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12.—The Distribution and Production of Submerged Macrophytes in Loch Leven, Kinross.

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Synopsis

The distribution and production of submerged macrophytes in Loch Leven has been investigated using drag-rake surveys and biomass measurements. Survey data suggest that changes in the species diversity of the loch have occurred since the earlier records. There appears to have been a decline in some species with an increase in others.

In general there has been an overall loss in species diversity which may be correlated with the increasingly eutrophic status of Loch Leven. At present the macrophyte flora is dominated by a few species, notably *Potamogeton filiformis*, *Zannichellia palustris*, *Nitella opaca* and algal periphyton, with declining, though still significant amounts of *Chara aspera*. It is probable that the species diversity is in the process of adjusting to the eutrophic status of the loch and that *P. filiformis* in particular is in an expanding condition.

Introduction

Studies are reported here on the distribution and production in Loch Leven of submerged macrophytes, which consist of angiosperms, pteridophytes, bryophytes, filamentous algae and Characeae. Interest in the submerged macrophytes arose after indications that increases in some plants had occurred since 1966 and the present studies were initiated as part of the IBP Project to investigate the present status of submerged macrophytes in Loch Leven.

Loch Leven is a nutrient rich lowland loch situated about 40 km north of Edinburgh at latitude 56°10′N and longitude 3°30′W. The main environmental and biological characteristics of the loch have been described by Morgan (1974) and Smith (1974). Macrophytes, in general, are sparse but there are well-established stands of *Potamogeton filiformis* to the north of St Serf's Island and along the shallow north-east shore near Grahamstone (latitude 56°12′N, longitude 3°21′W) to a depth of about 70 cm. Morgan (1970) has reviewed some of the information available on submerged macrophytes in Loch Leven from 1910 to 1966. In fact, records of aquatic plants in Loch Leven date back to those of Hooker (1821). West (1910*a*) carried out a thorough survey of Loch Leven and noted, in general terms, the abundance of some species of macrophytes in the loch. Aerial photographs, which show vegetation down to about 1 m depth of water, have been used in the present study, in conjunction with surveys, to study vegetation changes in the loch.

Detailed surveys began with those of D. F. Pollard in 1966 who used a drag-rake method to assess the distribution and occurrence of submerged macrophytes. These surveys have been repeated in 1971 and 1972. This paper attempts to assess the present status and production of aquatic macrophytes and to analyse the changes in species diversity that have occurred in Loch Leven over the last 150 years.

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MATERIALS

A NOTE ON IDENTIFICATION

The long-term changes in the submerged macrophytes of Loch Leven have both quantitative and qualitative aspects. Since some of the qualitative changes that have been recorded result from drastic alterations in the amounts and even the disappearance of related species it is advisable to outline some of the problems of identity involved.

*Potamogeton filiformis** and *P. pectinatus*

George West (1910*a*) recorded *P. filiformis* in Loch Leven in unspecified quantities and with no indication of its distribution, but did not record *P. pectinatus*, although this was found in Loch Fitty which lies 7 km south of Loch Leven. During a brief sampling of the shore south of Kinross House in July 1959, in under 1 m of water, both *P. filiformis* and *P. pectinatus* were recorded (data incorporated in Spence1964). Then in 1966 Pollard recorded *P. filiformis* once in his July survey 'growing strongly in a single station off the east end of St. Serf's Island' but he did not mention *P. pectinatus*. A hand-written note on Pollard's typescript says that *P. filiformis* was more abundant in September and October than in July 1966.

In 1971 the material from the drag-rake survey was uncertainly determined as *P. pectinatus* although no fruits were available. Re-examination of material collected in 1972 and 1973 has shown that most of the plants to the north of St Serf's Island and along the east shore are *P. filiformis*, whilst *P. pectinatus* has been found in 1973 in dense but isolated patches along the south and south-east margins of the loch. Confusion between these two species, especially in the sterile state, may have occurred during the rapid drag-rake surveys of the loch so that the exact proportion of either which makes up the total is therefore unknown, but *P. filiformis* appears to predominate. It is also possible that a sterile hybrid of *P. filiformis* × *P. pectinatus* occurs in the loch.

Chara aspera and *Nitella opaca*

George West (1910a) commented several times on the abundance of *Chara aspera* and *Nitella opaca*. Much of the material of these species collected in recent surveys was fragmentary and difficult, if oogonia were absent, to identify macroscopically. The proportions of the two species recorded during the 1 minute available on each drag-rake tow (see Methods) were based as far as possible on fruiting material.

Isoetes lacustris

This species was recorded by Hooker (1821) but at that time it was not separated from *I. echinospora* Durieu so that this record may refer to either species.

* Nomenclature as follows:

Angiospermae, Pteridophyta—Clapham, A. R., Tutin, T. G. and Warburg, E. F., 1962. *Flora of the British Isles*, C.U.P.

Characeae—Groves, J. and Bullock-Webster, G. R., 1924. *British Charophyta*. Ray Soc. Allen, G. O., 1950. *British Stoneworts*. Arbroath.

Bryophyta—Watson, E. V., 1963. *British Mosses and Liverworts*. C.U.P.

Juncus bulbosus and Eleocharis acicularis

J. bulbosus has only ever been recorded in Loch Leven by Pollard (1966, unpublished) and he found it to be the most widespread of the admittedly limited angiosperms. This material was authenticated by C. Ferreira and J. G. Roger but is not now available. An uncertain identification of sterile *J. bulbosus* in 1971, may have been confused with *Eleocharis acicularis* which was recorded by West (1910a). Dense carpets of *E. acicularis* have been found in 1973.

METHODS

Drag-rake Surveys, Maps and Aerial Photographs

The drag-rake surveys of 1971 were carried out using similar apparatus to that used by Pollard (1966 unpublished) in his survey. Each double-sided drag-rake employed was made from two garden rake-heads wired up back to back with wire mesh screen attached to the faces. Lead strip was wired to the assembly to keep the drag-rake on the bottom. A strong wire loop was hooked on to the head sockets for a line attachment. The dimensions of the drag-rakes varied from survey to survey, and members of each pair used at any one time were sometimes somewhat dissimilar. The ranges of dimensions of rakes used from 1966 to 1972 are given below:

Weight (g)	1240–1923
Width (cm)	19·0–28·7
Depth (cm)	14·0–19·0
No. of prongs per side	8–12
Prong shape	Straight, strongly curved
Screen mesh (cm)	1–2·5

Surveys were carried out using as far as possible the same transects and landmarks of Pollard. Transects around the periphery of the loch ran parallel to the shore at a distance of 20 m to 100 m out. Individual samples were taken from a continuously moving boat with the engine held at a constant (low) speed. Drag-rakes were dropped into the water alternately at one-minute intervals so that there was always one drag-rake on the bottom throughout the transect. Each sample drag covered from 50 m to 100 m. The maximum depth to which the drags sampled was about 5 m, which is well below the lower limit of about 1 m to 2 m for submerged macrophytes at Loch Leven.

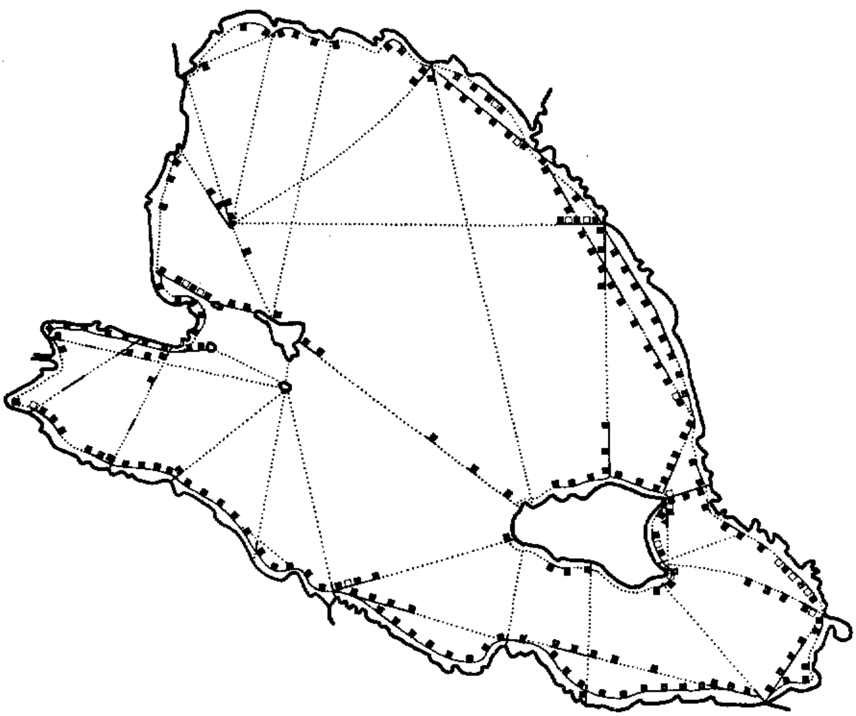
The amount of material for each species was subjectively assigned to one of four semi-quantitative classes of abundance. The following cover classes were used, based on the rake-head area:

1. Fully laden	3. $>\frac{1}{4}$, $<\frac{1}{2}$ laden
2. $>\frac{1}{2}$ laden	4. $<\frac{1}{4}$ laden

Pollard attempted in his 1966 survey to calculate the biomass of species from drag-rake data but this was not attempted in later surveys. Pollard compared yields from drag-rake samples with those obtained by the Ekman dredge and found that, in general, the former were considerably lower. He concluded that the drag-rake is a more suitable device for investigating large areas of sparse vegetation. Spence (unpublished data) found that rakes recovered only about 20 per cent of the biomass obtained by hand from the same macrophyte bed. It is clear, therefore, that quantitative results from drag-rakes can be used only with caution.

The results of various surveys, carried out in 1966, 1971 and 1972 are presented in text-figs 1, 2 and 3. For the reduced scale of these text-figures only the dominant species are represented, with some grouping of samples, from the original surveys.

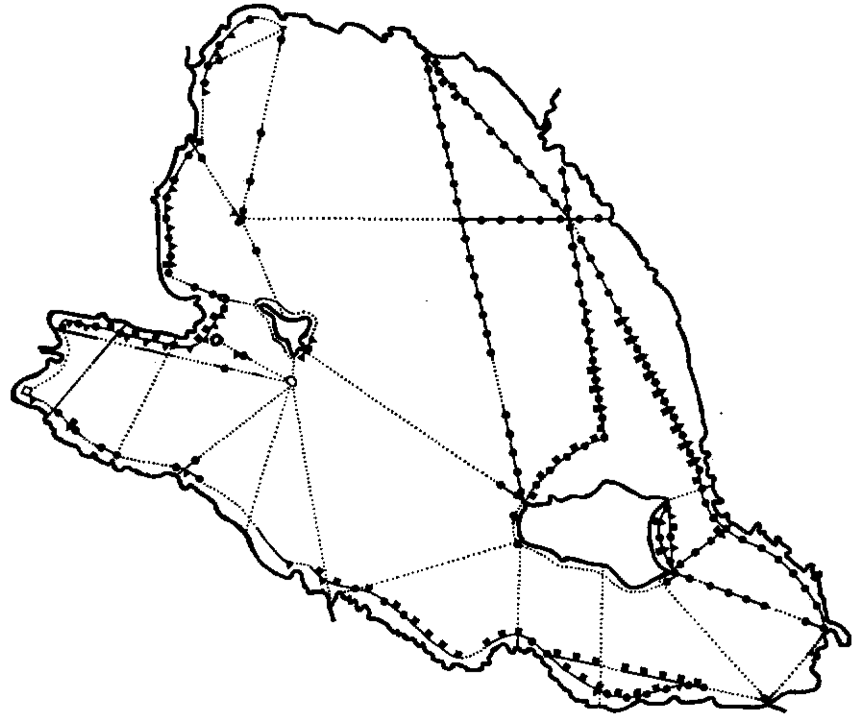
Aerial photographs have been taken over Loch Leven on several occasions. Some of these have been used (Pls 1, 2, 3 and 4), with stated reservations, to assess changes in vegetation over the period 1949 to 1972.



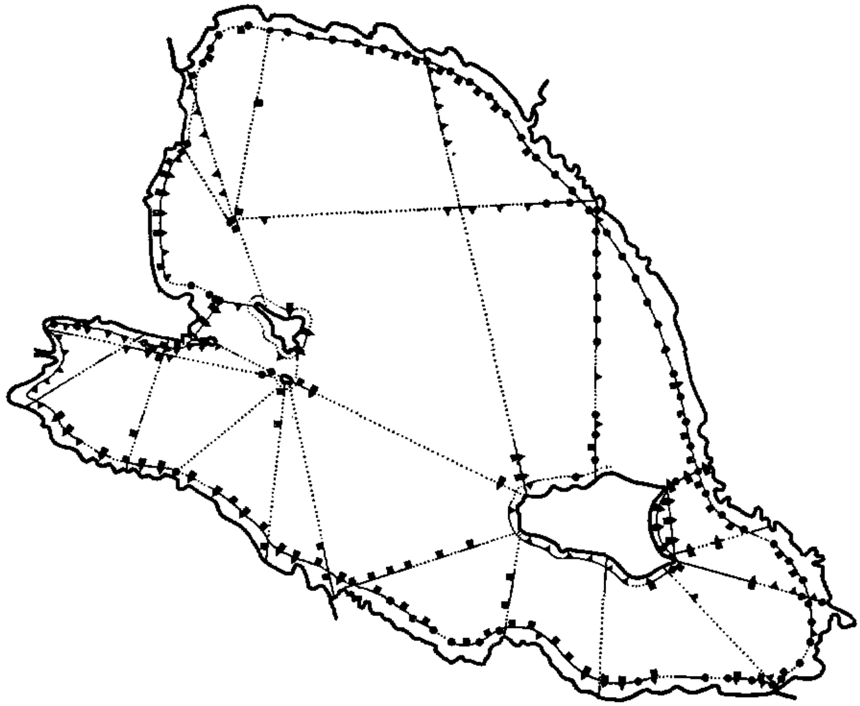
TEXT-FIG. 1.—Distribution of submerged macrophytic vegetation in Loch Leven in July 1966 Transect with vegetation recorded: ——; Transect without vegetation: ......; *Zannichellia palustris*: ▲; *Chara aspera*: ■; *Juncus bulbosus*: □; *Potamogeton filiformis*: ○.

Biomass Measurements

Biomass data for *Potamogeton filiformis*, which is one of the most abundant macrophytes in the loch, were collected using two square 0·5 m^2 quadrats (side of 70·7 cm) placed at alternate 1-m intervals along a string laid parallel to and 100 m out from the east shore at Grahamstone (see Pl. 4). This area, with a mean water depth of 50 cm falling to 30 cm to 40 cm in the summer, is well colonised by *Potamogeton filiformis* and was thus selected to obtain biomass data. Material was collected every two weeks from 20 June to 4 October 1972 using a spade to dig up rhizomes and overwintering tubers found at depths of 10 cm to 15 cm in the sand. Material collected was dried in an air-circulating oven at 80°C.



TEXT-FIG. 2.—Distribution of submerged macrophytic vegetation in Loch Leven in October 1971. Transect with vegetation recorded: ——; Transect without vegetation: ......; *Zannichellia palustris*: ▲; *Chara aspera*: ■; *Juncus bulbosus*: □; *Potamogeton filiformis*: ●.



TEXT-FIG. 3.—Distribution of submerged macrophytic vegetation in Loch Leven in July 1972. Transect with vegetation recorded: ——; Transect without vegetation: ......; *Zannichellia palustris*: ▲; *Chara aspera*: ■; *Potamogeton filiformis*: ●.

TABLE 1

List of submerged macrophytes recorded from Loch Leven at various dates
(Record of *R. aquatilis* for 1972 by G. H. Ballantyne, pers. comm.)

	Hooker 1821	*New Statistical Account* 1836	Balfour and Sadler 1863	Sonntag 1894	Balfour 1894	West 1910	Young 1936	Spence (1964) 1959	Pollard (unpubl.) 1966	1971	1972
CHARACEAE											
Chara aspera Willd.						×		×	×	×	×
C. fragilis Desv.						×			?		
C. vulgaris L.						×			?		
Nitella flexilis Agardh.			×								
N. opaca Agardh.						×			×	×	×
Tolypella glomerata Leonh.						×					
BRYOPHYTA											
Fontinalis antipyretica Hedw.										×	×
PTERIDOPHYTA											
Isoetes lacustris L.	×										
Pilularia globulifera L.		×									
ANGIOSPERMAE											
Callitriche hermaphroditica L.						×				×	×
Ceratophyllum demersum L.				?					×		
Eleocharis acicularis (L.) Roem. Schult.	×		×			×				?	?
Elodea canadensis Michx						×			×	×	×
Juncus bulbosus L.									×	?	
Littorella uniflora (L.) Aschers						×		×		×	×
Lobelia dortmanna L.					×						
Myriophyllum alterniflorum DC				×		×				×	×
M. spicatum L.		×				×			?×		
Nymphaea alba							×				
Potamogeton berchtoldii Fieb.						×					
P. crispus L.									×	×	×
P. filiformis Pers.						×		×	×	×	×
P. gramineus L.			×			×					
P. lucens L.						×					
P. obtusifolius Mert & Koch						×				×	×
P. pectinatus L.								×		×	×
P. perfoliatus L.						×				×	×
P. praelongus Wulf.						×					
P. × *zizii* Koch ex Roth.						×					
Ranunculus aquatilis L.						×					×
Subularia aquatica L.		×									
Utricularia vulgaris L.			×								
Zannichellia palustris L.								×	×	×	×

Enclosure Experiment

An enclosure experiment was carried out in 1972 to investigate the possible effect of wildfowl grazing on the biomass of *Potamogeton filiformis*. Two 1 m^3 duck-proof cages constructed of 'Dexion' and 'Weldmesh' were sunk into the east shore near the biomass transect line (Pl. 4). Two unprotected control quadrats were placed about 3 m from the cages. The experiment was set up on 4 May 1972 and terminated on 9 October 1972 when biomass and density in the two treatments were measured.

Bomb Calorimetry

The calorific content of tissues of *Potamogeton filiformis* was determined using a Gallenkamp CB–370 Ballistic Bomb Calorimeter. Values were converted assuming an average organic content of 80 per cent of the dry weight (Westlake 1965).

Results

Macrophyte Surveys

Table 1 shows the records of submerged macrophytes in Loch Leven from 1821 to 1972. The earlier records show several species which are indicative of nutrient-poor waters whilst more recent records of species reflect the increasing nutrient content of the water. West (1910*a*) found a diverse flora with 20 species of submerged

Table 2

List of macrophyte species lost, with last record, and macrophyte species gained, with first record, in Loch Leven since 1821 compiled with data from table 1

Species lost	Last record	Species gained	First record
Isoetes lacustris	1821	*Potamogeton pectinatus*	1959
Pilularlia globulifera	1836	*Zannichellia palustris*	1959
Subularia aquatica	1836	*P. crispus*	1966
Nitella flexilis	1863	*Fontinalis antipyretica*	1971
Utricularia vulgaris	1863		
Lobelia dortmanna	1894		
Potamogeton berchtoldii	1910		
P. gramineus	1910		
P. lucens	1910		
P. praelongus	1910		
P. × zizii	1910		
Tolypella glomerata	1910		
Nymphaea alba	1936		
Ceratophyllum demersum	1966		
Myriophyllum spicatum	?1966		

macrophyte including eight *Potamogeton* species. The dominant species were *Chara aspera, Elodea canadensis, Potamogeton perfoliatus* and *Nitella opaca.*

In July 1966 Pollard recorded 10 species of submerged macrophyte including only two species of *Potamogeton*. In 1971 there were 13 submerged macrophytes with five *Potamogeton* species and much the same macrophyte flora was present in 1972. Thus it would appear that from 1910 to 1972 there has been a net loss of species diversity with the loss and gain of the species included in table 2.

Table 3 shows the drag-rake data for more recent surveys. In July 1966 the dominant species was *Chara aspera* with *Juncus bulbosus* (see Note on Identification) as the only other significant macrophyte present. *Potamogeton filiformis* and *Zannichellia* *palustris* were recorded as growing strongly in two isolated regions near St Serf's Island but were more widespread in September and October of 1966.

In October 1971 the macrophyte population was dominated by *Potamogeton filiformis*, *Chara aspera*, *Zannichellia palustris* and *Nitella opaca*. Angiosperms were found in much greater proportions than in 1966. The surveys in 1972 showed much the same macrophyte flora as that in 1971. Filamentous algae were found in the

TABLE 3

Results of drag-rake surveys of submerged vegetation from 1966 to 1972

Species	No. of samples in which each species was found and in brackets this number as a percentage of the total number of samples in each survey			
	Pollard Jul 1966	Oct 1971	Jul 1972	Oct 1972
Chara aspera	362 (42·4)	110 (20·8)	184 (24·7)	99 (18·3)
Chara sp.	8 (0·9)	—	—	—
Nitella opaca	2 (0·2)	47 (8·9)	78 (10·5)	42 (7·8)
Fontinalis antipyretica	—	8 (1·5)	2 (0·3)	18 (3·3)
Callitriche hermaphroditica	—	11 (2·1)	13 (1·8)	5 (0·9)
Ceratophyllum demersum	1 (0·1)	—	—	—
Elodea canadensis	4 (0·5)	7 (1·3)	4 (0·5)	3 (0·6)
*Juncus bulbosus**	18 (2·1)	?1 (0·2)	—	—
Littorella uniflora	—	1 (0·2)	2 (0·3)	18 (3·3)
Myriophyllum alterniflorum	—	—	2 (0·3)	1 (0·2)
Myriophyllum spicatum	?1 (0·1)	—	—	—
Potamogeton crispus	4 (0·5)	3 (0·6)	5 (0·7)	—
*P. filiformis**	1 (0·1)	} 220 (41·5)	} 153 (20·6)	} 243 (45·0)
*P. pectinatus**	—			
P. perfoliatus	—	6 (1·1)	6 (0·8)	—
P. obtusifolius	—	6 (1·1)	1 (0·1)	—
Zannichaellia palustris	1 (0·1)	69 (13·0)	184 (24·7)	19 (3·5)
Total No. of samples	853	530	744	540

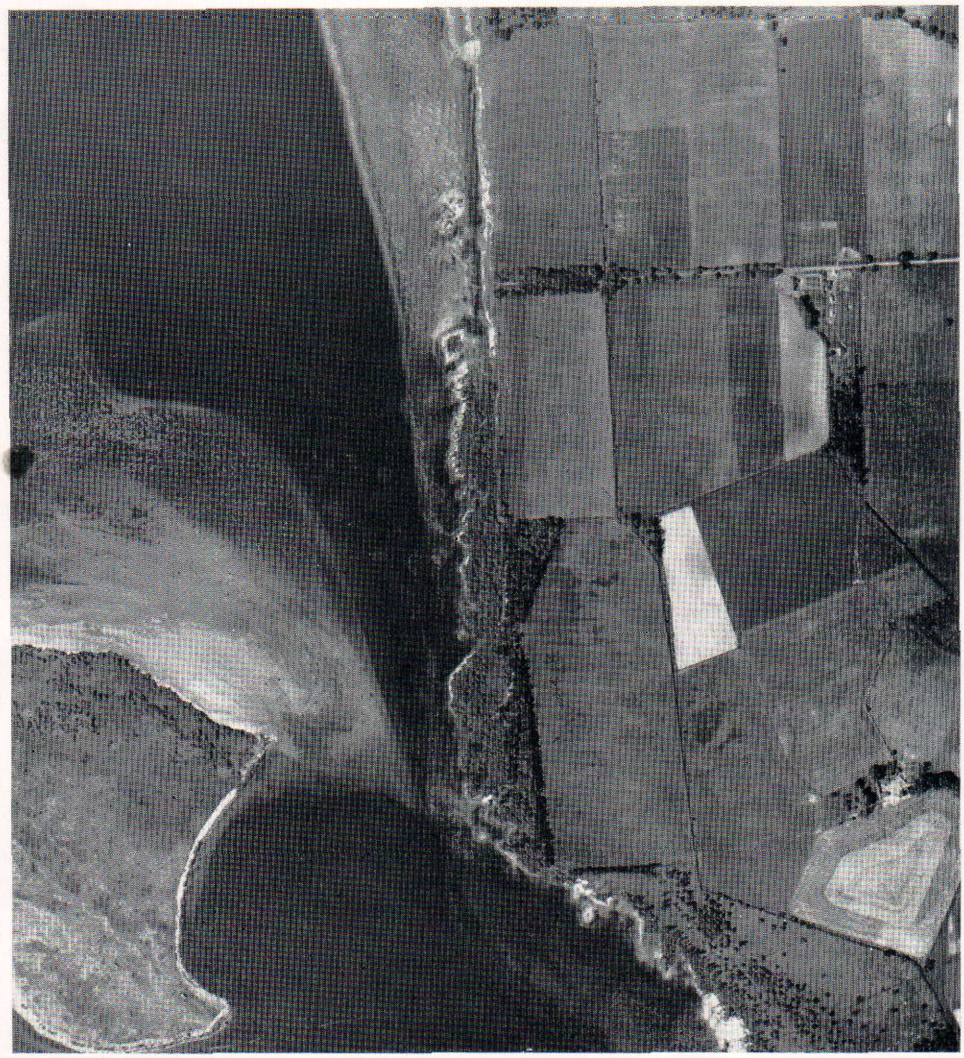
* see Note on Identification.

highest proportion of samples in 1972 and were present, though unrecorded, in significant amounts in 1971.

In table 4 semi-quantitative data for one of the dominant species, *Potamogeton filiformis*, are given foı 1971 and 1972 surveys in terms of the relative occurrence of samples in high and low cover classes. This indicates that in July the maximum percentage frequency occurs in the upper cover classes, i.e. greater than ¼ full, whilst in October 1972 the situation is reversed with a maximum frequency in the low cover class, i.e. less than ¼ full. Thus it can be seen that a considerable decline in quantities of *P. filiformis* occurred between July and October 1972 (see also table 5). Comparing estimates for the high cover class in October 1971 and October 1972 it can be seen that the quantities of *P. filiformis* were greater in 1971 than in 1972.

Biomass and Production of Potamogeton filiformis

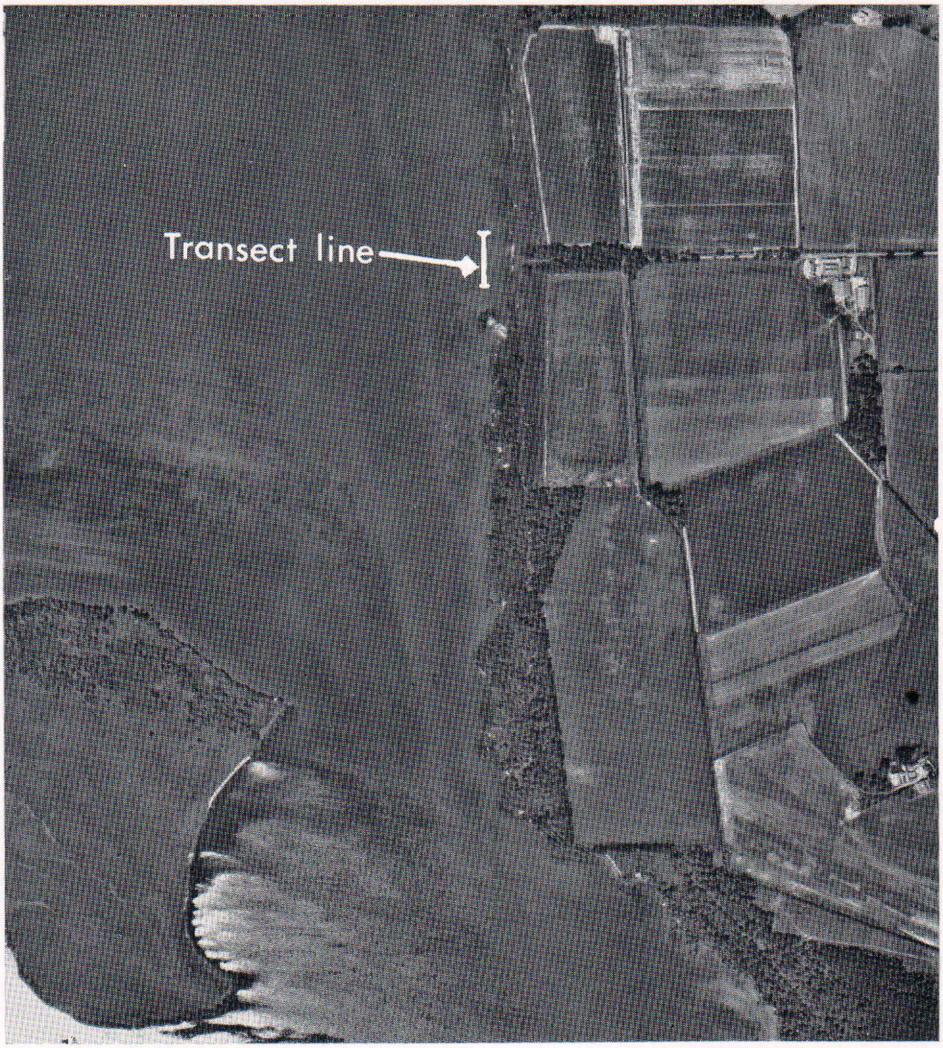
Table 5 indicates the biomass and density data collected in 1972 for *P. filiformis*. The biomass includes shoots and rhizomes which die down during winter months when only the subterranean storage tubers are found. The maximum biomass of these tubers so far recorded is 1·3 g dry wt/m^2 with a maximum density of 48/m^2.



Aerial photograph taken at 16 600 ft (5060 m) on 21 June 1949 of area of Loch Leven showing submerged shore to a depth of 1 m along the north-east of St Serf's Island and part of the eastern shoreline of the loch. Scale approximately 1 : 10 000.

Aerial photograph taken at 16 600 ft (5060 m) on 12 September 1960 of approximately the same area as Plate 1. A similar pattern of vegetation is visible on parts of the E. shore towards the top of the photograph to that present in 1949. The extent of the vegetation is, however, more difficult to ascertain because of increased water turbidity, but a slight decline has probably occurred.

Aerial photograph taken at 17 000 ft (5180 m) on 21 September 1964 of the same area as Plates 1 and 2 and on approximately the same scale of 1 : 10 000. There are no simultaneous survey data to ascertain, with any certainty, the vegetation type represented here but the overall decline in percentage cover by attached submerged plants in the same area since 1949 and 1960 is clearly seen.



Aerial photograph taken on 21 July 1972 at a scale of approximately 1 : 10 000. Even allowing for seasonal differences, note the marked increase in abundance of submerged vegetation over all shores down to 1 m since September 1964. The diffuse vegetation patches on the east shore above St Serf's are almost certainly *P. filiformis*. The transect line where biomass data for *P. filiformis* was collected is indicated on this diagram.

TABLE 4

The number of times Potamogeton filiformis *occurred in high and low cover classes, with respect to the area of the rake head used in the drag-rake survey (see Methods and Note on Identification) in 1971 and 1972*

Cover class	Oct 1971		Jul 1972		Oct 1972	
	Number	%	Number	%	Number	%
>¼ full	90	41	98	64	31	13
<¼ full	130	59	55	36	212	87
Total	220		153		243	

TABLE 5

Seasonal biomass and density data per unit area for Potamogeton filiformis *along a transect at 30 cm to 40 cm below O.D. on east shore of Loch Leven from June to October 1972. Data include the standard error of the mean*

Data	Biomass (g dry wt/m^2)	Density (no. of plants/m^2)
20 Jun	17·8 ± 2·9	334 ± 47
27 Jun	11·5 ± 3·8	319 ± 118
14 Jul	16·9 ± 1·3	332 ± 64
26 Jul	13·2 ± 2·4	260 ± 40
8 Aug	36·9 ± 16·4	570 ± 160
22 Aug	43·5 ± 4·4	475 ± 33
5 Sep	15·6 ± 0·5	266 ± 6
19 Sep	2·1	33
4 Oct	0·7 ± 0·06	18 ± 2

Data for the enclosure experiment are given in table 6. It is apparent that the maximal potential density is drastically reduced in the unprotected quadrats and that up to 94 per cent of the protected biomass is lost. Assuming that little loss occurs up to August, and the density data in table 5 indicate this, then the maximal biomass figure for *P. filiformis* of 43·5 g dry wt/m^2 obtained in August gives a tentative and minimum net annual production of 0·44 m.t. dry wt/ha/year (or 0·35 metric tonnes organic matter/ha/year, assuming an average organic content of 80 per cent of the dry weight, Westlake 1965). This figure may be converted to a value for whole

TABLE 6

Initial and final density (number plants/m^2) and final biomass (g dry wt/m^2) of Potamogeton filiformis *in two wire-netting cages, each of ground area 1 m (see Methods), and in two unenclosed quadrats of similar ground area. Experiment set up on 4 May 1972 and harvested on 9 October 1972*

Date	Parameter	Cages	Unenclosed quadrats
4 May 1972	Initial density (No./m^2)	45	39
9 Oct 1972	Final density (No./m^2)	224	39
9 Oct 1972	Final biomass (g dry wt/m^2)	21·9	1·2

loch areal production. The lower depth limit of *P. filiformis* from drag-rake surveys and diving is about 1·5 m, where only scattered plants were found, and the area of the loch to this depth is $3\cdot6\times10^6$m^2. Using a calorific content for *P. filiformis* of 3·28 kcal/g dry wt or 4·1 kcal/g organic matter, from bomb calorimetry (this value being comparable to those for submerged macrophytes, including *Potamogeton* species, of between 4·2 and 4·9 kcal/g organic matter given by Boyd 1970 and Straškraba 1968):

Net annual calorific production = 142·68 kcal/m^2.year or 596 973 J/m^2.year.
Therefore, whole loch production for colonisable area = $596\,973\times3\cdot6\times10^6$ J/loch year.
$2\cdot15\times10^{12}$ J/loch year.

This value, however, must be regarded as extremely tentative. It is an underestimate to the extent that protection from grazing or 'grubbing' by duck, or from wave action, increased unprotected biomass in October 1972 by 94 per cent at 30 cm; it is an overestimate in so far as *P. filiformis* (*a*) covers less than 100 per cent of the floor of the loch above 1·5 m depth of water and (*b*) is almost certainly less productive in deeper water than the biomass sampling depth. In fact, sampling in 1973 showed that very few plants occurred below 70 cm.

Discussion

From the records and survey data presented it is apparent that there have been changes in the submerged macrophyte flora of Loch Leven from the first records of the last century. Before discussing long-term changes it would seem apposite to stress the often large within-season changes that can occur in macrophyte populations. Data presented show that a higher frequency of occurrence is found for *P. filiformis* in October than in July (table 3) but that this probably represents many small fragments of broken, moribund stems and that biomass is at a minimum at this time is seen from data in tables 4, 5 and 6. Thus comparisons of percentage frequency for various species over several years are complicated by this within-season variation. This notwithstanding, it appears that changes in the quantities of species and in species diversity have occurred in the loch.

For convenience a chronological table (table 7) is indicated at this point to show when various surveys and aerial photographs were taken at Loch Leven from 1910 to 1972.

The early records of aquatic macrophytes in Loch Leven include species such as *Isoetes lacustris, Pilularia globulifera, Lobelia Dortmanna* and *Subularia aquatica* which are characteristically found in nutrient-poor waters with an alkalinity of less than 0·4 mMHCO_3^- (Spence 1967; Seddon 1972).

Most of the species recorded in the nineteenth century had disappeared by 1910 when West recorded 20 species of submerged macrophyte including five species of the *Potamogeton filiformis–Chara* association (pH 7·7 to 9·6, alkalinity >0·74 mM HCO_3^-, Spence 1964, 1967). West's notes indicate prolific growths of macrophytes in Loch Leven with particularly abundant amounts of *Chara aspera, Elodea canadensis, Nitella opaca* and *Potamogeton perfoliatus*. The most abundant species present was *Chara aspera*, the growth of which was described as prodigious especially at 1·2 m to 2·4 m, and which covered 'hundreds of acres' of the loch down to 4·6 m (West 1910*b*). In shallow areas where the bottom was of mud (e.g. the bay at the east end of St Serf's Island, see Pl. 1) beds of *Elodea canadensis* grew 'with such extraordinary vigour' that it was 'very difficult to tow a boat through them' (West 1910*b*). At that time it appeared that *Elodea* had been accidentally introduced into the loch and had partially exterminated the previously abundant *P. perfoliatus* (West 1910*a*). During the winter months large quantities of *Chara* and *Elodea* were found on the shore. The water was described as fairly clear and the euphotic layer probably extended to the lower depth limit of vegetation at about 5 m.

TABLE 7

Chronological list of vegetation surveys and aerial photographs of Loch Leven from 1910 to 1972

Date	Survey	Aerial photograph	Plate or text-figure number
1910	+	–	–
21 Jun 1949	–	+	Pl 1
3 Jul 1959	+	–	–
12 Sep 1960	–	+	Pl 2
21 Sep 1964	–	+	Pl 3
11–20 Jul 1966	+	–	Text-fig. 1
11–15 Oct 1971	+	–	Text-fig. 2
Jul 1972	+	+	Text-fig. 3, Pl 4
6–13 Oct 1972	+	–	–

The aerial photograph taken in 1949 (Pl. 1) indicates the water was still relatively clear and the reticulate pattern of submerged vegetation carpeting the inshore zone was probably *Chara aspera* although, with no concomitant survey data, no positive identification can be made. Aerial photographs taken in September 1960 (Pl. 2) show similar vegetation patterns in the shallow, sandy areas to those seen in 1949, but the cover of submerged plants is less and there are areas of relatively unvegetated sand.

In a brief visit in July 1959 Spence recorded extensive stands of the open *Potamogeton filiformis–Chara* association (Spence 1964) at around 50 cm depth of water along the shore south of Kinross House. This open community type (cover <40 per cent) is found in sands in shallow, nutrient-rich and moderately alkaline to alkaline waters (0·7 to 3·1 mM HCO_3^-), being recorded (1959–61) for some 14 lochs, including Lochs Lindores, Rescobie and Forfar. *Zannichellia palustris*, apparently recorded for the first time in 1959, is also present in the over-enriched Lochs Rescobie and Forfar in Angus.

The aerial photograph taken in September 1964 (Pl. 3) indicates a much reduced cover of submerged vegetation compared with that taken in June 1949 (Pl. 1), and the areas on the north-east shore consist largely of bare sand. In the course of his July survey in 1966 Pollard ran five transects over the area above the 1 m depth contour visible in this photograph. Assuming that no great changes in the macrophyte flora had occurred from 1964 to 1966 Pollard's survey data can be used to identify the vegetation in Pl. 3. Thus, by interpolation of Pollard's data there was a total of 85 samples over this visible part of the shore and 67 (79 per cent) of these contained *Chara aspera*. The only other species he recorded in this region were *Juncus bulbosus* (four times), *Elodea canadensis* (once) and *Potamogeton filiformis* (one out of four records for the whole loch). In spite of the differences in season and year it seems reasonable to suggest that the submerged vegetation in this photograph of 1964 was mainly *Chara aspera*.

In 1970 and 1971 there were reports that the amounts of submerged macrophytes had increased since 1966 and surveys were carried out in October 1971 and in July and October 1972 (text-figs. 1, 2 and 3). In 1971, it was apparent that the percentage frequency of *Potamogeton filiformis*, *Zannichellia palustris* and *Nitella opaca* had increased since 1966, whereas *Chara aspera* had declined. These species had similar frequencies in 1972 to those in 1971 except for a reduction in *Zannichellia*. Filamentous algae are an important constituent of the macrophyte flora and consist of generally small fragments (<¼ full drag-rake) with occasionally large amounts (>¼ to full drag-rake) of algae such as *Rhizoclonium*, *Cladophora* and *Oedogonium*.

The aerial photograph taken in July 1972 (Pl. 4) shows that vegetation had reappeared on the sandy north-east shore but the pattern there is very different from that prior to September 1964 (Pl. 3). The 54 samples from the July 1972 survey which fall within the 1 m zone seen in Pl. 4 (*N.B.* both survey and photograph were taken in the same month) give *Potamogeton filiformis* a frequency of 61 per cent and 41 per cent for *Chara aspera*. Apart from the shallow area to the north of St Serf's Island, the survey covered all the 1 m depth zone including the biomass transect line shown on Pl. 4 near the Grahamstone access point. The survey data, biomass studies and observations confirm that the diffuse vegetation areas found down to 1 m on this shore are comprised of *P. filiformis*, whilst *Chara aspera* was only recorded twice in the drag-rake transect along this part of the east shore. By comparison with aerial photographs of shallow-water vegetation in Durness limestone lochs the dark patches to the north of St Serf's Island probably consist of *Chara aspera* and *Potamogeton* sp.

Thus from the various surveys and photographic evidence given it would seem that *Chara aspera* has significantly declined in Loch Leven from extensive amounts in 1910 to the sparse amounts found in 1971–72. Loch Leven has become increasingly eutrophic (Morgan 1970) and it is possible that the decline in the amount of *Chara* species is related to this increased eutrophication. In particular it is likely that the decline of *Chara* can be linked to increased levels of phosphate-phosphorus. Forsberg (1964*a*, *b*; 1965) has correlated the sensitivity of several *Chara* species, including *C. aspera*, to phosphorus with their decline in polluted waters. From experimental evidence Forsberg (1965) found that *Chara* plants grew optimally at or below 20 μg P/l and this level in natural waters has been selected as the critical concentration for growth (Forsberg 1964*b*).

In table 8 the number of months per year since 1964 that Loch Leven water has exceeded 20 μg P/l is shown (see Holden and Caines 1974). It can be seen that in some years this level has frequently been exceeded so that it would seem plausible to suggest that the decline of *Chara* is correlated with the inhibitory levels of phosphorus in Loch Leven. The poor underwater irradiance in Loch Leven, due mainly to high levels of phytoplankton and sometimes to stirred sediments, may have also contributed to this decline.

The other significant feature in the dynamics of the macrophyte population is the recent increase in the amounts of *Potamogeton filiformis*. The production estimate given for *P. filiformis* of 0·35 metric tonnes organic matter/ha/year is at the lower end of the average range for aquatic macrophytes (1–7 metric tonnes organic matter/ha/year, Westlake 1963) and, combined with the relatively shallow lower depth limit of about 0·7 m to 1·5 m, indicates that, despite an increase in abundance of the plant, its production is quite low. The maximum biomass approaches the oligotrophic level (Westlake 1963). The enclosure experiment showed that the maximal potential density is drastically reduced in the unprotected quadrats and that up to 94 per cent of the potential biomass is lost. These cages afford some protection from wave action but also prevent the uprooting of plants by wildfowl such as pochard (*Aythya ferina* (L.))

TABLE 8

The number of months in the stated years where phosphate-phosphorus in Loch Leven exceeded 20 µg/l. At least two estimates were made in each month. Data of Holden and Caines (1974)

Year	1964	1965	1966	1968	1971
Number of months with more than 20 μg PO_4-P/l.	5	6	2	3	6

coot (*Fulica atra* L.) and mute swan (*Cygnus olor* Gmelin), which are mainly vegetarian. The cages do not assess which factor is the most important but large amounts of *P. filiformis* were found washed up on the east shore in September and October 1972. It is possible that wave action removed some plants from the substrate but the weather was calm throughout this period so that foraging by wildfowl was probably responsible for most of the plant debris subsequently found on the shore. It is also possible that *P. filiformis* is as yet at an early stage of colonisation in the loch.

That algal competition for light is an important factor in limiting the growth of submerged macrophytes in eutrophic conditions is well documented and is in fact used as a control measure (Smith and Swingle 1941; Olsen 1964). The depth of the euphotic zone in Loch Leven averages 2·5 m but can be as shallow as 1·5 m and this shallow euphotic zone has been correlated with the often concentrated blooms of phytoplankton (Morgan 1970). It is suggested that the reduced quantities of *P. filiformis* in October 1972 compared with October 1971 (table 4) may be associated with the occurrence, for the first time since 1967, of surface blooms of gas-vacuolate blue-green algae in 1972 (*Anabaena* sp., see Bailey-Watts 1974). These species on calm days form a dense floating layer which will undoubtedly reduce the amount of available light to macrophytes below it.

REFERENCES TO LITERATURE

ANON., 1836. *New Statistical Account of Scotland*, **9**, Fife and Kinross, 1845. Edinburgh: Blackwood.
——, 1971. Loch Leven I.B.P. Project. *A. Rep. Nat. Conserv. Edinb.*
——, 1972. Loch Leven I.B.P. Project. *A Rep. Nat. Conserv. Edinb.*
BAILEY-WATTS, A. E., 1974. The algal plankton of Loch Leven, Kinross. *Proc. Roy. Soc. Edinb., B*, **74**, 135–156.
BALFOUR, I. B., 1894. An old list of stations of rarer plants, ascertained to grow around Inverkeithing and North of the Forth by A. Robertson. *Trans. Proc. Bot. Soc. Edinb.*, **20**, 84–90.
BALFOUR, J. H. and SADLER, J., 1863. *Flora of Edinburgh*. Edinburgh: Black.

BOYD, C. E., 1970. Amino acid, protein and caloric content of vascular aquatic macrophytes. *Ecology*, **51**, 902–906.

FORSBERG, C., 1964*a*. Phosphorus, a maximum factor in the growth of the Characeae. *Nature, Lond.*, **201**, 517–518.

——, 1964*b*. The vegetation changes in Lake Tåkern. *Svensk. Bot. Tidskr.*, **58**, 44–54.

——, 1965. Nutritional studies of *Chara* in axenic cultures. *Physiologia Pl.*, **18**, 275–290.

HOLDEN, A. V. and CAINES, L. A., 1974. Nutrient chemistry of Loch Leven. *Proc. Roy. Soc. Edinb.*, *B*, **74**, 101–121.

HOOKER, W. J., 1821. *Flora Scotica: or a description of Scottish Plants*. London.

MACLEAY, K. N. G., 1953. Additions and emendations to the comital flora for Fife and Kinross (V.-C. 85). *Watsonia*, **2**, 398–410.

MORGAN, N. C., 1970. Changes in the fauna and flora of a nutrient enriched lake. *Hydrobiologia*, **35**, 545–553.

——, 1974. Historical background to the International Biological Programme Project at Loch Leven, Kinross. *Proc. Roy. Soc. Edinb.*, *B*, **74**, 45–55.

OLSEN, S., 1964. Vegetation saendringer i Lingby Sø. Bidrag til analyse af kulturpavirkninger pa vand-og sumpplante vegetationen. *Bot. Tidsskr.*, **59**, 273–300

SEDDON, B., 1972. Aquatic macrophytes as limnological indicators. *Freshwat. Biol.*, **2**, 107–130.

SMITH, E. V. and SWINGLE, H. S., 1941. The use of fertilizer for controlling several submerged aquatic plants in ponds. *Trans. Am. Fish Soc.*, **71**, 94–101.

SMITH, I. R., 1974. The structure and physical environment of Loch Leven, Scotland. *Proc. Roy. Soc. Edinb.*, *B*, **74**, 81–100.

SPENCE, D. H. N., 1964. The macrophytic vegetation of freshwater lochs, swamps and associated fens. In *The Vegetation of Scotland*. (Burnett, J. H., Ed.) Edinburgh: Oliver & Boyd.

——, 1967. Factors controlling the distribution of freshwater macrophytes with particular reference to the lochs of Scotland. *J. Ecol.*, **55**, 147–170.

STRAŠKRABA, M., 1968. Der Anteil der höheren Pflanzen an der Produktion der stehenden Gewässer. *Mitt. Int. Verein. Theor. Angew. Limnol.*, **14**, 212–230.

WEST, G., 1910*a*. A further contribution to a comparative study of the dominant phanerogamic and higher cryptogamic flora of aquatic habit in Scottish lakes. *Proc. Roy. Soc. Edinb.*, **30**, 65–182.

——, 1910*b*. An epitome of a comparative study of the dominant phanerogamic and higher cryptogamic flora of aquatic habit, in seven lake areas in Scotland. In *Bathymetrical Survey of the Scottish Freshwater Lochs*, **1**. (Murray, J. & Pullar, L.) Edinburgh: Challenger Office.

WESTLAKE, D. F., 1963. Comparisons of plant productivity. *Biol. Rev.*, **38**, 385–425.

——, 1965. Some basic data for investigations of the productivity of aquatic macrophytes. *Memorie Ist. Ital. Idrobiol.*, **18**, *Suppl.*, 229–248.

YOUNG, W., 1936. A list of the flowering plants and ferns recorded from Fife and Kinross. (V.-C. 85). *Trans. Proc. Bot. Soc. Edinb.*, **32**, 3–173.