MONOCOTYLEDONS							
Juncus bulbosus var. fluitans	1985	-	2.6	-	-	-	0.9
	1986	14.3	-	-	-	-	2.3
	1987	36.8	12.2	-	-	-	8.5
	1988	15.0	3.8	1.9	-	-	3.8
Potamogeton polygonifolius	1985	-	-	-	-	-	-
	1986	-	-	-	-	-	-
	1987	-	-	-	-	-	-
	1988	(3.6)*	-	-	-	-	(0.6)*

* data from embayment 9.

Number of Ekman grab samples (n)	1985	31	39	16	14	7	107
	1986	14	22	22	20	9	87
	1987	19	49	54	23	8	153
	1988	20	52	53	24	8	157

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