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27.—A Summary of the Loch Leven IBP Results in relation to Lake Management and Future Research.

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Synopsis

The International Biological Programme provided resources and enabled the work of a considerable number of researchers to be focused on physical, chemical and biological studies on Loch Leven, Kinross. In this paper the results are summarised with the help of an energy flow diagram and relationships between different trophic levels discussed. Major gaps in our knowledge, which have still to be worked on before all the relationships between different trophic levels can be well understood, have been highlighted. The causes of changes which have been recorded at Loch Leven and the unusual variability in the ecosystem are discussed and hypotheses presented. Profitable lines for future research are suggested, particularly in relation to the management of the loch as a National Nature Reserve and a brown trout fishery.

Introduction

The International Biological Programme has enabled the concentration of a large effort on many aspects of the ecology of one lake. The work has been undertaken by people from a considerable number of organisations (N. C. Morgan 1974) who have voluntarily agreed to work together. It has enabled some of the major sources of production in the loch to be measured and steps have been made towards understanding the links between the trophic levels. Inevitably with increased understanding many more gaps in our knowledge have been highlighted and many new problems defined. Because of limited resources certain obvious areas for research such as microbial decomposition and the input of allochthonous matter have been neglected.

The purpose of this summary paper is to bring together the production estimates of the different components in the form of a flow diagram and to thereby outline the gaps where future research might usefully be concentrated. A great deal has been learnt in terms of organisation which is of value in planning future studies of this sort.

Loch Leven is a National Nature Reserve and the study has provided useful information for improved management and also detected problems of which we were not aware beforehand. Future research which will be an important adjunct to management is recorded.

Summary of Relationships at Loch Leven

A summary of the relationships studied for the year 1971 at Loch Leven is shown in text-fig. 1. The values are all expressed as $kJ/m^2/yr$, and have been taken from the papers of Smith, Bindloss, Jupp *et al.*, Britton, Maitland and Hudspith, Charles *et al.*, McLusky and McFarlane, Thorpe, R. I. G. Morgan, and Laughlin (all 1974). All the values given are for 1971, except for macrophytes and nematodes which are

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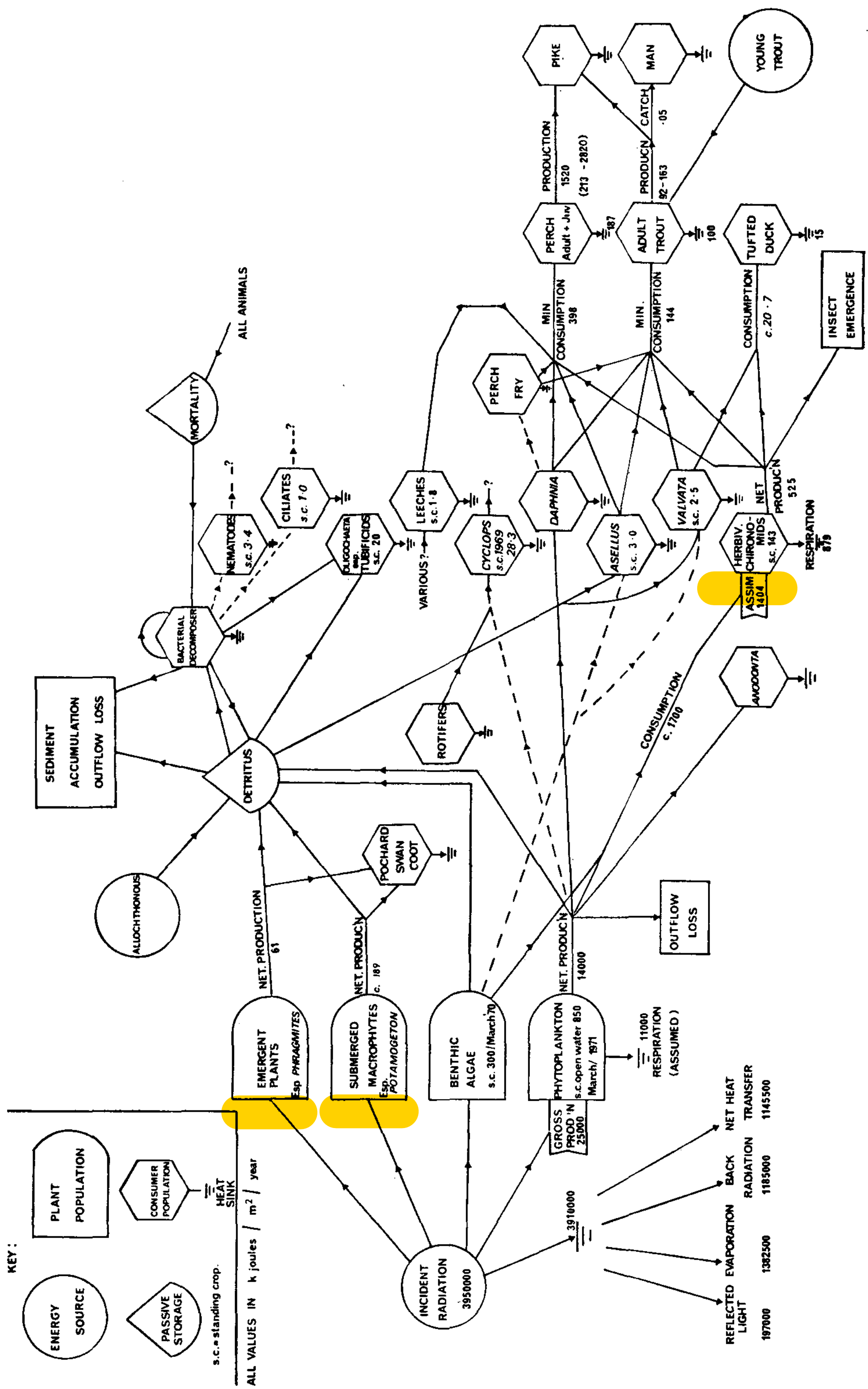

TEXT-FIG. 1.—Summary of the relationships studied at Loch Leven, Kinross, for the year 1971. Values are expressed as kJ/m²/year. For further explanation, see text.

for 1972, and tufted duck which are modified from the 1970 figure. The energy circuit language symbols of Odum (as in Jansson 1972) have been used in the diagram, as explained in the insert key. Known feeding relationships are shown by a solid arrow, and hypothetical ones by a hatched arrow. Data for years other than 1971 are shown in italics.

The main aim of the International Biological Programme at Loch Leven was to measure production and relationships in the food chain; phytoplankton—Chironomidae—fish and diving duck.

The phytoplankton productivity and incident radiation values are as given by Bindloss, with the losses of incident energy calculated from the percentages given by Smith. Net production of phytoplankton has been derived by subtraction of the assumed respiration rate of the phytoplankton from gross production. The net production of submerged macrophytes has been calculated from the figure of 597 kJ/m^2/yr for the depth zone 0–30 cm (Jupp pers. com.), which gives a production of 63 kJ/m^2/yr when calculated for the whole loch. Macrophyte growth takes place down to about 150 cm in Loch Leven and allowing for decreasing production with depth an approximate total production has been estimated of 3×63 kJ/m^2/yr. The production of chironomids has been computed from 1971 data by Maitland and Hudspith on sand species which represent 42 per cent of the loch area, and from data by Charles *et al.* on total mud species, which represent 57 per cent of the loch. Respiration values for the chironomid larvae are derived from McLusky and McFarlane (1974). Assimilation for chironomids is derived by summation of respiration and production. Assimilation has then been converted into consumption by the addition of 20 per cent, which gives a value of approximately 1700 kJ/m^2/yr. Using Maitland and Hudspith's 1970 data on production of the total zoobenthos in the sand, a speculative figure of approximately 2500 kJ/m^2/yr may be suggested for total zoobenthos energy requirements in 1971. This figure is based on the unlikely assumption that the proportion of macro-zoobenthos production formed by the chironomids is the same for mud sediments as for sand. However, this is the best estimate to date. The values for standing crop of the other zoobenthos are derived from Maitland and Hudspith's 1971 data for sand areas and are calculated on the assumption that the ratio of zoobenthos other than Chironomidae in sand to those in mud was the same as they found in 1968.

Laughlin (1974) calculated the total energy requirements for tufted duck in 1970 as 29·4 kJ/m^2/yr, but regarded this as exceptional, and his modified value of 20·7 has been included on the diagram. Thorpe (1974) calculated fish production of adult perch and trout in units of g wet wt/m^2/yr, which have been converted to kjoules (R. I. G. Morgan 1974). Morgan calculated minimum total energy requirements for trout and perch, utilising the mean production values of Thorpe and adding minimum values for respiration, gonad production, excretion and specific dynamic action.

Of the 40 000 kJ/m^2/yr incident radiation which are available for primary production a significant proportion, 25 000 (62 per cent), are utilised by the phytoplankton. Approximately 4 per cent of the available incident energy ends up in fish production and 0·00001 per cent in the angler's annual catch of brown trout. It can be seen from the diagram that if chironomids were to feed on phytoplankton alone they would consume approximately 12 per cent of the phytoplankton net production, and that if the perch and trout fed on chironomids alone they would need to consume more than the chironomid production. Thorpe indicates that the adult fish feed on young perch, *Asellus*, leeches and *Daphnia* as well as chironomids. A high phytoplankton crop is present at all times of year (Bailey-Watts 1974). In addition, it has been shown that at Loch Leven the chironomidae also fed on significant amounts of detritus, epifauna on sand grains and benthic algae (Morgan 1972) so food supply does not appear to be the factor limiting chironomid production. On the other hand the fish may be consuming a high proportion of the available food supply which may well be the limiting factor to their production. If the tufted duck fed on chironomids alone they would consume 4 per cent of the chironomid production, but it must be borne in mind that about half the loch is below the maximum feeding depth of the tufted duck, and within the other half many of the chironomids may be unavailable to the ducks because of the behaviour of the larvae.

Major Gaps in our Knowledge about the Loch Leven Ecosystem

The energy flow diagram, which is speculative in some parts, emphasises many gaps in our knowledge of Loch Leven. In particular, it illustrates our lack of knowledge of the feeding relationships between its major trophic levels. Data on the feeding relationships and production of zooplankton are required. It is clear that the role of the zooplankton (*Cyclops* and *Daphnia* principally) as feeders on phytoplankton and bacteria is little understood. The diagram suggests a position in the feeding chain for *Daphnia hyalina* var. *lacustris* Sars., but indicates the lack of knowledge of the feeding of *Cyclops strenuus* var. *abyssorum* Sars., which has usually been reported as a carnivorous species in the adult stage but at Loch Leven adults certainly ingest some algae. The food of these two species at Loch Leven is briefly discussed by Bailey-Watts (1974) and Johnson and Walker (1974). The role of zooplankton as food for fish, in particular perhaps young perch, has not been studied. The young perch, in turn, may be an important food item for adult perch and adult trout and may thereby be one of the major energy transfer pathways. Studies in progress by D. Johnson will provide data on zooplankton production for 1972–73.

Asellus has been found in many of the fish stomachs examined by Thorpe, but almost nothing is known about the feeding or production of this species. *Valvata* has been reported by Laughlin as an important food item for tufted duck but little is known about its production. Both these invertebrates are believed to feed on attached algae and detritus. Samples of these species from the sandy areas have been collected in 1970 and 1971, with which it may be possible to obtain production estimates.

An important part of the energy flow in the loch must be passing through the microbial decomposers which receive their energy supply from the accumulation of detritus derived from plant and animal material, and the inputs of allochthonous material into the loch. The micro-organisms provide food for ciliates and nematodes.

It was not possible to carry out studies on the production of the benthic algae during the IBP programme. However, Bailey-Watts' value for standing crop in March 1970 is included on the diagram, and indicates that the benthic algae may be a significant part of primary production. They are important in the food of some chironomids, such as *Stictochironomus* and *Glyptotendipes* at Loch Leven (Maitland pers.

com.) and other zoobenthos. On the other hand preliminary studies show that the production of submerged and emergent macrophytes is negligible in terms of total primary production. This may be a limiting factor for species of grazing wildfowl.

Tubificid worms are a significant part of the zoobenthos biomass, feeding on detritus and micro-organisms, but Jónasson (1972) showed that in Lake Esrom their production is relatively slow. *Anodonta* is probably an important filter feeder, utilising phytoplankton for its food supply, but little is known of its population or energy requirements.

The link from incident radiation to phytoplankton to chironomids and then on perhaps to fish has been the most intensively studied food chain at Loch Leven; but it is clear that other inputs of energy, especially from allochthonous material and attached algae, may also be important in the food chain. Both the studies of fish stomachs and the bioenergetics of fish have indicated that chironomids are not now the sole principal fish food item as was suspected at the beginning of the Loch Leven programme. Data on the production and feeding of other zoobenthos, zooplankton and also young fish are important gaps and it is not clear what are the limiting factors for the production of zoobenthos or zooplankton. It may be that a seasonal energy demand, such as the autumnal peaks in energy requirements shown for chironomids by McLusky and McFarlane, may be critical for benthic production.

Variability of the Ecosystem

The variability of the Loch Leven ecosystem from year to year has been indicated clearly by the IBP studies and is a major feature of the lake. This instability of both the quality and quantity of the flora and fauna is a characteristic of all the groups investigated. Some of the changes seem to be long-term or permanent trends such as the increase in the phytoplankton density, the decline in submerged and emergent macrophytes, the virtual disappearance of Odonata and Ephemeroptera, the decline in Trichoptera and Gastropoda and the disappearance of charr, *Salvelinus alpinus* (L.). Others seem to be cyclical, such as the year-to-year fluctuations in the composition of the dominant phytoplankters, the disappearance of *Daphnia hyalina* var. *lacustris* between 1954 and 1966 and its reappearance in 1970, and the fluctuations in the annual catches of brown trout. This means that things which are normally predictable in lakes, such as the seasonal changes in the major components of the phytoplankton, are so far unpredictable at Loch Leven.

The causes of these changes and fluctuations may be related to the increase in plant nutrients recorded by Bindloss *et al.* (1972). The high phytoplankton densities and the appearance of such species as the tubificid worm *Potamothrix hammoniensis* (Michaelsen) (Morgan 1970), which is associated with eutrophication, almost certainly relate to this increase. A reason for 'instability' in phytoplankton annual successions may be the shallowness of the loch so that an excess of production over loss can occur at all times of year, as is shown by Bailey-Watts (1974). Thus short-term effects can be important at any time of year. This is a situation comparable to deeper lakes in summer. In deeper, more flushed lakes, the phytoplankton is reduced to small numbers in winter. Thus the late winter-early spring situation in these lakes is an 'open field' for organisms able to grow rapidly in cold water and short days (e.g. diatoms). This in turn may induce further changes later on. We have as it were a single potential set up in winter which is discharged in spring. Thereafter a series of diverse potentials are set up and discharged in summer. The latter situation is similar to Loch Leven all the year since light conditions remain relatively good in the shallow water in winter and nutrients are plentiful. On top of this is a qualitative stability factor, the chemistry of the water, which permits some but not other algae to flourish.

The decrease in the depth at which macrophytes are recorded (Morgan 1970; Jupp *et al.* 1974) most probably relates to the shading effect of the dense phytoplankton but the complete disappearance of species with floating leaves is less easy to explain. Certainly some of these produce submerged leaves before reaching the water surface but most have tuberous roots which act as storage organs and might be expected to support growth of the plant stem to the surface.

The fluctuations in the zoobenthos may also relate indirectly to the increasing nutrient status as addition of fertilisers to lochs can cause big changes in benthos numbers and the predominance of different species from year to year (Morgan 1966), and the instability of the loch may well be caused by the relatively rapid increase in nutrient level which has taken place. Many of the groups of zoobenthos which have declined live on vegetation and their decline may be associated with this.

There are other important factors such as the influence of parasites and grazers, such as *Daphnia hyalina*, on the composition of the phytoplankton which are imperfectly understood. The decline in the remnants of the emergent vegetation appears to be associated with erosion of the edges of the reed beds by wave action combined with grazing on the young shoots by wildfowl (Britton 1974). A dense bed of either submerged or emergent vegetation will in itself give mutual protection to the individual plants from damage by wave action by damping down such action. Once this protection has gone, following the decline in vegetation, that which remains is more vulnerable and it may be extremely difficult for it to re-establish naturally. It is possible that the discharge of dieldrin into the loch between 1958 and 1964 (Holden and Caines 1974) may have caused a decline in the fecundity of *Daphnia hyalina* although the levels would appear to have been too low to directly kill the *Daphnia*. This could have contributed to the temporary disappearance of this species.

The evidence suggests that, because of its shallowness and exposure, Loch Leven is unable to absorb environmental stress and storms may have unpredicted effects on the flora and fauna, causing crashes in populations which would not otherwise happen. The sudden and complete disappearance of *Endochironomus* during the course of this study is an instance of the speed and magnitude of change. The imposition of other factors such as high nutrient loading during the present century may have imposed additional stresses which bring about the unstable situation exhibited now. Experimental work is required on the causal relationships affecting the stability of the system in order to provide information for the proper management of the lake system. Few other shallow exposed lakes have been studied in great detail so that it is too soon to know whether this situation at Loch Leven is a feature of lakes of this type.

Management of the Ecosystem

Loch Leven is a National Nature Reserve and a brown trout fishery. The IBP project has provided valuable information relating to the management of both and has highlighted areas where further research and experimental management are required. The need for research on the causes of the lake instability has been mentioned. Other problems are listed below:

1. Methods of control of the high populations of diatoms and blue-green algae which may limit macrophyte re-establishment and are said to be detrimental to the trout fishery. An approach to this problem is to look for limiting factors and to investigate the best ways of reducing the phosphate input from the woollen mills and sewage. Reduction of the amount of nitrate entering the lake, primarily from agricultural sources, could assist significantly in controlling algal populations, but is not practicable at the present time.

2. Reduction of the total amount of a nutrient, such as phosphorus, entering the water from sources outside the lake is only worthwhile as a method of controlling algal populations if it is known that such sources are the most important. In Loch Leven, phytoplankton populations appear to obtain much of their phosphate from the sediments, which contain large quantities. Further work is required on the release and uptake of phosphate (and other nutrients) by the mud. Knowledge of the biological factors in sediments affecting the rates of release and uptake of nutrients is important together with the relative importance of physical factors such as adsorption, gas bubble evolution and sediment disturbance by wind-generated currents. The activity of sediment bacteria (particularly under aerobic conditions), benthic algae, phytoplankton and zoobenthos (particularly chironomids and tubificids) in the translocation of nutrients must be determined in order that the most important factors controlling nutrient levels in the ecosystem can be ascertained. For example, preliminary laboratory studies have indicated that assimilatory nitrate reduction and then nitrification by sediment micro-organisms may play important roles respectively in the reduction in nitrate concentration in the open water in the spring and the increase in the late summer shown by Holden and Caines (1974) (Holding pers. com.).

3. The re-establishment of submerged macrophytes. This is particularly important in relation to diversifying the invertebrate faunas which in turn are important for the fish and wildfowl. The work described by Jupp *et al.* (1974) on the present distribution of macrophytes and the factors limiting this is a first step towards solving this problem.

4. The re-establishment of emergent vegetation is also important and work has commenced on this (Britton 1974).

5. Concurrent studies are required on the utilisation of macrophytes by wildfowl.

6. *Daphnia hyalina* is probably a more available food for young perch than *Cyclops strenuus* var. *abyssorum*. As this may be one of the major routes of energy flow through the ecosystem at Loch Leven it is important to investigate ways of maintaining *D. hyalina* as the dominant zooplankter and preventing *C. strenuus* var. *abyssorum* taking on this role.

7. In conjunction with the work on macrophytes, Odonata and Ephemeroptera. should be reintroduced into the loch and the species range of other groups such as Trichoptera and Gastropoda increased. This is in keeping with the general principle of maintaining a wide diversity of species in National Nature Reserves and to provide food for fish and diving duck.

8. The low hatching and fledging success of ducks at Loch Leven is related to

heavy predation on the eggs by avian predators and losses of young by predation and mortality due to the very exposed conditions at the loch. Management has commenced on protecting areas of shallow water along the shoreline from wave action in order to provide sheltered places for the young to feed. Several helminths have been found in immature birds which are known to cause nestling mortality (Fraser pers. com.) and an investigation of the parasites of young ducklings is required.

9. Large numbers of brown trout have been found to die at spawning time. Initial studies suggest that these deaths may be caused by hormonal factors similar to those described in the Pacific salmon, *Oncorhynchus* spp. (Robertson and Wexler 1960). The loch provides a natural population of fish in which to study the changes occurring in the fish at spawning time and the relationship of these changes to disease resistance.

10. A comprehensive picture of the parasites infecting trout, perch and birds at Loch Leven has now been obtained (Campbell 1974; Fraser 1974). The circulation patterns between hosts, particularly of helminth parasites, should now be investigated as an aid to management of secondary producers. There is some evidence that the same path is being used by different families of trematode, as instanced by some species of Diplostomatidae and Strigeidae using the same mollusc, fish and bird hosts (Fraser pers. com.). Production estimates of strigeid metacercariae in trout and perch and of the trematode *Bunodera luciopercae* (Müller) in perch can be made if fish population estimates are concurrently available. The present incidence of parasites in the major fish species at Loch Leven is relatively low and it is important to monitor the incidence over a period of time to determine long-term variations.

11. The effects of water level fluctuations on shallow littoral flora and fauna needs fuller investigation and determination of their rate of recovery from drying out.

12. The impact of wave action on the macrophytes and zoobenthos and the resistance of different species should also be determined. This should be related to the problem of re-establishment of macrophytes.

13. There is an overall need to monitor the ecosystem at the major trophic levels to detect significant changes which may require changes in management. Analysis of the long runs of chemical, phytoplankton, zoobenthos and fish data, which are now available, will enable us to determine the best methods, coverage and sampling time intervals to use to detect change with the minimum of effort. Monitoring of the macrophytes may be feasible by aerial photography.

Observations

The Loch Leven project has shown that in ecosystem studies of this type the basic concept of obtaining data on physical and chemical conditions before starting detailed biological studies is correct, particularly in order to produce detailed bathymetric and sediment maps from which sampling programmes can be determined for production studies. Detailed land use studies and survey of the catchment area would have been valuable adjuncts in calculating the sources and amounts of nutrients such as nitrogen and organic allochthonous material entering from the catchment, and would have been most valuable if done at the beginning. As indicated under 'management problems', interpretation of the chemical data and the relationship of phytoplankton blooms to nutrient supply would have been greatly facilitated by estimates of the quantity and quality of allochthonous materials entering the loch and the exchange of nutrients at the mud/water interface, including the physical and biological (bacteria and zoobenthos) factors influencing it. These, however, would have been large and comprehensive studies in themselves.

If resources had allowed it, concurrent studies on feeding and assimilation by all the major secondary producers being studied should have been carried out and in particular more extensive studies on the feeding of fish should have been made at the outset of this study to determine all the major energy pathways to fish.

The levels of accuracy of measurement of the populations and production of chironomids which has been achieved has fully justified the large effort put into determining the sampling strategy and methods, particularly for the mud (Charles *et al.* 1974; Maitland 1974). It will seldom be possible to put this amount of effort into such studies and it will now be possible to analyse the results to determine what would have been lost by omitting the larvae which pass through different mesh sizes and by reducing the number of samples or frequency of sampling. This should provide a valuable guide to the design of sampling programmes in the future to achieve particular levels of accuracy.

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References to Literature

Bailey-Watts, A. E., 1974. The algal plankton of Loch Leven, Kinross. *Proc. Roy. Soc. Edinb., B*, **74**, 135–156.

Bindloss, M. E., Holden, A. V., Bailey-Watts, A. E. and Smith, I. R., 1972. Phytoplankton production, chemical and physical conditions in Loch Leven. *Proc. IBP–UNESCO Symp. on Productivity Problems of Freshwaters*, Kazimierz Dolny, 639–659.

Bindloss, M. E., 1974. Primary productivity of phytoplankton in Loch Leven, Kinross. *Proc. Roy. Soc. Edinb., B*, **74**, 157–181.

Britton, R. H., 1974. Factors affecting the distribution and productivity of emergent vegetation at Loch Leven, Kinross. *Proc. Roy. Soc. Edinb., B*, **74**, 209–218.

Campbell, A. D., 1974. The parasites of fish in Loch Leven. *Proc. Roy. Soc. Edinb., B*, **74**, 347–364.

Charles, W. N., East, K., Gray, M. C. and Murray, T. D., 1974. The production of larval chironomidae in the mud at Loch Leven, Kinross. *Proc. Roy. Soc. Edinb., B*, **74**, 241–258.

Fraser, P. G., 1974. The helminth parasites of aquatic birds from Loch Leven, Kinross. *Proc. Roy. Soc. Edinb., B*, **74**, 391–406.

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

Jansson, B. O., 1972. Ecosystem approach to the Baltic problem. *Bull. Ecol. Res. Comm., (Swedish Nat. Sci. Res. Council)*, **16**, 1–82.

Johnson, D. and Walker, A. F., 1974. The zooplankton of Loch Leven, Kinross. *Proc. Roy. Soc. Edinb., B*, **74**, 285–294.

Jónasson, P. M., 1972. Ecology and production of the profundal benthos in relation to phytoplankton in Lake Esrom. *Oikos, Suppl.*, **14**, 1–148.

JUPP, B. P., SPENCE, D. H. N. and BRITTON, R. H., 1974. The distribution and production of submerged macrophytes in Loch Leven, Kinross. *Proc. Roy. Soc. Edinb.*, *B*, **74**, 195–208.

LAUGHLIN, K. F., 1974. The bioenergetics of the tufted duck (*Aythya fuligula*) at Loch Leven, Kinross. *Proc. Roy. Soc. Edinb.*, *B*, **74**, 383–389.

MAITLAND, P. S. and HUDSPITH, P. M. G., 1974. The zoobenthos of Loch Leven, Kinross, and estimates of its production in the sandy littoral area during 1970 and 1971. *Proc. Roy. Soc. Edinb.*, *B*, **74**, 219–239.

MCLUSKY, D. S. and MCFARLANE, A., 1974. The energy requirements of certain larval chironomid populations in Loch Leven, Kinross. *Proc. Roy. Soc. Edinb.*, *B*, **74**, 259–264.

MORGAN, N. C., 1966. Fertilization experiments in Scottish Freshwater Lochs II. Sutherland, 1954, 2. Effects on bottom fauna. *Freshwat. Salm. Fish. Res.*, **36**, 19 pp.

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

——, 1972. Productivity studies at Loch Leven (a shallow nutrient rich lowland lake). *Proc. IBP–UNESCO Symp. on Productivity Problems of Freshwaters*, Kazimierz Dolny, 183–205.

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

MORGAN, R. I. G., 1974. The energy requirements of trout and perch populations in Loch Leven, Kinross. *Proc. Roy. Soc. Edinb.*, *B*, **74**, 333–345.

ROBERTSON, O. H. and WEXLER, B. C., 1960. Histological changes in the organs of migratory and spawning Pacific salmon, (*Oncorhynchus* spp.). *Endocrinology*, **66**, 222–239.

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

THORPE, J. E., 1974. Trout and perch populations at Loch Leven, Kinross. *Proc. Roy. Soc. Edinb.*, *B*, **74**, 295–313.