PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Productivity of Freshwater Communities [and Discussion]

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The productivity of freshwater communities

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Research into the productivity aspects of aquatic ecology began with Danish studies in the sea and was developed up to 1942 especially in Russia and North America. The I.B.P.-P.F. (Productivity of Freshwaters) section planned to use new methods to test and develop the 'trophic-dynamic ecosystem' concept in a wide range of fresh waters. Apart from the Lake George project, the United Kingdom's projects were centred on Loch Leven and the River Thames at Reading. At both places estimates were made of energy flow through several main components of the ecosystem; in Loch Leven from phytoplankton through benthic chironomids to trout, perch and tufted ducks; in the River Thames from phytoplankton, weed beds and detritus through crustacea and benthic invertebrates to fish. Intensive studies on all the forms of primary production in ponds near Bristol, several supporting projects (some in applied limnology) and a share in the Netherlands' studies of Tjeukemeer were other U.K. contributions. Though the over-simplicity and other weaknesses of the original concepts of I.B.P.-P.F. and basic problems in methodology and the comparability of data have been revealed, many valuable results were achieved. The programme has also been a stimulus to limnology in general through the handbooks and through its enthusiastic teams of young limnologists.

1. Introduction

One of the sections of the International Biological Programme was entitled 'The Productivity of Freshwaters' and abbreviated the 'P.F. Section'. I will attempt, in this paper, to review the United Kingdom's contribution to the work of the P.F. Section, but it will be impossible in a short paper, written before all the results are published, to do justice to the detailed scientific findings of the several research projects involved. Rather, therefore, will I try to sketch the scientific context in which the P.F. programme was planned and carried out, then describe a few of the U.K. projects and finally comment on some of the more general aspects of the programme and its successes and failures.

Inevitably I have indulged in personal bias, especially in the selection of particular parts of the programme for more detailed description. By its nature the I.B.P. was a team effort and I am very conscious that I am reporting about the work of others. To many of these I am indebted, not only for help in the preparation of this paper but for the discussion and involvement over the past twelve years that provided essential background information. I am particularly grateful to Dr J. W. G. Lund who was the Chairman of the U.K. I.B.P.-P.F. Subcommittee in its vital earlier days, to Dr J. F. Talling who inspired and guided much of the work, Dr K. H. Mann and Dr A. D. Berrie who were responsible for the project on the River Thames, Mr N. C. Morgan and Dr P. S. Maitland who led the Loch Leven team, Mr D. F. Westlake who has done much in the primary production field, Dr J. Rzoska who, as Sectional Coordinator played a major role, not only in the whole international P.F. programme, but also in that of the U.K., and many others too numerous to mention by name. I must also draw attention to the wise guidance, practical assistance and financial support given to the U.K.s I.B.P.-P.F. programme by the Council, Officers and staff of the Royal Society. It is important to

emphasize at the outset that, both nationally and internationally, the informal spirit of cooperation and goodwill, leading in many cases to the development of real personal friendships, has been an outstanding feature of the I.B.P.

2. The historical and scientific context of the P.F. programme

The basic hypothesis behind much of the I.B.P. has been that of an *ecosystem* (Tansley 1935) made up of a series of *trophic levels* through which solar energy, fixed by photosynthesis, flows irreversibly. The measurement of the *biomass* of each of these trophic levels, and their *production*, was a major aim of the I.B.P. Especially was this so in the freshwater section as the '*trophic-dynamic*' model of the ecosystem had had special attention from aquatic ecologists. (It is important to note here that much of the fundamental progress in freshwater ecology is inextricably interwoven with parallel work in the sea. It is a paradox of the I.B.P. that there was not more contact between the P.F. and P.M. sections.) It is always difficult to trace the exact origins of general hypotheses in science and no brief review will present a complete or balanced picture, but I believe that an assessment of I.B.P. requires some note of the ancestry of its guiding themes.

The trophic-level structure of ecosystems formed much of the basis of the work in the sea of the Danish Biological Station under the original leadership of J. G. Petersen during the first decades of this century. Estimates were thus being made of the biomass of aquatic trophic levels some fifty years before the I.B.P. These general ideas had a place, too, in Elton's (1927) classic textbook. At about the same time direct measurements of planktonic primary production were being pioneered (e.g. Gaarder & Gran 1927). In freshwaters the Russian school led by Ivlev, and before and during the I.B.P. by Winberg, developed pioneer ideas and made what were probably the first measurements of freshwater production (Borutsky 1939; Ivlev 1945, 1966). In America the Wisconsin school, led by Juday, made some key pioneer experiments (Manning, Juday & Wolf 1938), constructed biomass pyramids for lake ecosystems (Juday 1940) and started to compile comparative biomass data. Conceptually a key paper was that of Lindeman (1942) and this has been a stimulus to much subsequent thought (even though some of this has pointed out limitations and errors in his ideas). Mann (1969) reviewed the general state of progress in the study of aquatic ecosystems just before I.B.P. results began to influence it.

Progress in the actual measurement of secondary production was next made for freshwater fish (Allen 1946, 1951; Ricker & Foerster 1948), and Allen's graphical method has been the basis for much work in the I.B.P. A major paper was that by Odum (1957) which described production in several trophic levels in Silver Springs. The methodology of production estimation in phytoplankton received a fillip with the introduction of the ^{14}C method by Steeman Nielsen (1952), though the rival 'oxygen' method was more widely used in the I.B.P.-P.F. The 'state of the art' in methodology just before the I.B.P. has been reviewed by Lund & Talling (1957) and Gessner (1955, 1959) for primary production, and by Ricker (1958) and Beverton & Holt (1957) for fish population dynamics. Another significant development of about this period was the introduction of effective mathematical modelling. In fishery ecology quantitative modelling began several decades earlier but became sophisticated only with the work of Beverton & Holt, Ricker and others. Riley (1946) modelled plankton production in the sea but probably the most significant influence for I.B.P.-P.F. in models of primary production has been the work of Talling (1957, etc.), whose models have been based on the empirical measurement of fundamental processes. In the 1960s ecologists were beginning to be aware of the potential provided by systems analysis and computers for the study of ecosystems. The general development of this approach came too late, however, for most of the national P.F. programmes with the exception of those on Marion Lake in Canada, Lake Dalnoe in Kamchatka and some of the late starters in the U.S.A.

It was thus in a context of a bold, simple conceptual framework of a trophic-dynamic ecosystem, waiting to be tested and developed with a wide range of new field data, that the I.B.P.-P.F. programme was conceived and planned. New methods of measuring populations and production rates were available and the computer, in the hands of geniuses in systems analysis, lay waiting to process the data into meaningful results. There was an optimism that we had only to measure enough of the relevant variables in a wide range of waters for the fundamental structure and functioning of freshwater ecosystems to be revealed. The time, too, was one when the first serious hints of man-induced environmental changes in lakes were beginning to be widely apparent (though the scientific study of water pollution had begun a century before). The understanding revealed by I.B.P.-P.F. might solve the practical problems of 'eutrophication' and other biological problems of water resource management.

3. The planning of the I.B.P.-P.F. programme

It is against this background of rather vague hypothesis that both the international and national planning of the P.F. took place. The initial ideas for the I.B.P. as a whole arose at and around the general Assembly of the International Union of Biological Sciences (I.U.B.S.) in Amsterdam in 1961, and the first meeting of the international P.F. Subcommittee took place in Madison, U.S.A., in August 1962. By June 1964 the proposed P.F. programme was published. It laid emphasis on the study of community structure, biomass, rates of biomass change, factors controlling these and 'utilization efficiencies'. There were to be between twelve and fifteen sites on representative standing or running water ecosystems distributed across the main climatic zones of the world. To this minimum programme were added a number of other projects, several of which reflected the specialized interests of some of those involved. There was emphasis on the use of recommended methods and training in them.

In the U.K., comments were made on this international programme and possible national contributions to it at meetings in August 1963 and April 1964. The idea of a project in East Africa, possibly somewhere on the Nile system was mooted early on, and this developed into the Lake George project (Greenwood, this volume). There is evidence in the records of these early meetings of concern for an adequate consideration of taxonomy, methodology and a U.K. role in training programmes. Dr Mann's project on the River Thames was mentioned, as was the potential for basic work on energy flow in fish ponds, e.g. at Malacca. The role of benthic algae and detritus in freshwater communities was also stressed.

Eventually the U.K./P.F. programme crystallized into four main projects:

(*a*) a study of all trophic levels on the River Thames at Reading;

(*b*) an 'all level' study of Loch Leven in Kinross-shire;

(*c*) an all level study of Lake George on the equator, jointly with Uganda, and

(*d*) a study of primary production in detail in two ponds near Bristol, which included special attention to non-planktonic forms of primary production.

To this main programme was attached a 'supporting programme'. This consisted mostly of projects in freshwater biology that were in progress or planned before the I.B.P. started but which had some relevance to it. Several involved research in applied problems, but some were projects in production ecology derived from the same basic concepts as the main I.B.P. programmes, e.g. the Freshwater Biological Association's programme at its River Laboratory in Dorset which had been planned between 1960 and 1963 and the work on the Thames Valley Reservoirs by the Metropolitan Water Board and Royal Holloway College. Mention must also be made of the I.B.P. project on Tjeukemeer in Friesland. This was part of the main programme of the Netherlands under the leadership of Dr H. L. Golterman, but the team included a number of British zoologists so became a joint Netherlands–U.K. project.

In the more detailed description of this programme that follows I shall concentrate on the Thames and Loch Leven projects with passing reference to some of the others. The Lake George project is the subject of a separate paper in this symposium, and the work on the ponds near Bristol awaits a general summary of its many detailed and specialized papers, which I shall not attempt to initiate here.

A bibliography of the papers originating from the U.K. main and supporting P.F. programme, arranged according to projects is given in pp. 526-536.

4. The Loch Leven project

Introduction

Loch Leven is a lake unique in Britain because it is relatively large (13.3 km^2) and yet shallow with a mean depth of only 4 m; moreover it rarely stratifies. It is thus very different from glacial valley lakes such as Windermere, Esthwaite Water, Loch Lomond or Llyn Tegid, that have been the sites for much previous limnological research in the U.K. The loch had long been famous for its fishery for trout (*Salmo trutta*) and its populations of waterfowl; in winter up to 20000 pink-footed geese (*Anser brachyrhynchus*) and other species may be present. In 1964 the loch became a National Nature Reserve by agreement with the owner, Sir David Montgomery. Regular observations on the loch began in 1963 because blooms of blue-green algae were becoming an increasing nuisance to the trout fishery. Out of these two events arose a proposal for an I.B.P. project on the loch, made jointly by the Nature Conservancy and the Freshwater Fisheries Laboratory of the Department of Agriculture and Fisheries for Scotland. This proposal was accepted by the U.K./P.F. Subcommittee and the original sponsors were joined by the Wildfowl Trust and eventually workers from nearly all the Scottish universities. A total of forty-one scientists from eleven organizations were involved. A small steering committee under the chairmanship of Dr Lund met six-monthly and there were also meetings of all those actively engaged in the project, culminating in a symposium meeting at Stirling University in June 1973. The proceedings of this meeting have been published (*Proc. R. Soc. Edinb.* B 1974, 43–416) and are the basis for much of the account that follows. (Full references will be found in this volume and are not given here.)

The physical and chemical features of Loch Leven

Considerable effort was expended in providing a morphological, physical and chemical description of the environment of the loch and its surroundings as a basis for the work on its production ecology. It was necessary first to make a new and detailed bathymetric map, a survey of the bottom sediments, and a study of the hydrological balance. Because of its exposed position and shallow depth over much of its area, wind-induced circulation is an important environmental factor. The rather complex pattern of horizontal circulation under the wind conditions commonly prevailing was worked out, as was the depth of the wave-mixed layer at different wind speeds.

The existence of algal blooms in Loch Leven and their increasing frequency over the last ten years roused interest in the nutrient chemistry of the loch. As much of the catchment for the loch lies on relatively fertile agricultural land the loch waters have probably long been fairly productive and this may have been enhanced recently by the increased use of mineral fertilizers. There is also nutrient input from two small towns and the phosphorus-rich detergents used in a small woollen mill. Estimates of the budgets for phosphorus and nitrogen showed that the sediments probably play a major role in both the release and uptake of nutrients, particularly phosphorus. At times there were rapid decreases in nitrogen or phosphorus in the water which could not be accounted for by loss in the outflow or uptake by algae. In general, however, the concentrations of plant nutrients and the quantities available were more than adequate to maintain plant growth and algal production did not appear to be limited by a lack of nutrients. Some evidence was obtained to suggest that, although the surface sediments were rarely de-oxygenated, there might have been a significant bacterial de-nitrification.

Primary production

Approximately 150 species of planktonic algae were found in Loch Leven in routine examinations, of which some twenty-five made significant contributions to the biomass. During the four years of observation diatoms were the major components especially in the winter and spring and they were frequently the smaller centric species, such as *Cyclotella pseudostelligera* and *Stephanodiscus* spp. Green algae were also abundant in the late summer and *Peridinium cinctum* dominated the plankton for one spell. However, the most noticeable algae were frequently blue-greens such as *Oscillatoria redekei* and *Synechococcus* n.sp. The small size of many of the abundant species may have been connected with the apparent lack of intensive grazing by zooplankton during much of the time. The biomass was high, typically 20 g m^{-2} of carbon in the summer phytoplankton.

Estimates of gross phytoplankton production showed the influence of the shallow well-mixed water and high nutrient levels. Some of the rates of production recorded approached the upper limits known for natural waters and the amount of phytoplankton present sometimes approached its theoretical maximum 'photosynthetic cover'. The rates observed ranged from 0.4 to 21 g O_2 m^{-2} d^{-1} (0.1–8 g C m^{-2} d^{-1}) and averaged over four years 5.8 g O_2 m^{-2} d^{-1} (2.2 g C m^{-2} d^{-1}). The average yearly total gross phytoplankton production was estimated as 2.1 kg O_2 m^{-2} a^{-1} (785 g C m^{-2} a^{-1}, or 33 MJ m^{-2} a^{-1}), just under 1 % of total incident radiation being fixed by photosynthesis. The high rates of gross primary production were probably due to the shallow mixed water column and relatively high nutrient loadings. There was evidence that at times photosynthesis was limited by high pH and thus possibly by the availability of carbon. The calculation of meaningful estimates for the rate of net primary production was difficult and only approximations were possible.

Sampling of the surface sediments of the loch revealed a biomass of benthic algae, mostly diatoms, which was frequently greater than that in the water column above. It is probable that they contribute significantly to the total primary production and to the food supply of benthic invertebrates.

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Loch Leven was at one time noted for its dense growth of littoral macrophytes, both emergent and submerged, but in the years preceding the I.B.P. observations these had become much reduced. The number of species had also decreased though some new species have appeared and the general balance has profoundly altered from a flora dominated by *Chara aspera* to one with relatively abundant *Potamogeton filiformis*, *Zannichellia palustris* and *Nitella opada*. The reasons for these changes are probably the increase in phosphate concentrations and shading by algal blooms (especially when *Anabaena* occurs). Wave action and the activities of ducks also influence the development of weed beds but cannot be a primary reason for the decline in abundance. Approximate estimates for the net primary production by submerged macrophytes average 0.6 MJ m^{-2} a^{-1}, considerably less than the contribution from the plankton. The total production of emergent aquatic macrophytes, chiefly *Phragmites communis*, is negligible compared with other sources.

Zooplankton

Collections of zooplankton made at various times had shown changes in the species of crustacea common in Loch Leven and notably the disappearance of *Daphnia hyalina* after 1954. During the main period of I.B.P. sampling the zooplankton was unusual in being virtually unispecific and consisting of the carnivorous copepod *Cyclops strenuus abyssorum* though small numbers of *Diaptomus gracilis* were present and also a number of rotifers. Estimates of zooplankton production were not made but summer population densities reached nearly 300 l^{-1}. In August 1971 *Daphnia hyalina* suddenly reappeared and was co-dominant with *Cyclops strenuus* in 1972. The total population densities were about the same as in 1969.

Zoobenthos

Studies on the production ecology of zoobenthos were concentrated on the two main substrata of the loch – sand and mud, and on the small number of species of Chironomidae that dominated the zoobenthos on each kind of bottom sediment. In the sandy areas *Limnochironomus*, *Glyptotendipes* and *Stictochironomus* were the genera which dominated the biomass and whose production was estimated in detail. There were considerable differences in both the total production and the relative importance of the species between 1970 and 1971. In 1970 the total production by the three genera was, in dry mass, 42 g m^{-2} a^{-1} whereas in 1971 it fell to 16 g m^{-2} a^{-1}. Extrapolating the data for these three dominant genera to the whole zoobenthos of the sand gives a production rate for 1970 of 46.5 g m^{-2} a^{-1} (equivalent to 1.0 MJ m^{-2} a^{-1}).

In the muddy sediments of the loch four genera were dominant – *Chironomus* (*C. anthracinus*), *Limnochironomus*, *Polypedium* and *Glyptotendipes*, and estimates of production were made for them. Dry mass production for the four genera totalled 29 g m^{-2} a^{-1} (equivalent to 580 kJ m^{-2} a^{-1}). Extrapolation to all the Chironomidae, which make up the bulk of the zoobenthos in the mud gives a total production of 34 g m^{-2} a^{-1} (680 kJ m^{-2} a^{-1}).

Laboratory estimates were made of the respiration rates of larval chironomids from Loch Leven so that approximate gross calculations of the total respiration and thus energy demands of the five most abundant benthic chironomids could be made. These total estimates were, for 1970 and 1971 respectively, 940 and 790 kJ m^{-2} a^{-1} for respiration and 1.25 and 1.02 MJ m^{-2} a^{-1} for total assimilation.

The stony littoral areas of Loch Leven occupy only a small proportion of the total area and the zoobenthos in the stones was not studied in detail quantitatively. It became apparent, however, that the stony areas may produce a significant part of the food of the trout (*Salmo trutta*) at a crucial part of their life history and thus be more important to the fish than would be apparent from their relatively small area.

Fish

Studies on the fish in Loch Leven concentrated on the two most important species, the trout (*Salmo trutta*) and perch (*Perca fluviatilis*). Estimates were made of the populations, growth and production of trout and perch and also calculations of their food consumption by two independent methods – stomach evacuation experiments in the loch and respirometry in the laboratory coupled with observations on the activity in the wild of individuals bearing sonic tags. Total annual (wet mass) production of adult trout ranged from 5.7 to 25.7 Mg a^{-1} of which 3.6–5.5 Mg was gonadal. Juvenile trout production in the loch was approximately 15–37 Mg a^{-1}. The production of adult perch was 37 Mg a^{-1}; that of juveniles lay between 30 and 860 Mg a^{-1}. Trout and perch feed on much the same prey; perch fry and *Asellus* making up about 50 % of the diet of each. The total energy consumption for both species was estimated as 1.8 MJ m^{-2} a^{-1}. The detailed data showed variation from year to year, with negative production over the winter half of the year. An estimate was also made of the production of the trout parasite *Eubothrium crassum* which was about 1 % of the production of its host.

Waterfowl

About thirty species of swans, ducks and geese occur on Loch Leven, though some of them only as rare vagrants. The tufted duck (*Aythya fuligula*) was studied in detail and an estimate made of its bioenergetics, because it is the commonest diving duck, nests on the islands and feeds almost entirely within the loch. The total energy requirements were estimated to average 20 kJ m^{-2} a^{-1}. Sixty per cent of the food of tufted duck was found to be chironomid larvae and the demands of the duck on the zoobenthos production is thus but a fraction of that imposed by the fish and negligible compared with the estimated production of chironomids.

Energy flow

The various estimates of biomass production and assimilation made in Loch Leven were combined into a summary diagram of energy flow through the loch ecosystem (figure 1). The year 1971 was chosen as a period when simultaneous estimates would be made of as many variables as possible with particular emphasis on the food chain: phytoplankton – chironomids – fish and tufted duck. The accuracy of the estimates varies greatly; in some organisms, such as the chironomids on the mud and adult trout, the estimates could be accompanied by calculations of statistical error which showed that, for field ecological sampling, the estimates were reasonably accurate. In other cases, 'order of magnitude guesstimates' are the best that could be made. The summary also serves to indicate the principal gaps in knowledge about the Loch Leven ecosystem. It was not possible to estimate the rate of production by benthic algae though this may have been significant. Apart from suggestive data on the nitrogen cycle no information on bacteria was obtained nor was it possible to estimate the allochthonous input of organic matter into the loch, though this may have contributed significantly, via microbes, to the food available for animals. The information on the diet of the main animal components was also inadequate.

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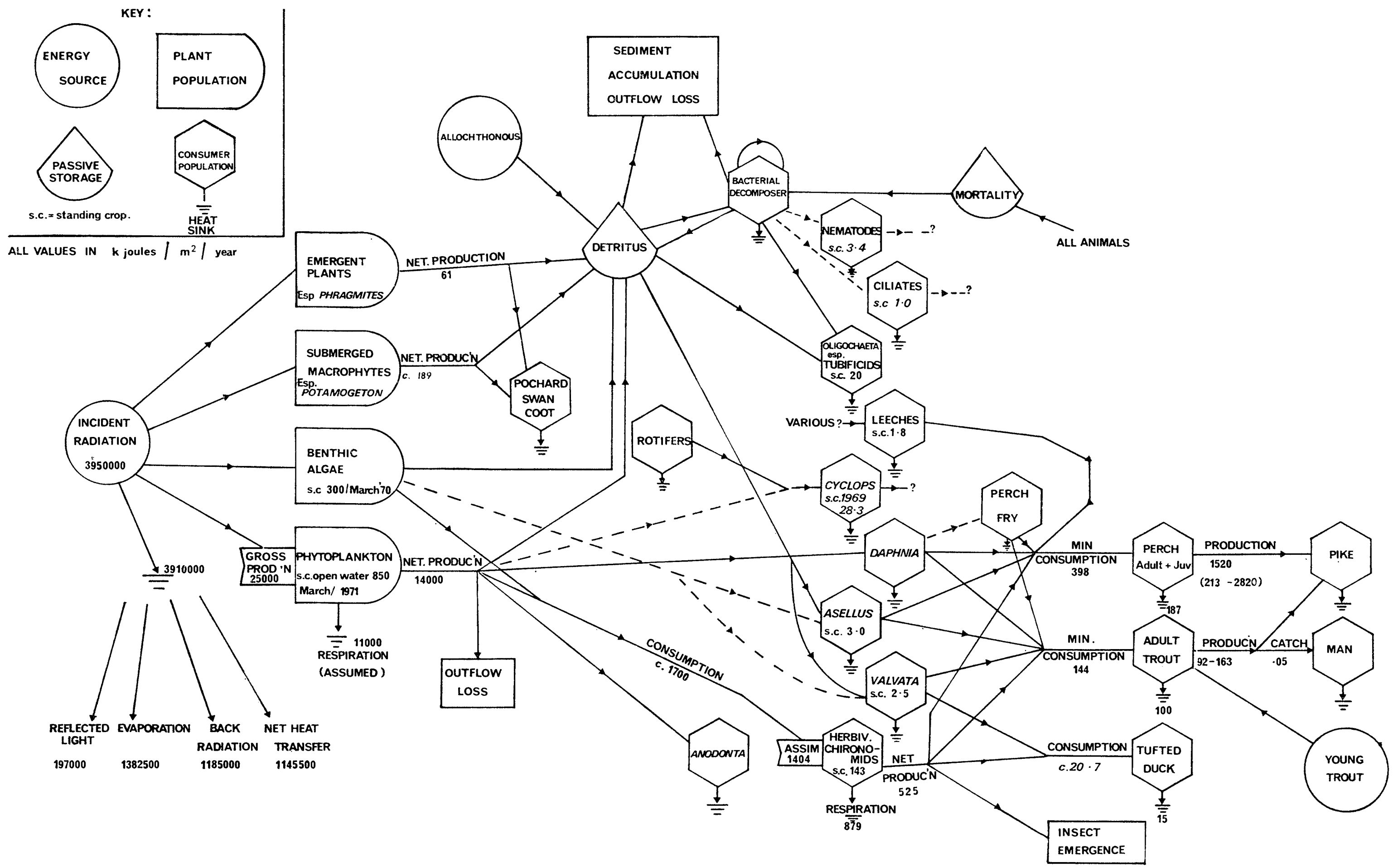

FIGURE 1. Summary of the relationships studied at Loch Leven for the year 1971. Values are expressed as kJ m^{-2} a^{-1}. (Reproduced from *Proc. R. Soc. Edinb.* (B) **74**, p. 408, by kind permission of The Royal Society of Edinburgh, Mr N. C. Morgan & Dr D. S. McLusky.)

Secular variability

Reference has already been made to the long-term ecological changes that have been observed in Loch Leven. Almost every one of the individual studies in the programme revealed major year-to-year changes in the species present and their population dynamics, and this was one of the principal discoveries of the whole project. For example; the pattern of the main phytoplankton species varied each year with some species occurring fairly regularly, others only once or twice over the four year period; a major zooplankton component (*Daphnia hyalina*) was absent for several years, but suddenly reappeared; submerged macrophytes increased markedly in the middle of the period; one of the dominant chironomids, *Endochironomus*, disappeared from the zoobenthos; there was considerable variation in the annual fish production and survival. It is not yet clear whether such variation is peculiar to Loch Leven and to particular man-made changes in it over the present period or if it is an inherent property of large shallow lakes of its type.

5. The River Thames project

Introduction

Work on the River Thames began several years before the start of the I.B.P. with studies on the fish populations and invertebrates by Dr Mann, Dr Williams and Miss Negus. With the advent of the I.B.P. these were developed into an investigation of the ecosystem at all trophic levels by a small team based on the Zoology Department of the University of Reading. The project was initiated and guided by Dr K. H. Mann, but he was succeeded in later years by Dr A. D. Berrie. Summaries of all but the latest stages of the project have been given by Mann *et al.* (1972) and Berrie (1972) and full lists of references will be found in these two accounts.

The River Thames at Reading is a eutrophic lowland river somewhat canalized for navigation. It is 40–80 m wide and 2–4 m deep with a discharge varying between about 12 and 120 $m^3\ s^{-1}$ but usually below 20 $m^3\ s^{-1}$ for the four summer months. The reach that has been studied is 4.2 km long between two sets of navigational locks, but the inflow of a major tributary, the River Kennet, renders the production ecology of the upper third rather different from that of the lower two thirds of the reach. Levels of dissolved oxygen are usually near saturation in spite of the sewage effluent in the R. Kennet, but suspended solids average 16.5 g m^{-3}, 40 % of which is organic. The mean nitrate concentration is over 4 mg l^{-1}, and that of phosphate over 2 mg l^{-1}.

Primary production

Throughout most of the year the river supports a phytoplankton population dominated by diatoms especially *Stephanodiscus hantzschii*, though in the middle of summer green algae are abundant. In April 1968 a peak abundance of 70000 diatom cells per millilitre was reached. Measurements of primary production by using suspended and rotated light and dark bottles were made throughout the year and the calculated net production above the Kennet inflow was 18 MJ $m^{-2}\ a^{-1}$ and below 8 MJ $m^{-2}\ a^{-1}$. The production of benthic algae, which are common over the bed of the river, was estimated using light and dark domed enclosures. The results showed that only in the shallow areas did gross primary production exceed community respiration and the total contribution of the benthos to primary production was very small. The shallow shelves along the banks of the river grow beds of the macrophytes *Acorus calamus* and *Nuphar lutea* and they produce an average of 184 kJ m^{-2} a^{-1}; again small relative to the phytoplankton production.

Studies were made of the contribution of allochthonous organic matter originating from the leaves of *Salix* spp. growing along the bank. This input at about 330 kJ m^{-2} a^{-1} is but a fraction of the phytoplankton production. No attempt was made to estimate other allochthonous input quantitatively but a very large quantity of dissolved and particulate organic matter must enter in the river water which is enriched by drainage from agricultural land and sewage treatment plants. A significant contribution to the food of the bleak (*Alburnus alburnus*) is the bread thrown in by anglers as ground bait!

Invertebrate secondary production

The macro-zoobenthos in the main part of the river was sampled to provide data from which the production of the principal invertebrates might be estimated. A large part of the biomass is made up of unionid mussels and other filter feeders. The total zoobenthos production was estimated at about 600 kJ m^{-2} a^{-1}. Separate studies were made of two components of the invertebrate fauna that were prominent in the food of the fish; the microcrustacea ('zooplankton') and the chironomid larvae that occurred mainly in the weed beds. The results for these have not yet been published in any detail but total larval chironomid production is about 80 kJ m^{-2} a^{-1}. The production of microcrustacea, mostly of species living in the littoral weed beds, is about 240 kJ m^{-2} a^{-1}, but there is also a large through-flow of microcrustacea produced in reaches up-stream.

Fish

Some effort was expended on the estimation of the population numbers, growth rates and diet of the main fish species, especially the bleak (*Alburnus alburnus*) and the roach (*Rutilus rutilus*). Both these species were very abundant, population densities for bleak over one year old being 2.5 m^{-2} and roach 1 m^{-2}. The estimates of production were 570 kJ m^{-2} a^{-1} for bleak and roach, 69 % of which took place in the first year of life. To this must be added 250 kJ m^{-2} a^{-1} for other species. Estimates were made, based on respirometry and dietary studies, of the consumption of various foods by the bleak and roach over one year old and these totalled respectively 1.5 and 2.2 MJ m^{-2} a^{-1}; major contributions to this were made by chironomid adults, terrestrial insects, particulate organic detritus and zooplankton.

Energy flow

The pattern of energy flow for the River Thames is summarized in figure 2. This diagram is notable for the emphasis on pathways leading to the fish and the importance of detritus and allochthonous materials relative to primary production in the reach of the river itself. The lack of any information on heterotrophic production and the pathways taken by allochthonous inputs into the system are obvious and acknowledged gaps in this study. The River Thames project, however, represents one of the very few river studies in I.B.P.-P.F. and is thus of particular interest and value.

6. Other projects

The Bere Stream

This, one of the supporting projects, was a study of a small chalk stream in Dorset. It is a continuing programme of research but was linked to the I.B.P. during its course because of the close resemblance of their basic concepts. This brief account is based on the summary of results up to 1970 by Westlake, Casey & Dawson (1972). Total primary production, mainly by the emergent macrophyte *Rorippa nasturtium-aquaticum*, totalled about 27 MJ m^{-2} a^{-1}. There was a large allochthonous input of fine organic detritus estimated at 800 MJ m^{-2} a^{-1}, an invertebrate production of about 3 MJ m^{-2} a^{-1} and a fish production of 140 kJ m^{-2} a^{-1}. It would seem that a major source of food for the invertebrates is allochthonous organic detritus (via micro-organisms) and that the fish consume about one third of the invertebrate production. A major component of the system could be dissolved organic matter, the throughput of which represents about half the total budget of organic matter. This study of small chalk streams thus supports the conclusions from the R. Thames project, that the energy dynamics of river ecosystems depend very much upon allochthonous inputs from terrestrial production or human activities in their catchments.

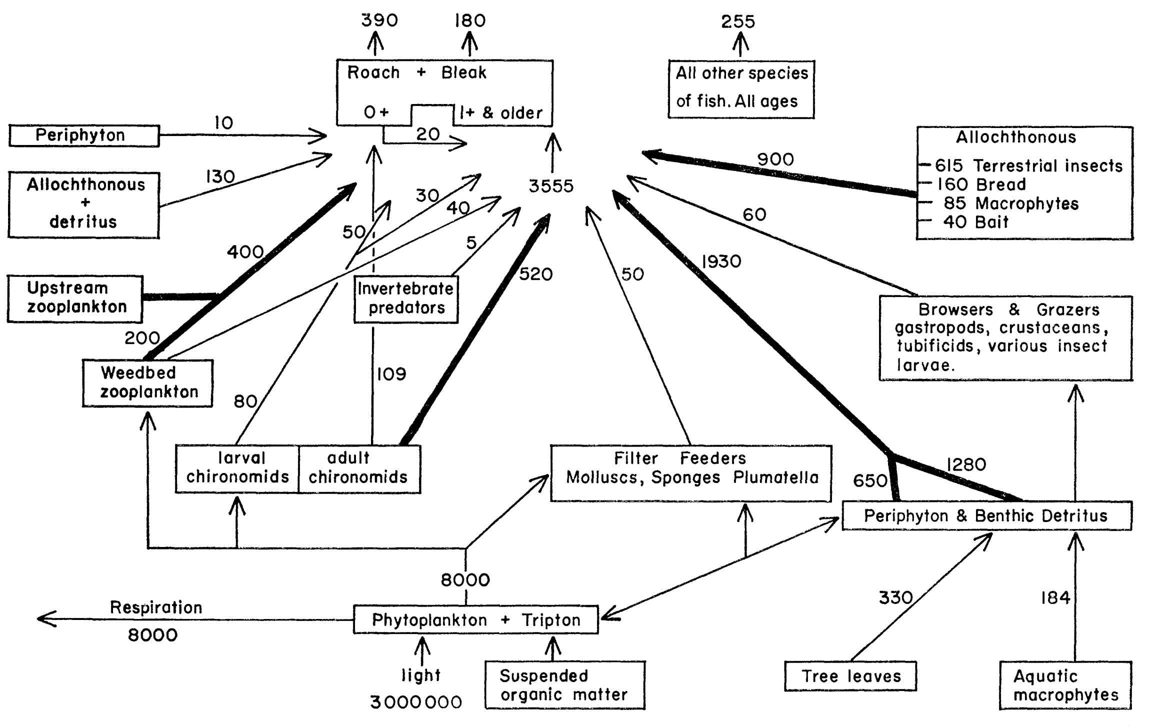

FIGURE 2. Energy flow chart for the River Thames below the R. Kennet mouth at Reading. The figures beside the arrows show estimates of energy flow in kJ m^{-2} a^{-1}; the heavy arrows show the larger channels of energy flow. (Adapted from Mann *et al.* 1952, Fig. 3, by kind permission of the authors, editors and publishers.)

Tjeukemeer

This Friesian lake is large (20 km^2) and shallow (2 m) so that it resembles Loch Leven morphologically. It differs, however, in having an unusual and complex hydrology (as it is connected with both a polder drainage system and the Ijsselmeer) and in its very peaty water. It has a high gross but low net primary production. The zooplankton production was studied as was that of benthic chironomids which had a very low production. Production of *Gammarus* and other invertebrates in the dense beds of littoral emergent macrophytes (*Phragmites communis* and *Typha latifolia*) may be important as a source of fish food. There are six dominant species of fish present in dense populations whose production may be food limited. The approximate rates of production in kJ m^{-2} a^{-1} were: primary production (gross) 1200, zooplankton 375, *Gammarus* 320, fish 45. In comparison with Loch Leven, Tjeukemeer appears to be much more

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stable biologically with rather consistent and typical seasonal periodicities in phyto- and zooplankton (Beattie *et al.* 1972; Golterman 1974).

The Thames Valley reservoirs

This project is of interest as it combines basic research on phytoplankton–zooplankton dynamics with the practical management of algal crops in storage reservoirs. An attempt was made to estimate the incoming and outgoing 'organic carbon fluxes' in terms of phytoplankton input and production, zooplankton production and grazing, and input and output of detritus (Steel, Duncan & Andrew 1972). In another paper Steel (1972) discusses the use of mixing jets in these storage reservoirs to maintain circulation of detritus and phytoplankton and perhaps practise zooplankton 'husbandry' as an aid to controlling phytoplankton populations by grazing.

7. The scientific achievements of the I.B.P.-P.F. programme

The original international P.F. programme planned to carry out intensive measurements of biomass and production at 'twelve to fifteen sites'. In the event, at the first summary and synthesis meeting in May 1970 results were presented from some thirty-six sites where more than one trophic level had been studied. At the second meeting, at Reading in 1972, about ninety data reports from different sites were deposited. In terms of effort then, the achieved programme substantially exceeded plans. Moreover, the sites were reasonably spread over the range of latitudes and types of lakes, from Char lake in the Canadian arctic, nearly 75° N, to Lake George on the equator, and from Tjeukemeer 1 m below sea level to Finstertaler See at 2250 m a.s.l. Inevitably north temperate lakes were over-represented and those from the tropics and southern hemispheres under-represented, as were ponds and especially rivers.

The extent and quality of the data available from the sites varied greatly. In spite of attempts to establish agreed methods, develop suitable new methods, and standardize the expression of results, there was considerable deviation in the details of methodology, the extent to which these details were adequately reported and the rigour and clarity with which the data reports were written up. This has rendered it difficult to make comparisons between many of the sites, especially when measures of statistical variation were rarely reported. On reflection, these shortcomings were largely inevitable. In making observations and experiments near the frontiers of knowledge, it will be necessary to improve and develop methodology to take advantage of new understanding of the processes being measured and new technology in measurement. Further, when measurements are made in new situations extrapolated beyond the limits of previous experience modifications of methodology are often essential.

For example, light and dark bottle measurements of photosynthesis and respiration were the most widespread and consistent observations made in the I.B.P.-P.F. This technique originated nearly fifty years ago, yet I believe it is not at all clear exactly what is being measured or estimated; indeed some plant physiologists would have us believe that the results are meaningless. Furthermore, the times of exposure and other details of the experiments may need to be adapted to suit particular conditions and the magnitude of the rates actually measured. Thus, even though this particular measurement may appear to be easy to standardize it may not be so simple to carry out in practice without experience and judgement, and the interpretation and synthesis of a wide range of data will not be easy. In international programmes this

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problem of standardization may be particularly acute, even if within certain countries, regions or research schools there is consistency in methodology.

The synthesis of the I.B.P.-P.F. data is not yet complete; the writing of the summary volume is nearly complete but its editing is only partially done. This volume will, however, represent only a small part of the results (and achievements) of the whole programme. The major part of these results will appear in the large number of individual scientific papers, some but not all of which have so far been published. I believe that it is fair to comment that the planning of I.B.P. grossly underestimated the share of the total effort that would be required for data analysis, interpretation, integration, writing up and publication. Some of this can be started only when most of the results from the individual projects have appeared in print. Nevertheless, I believe that a few further, more positive, generalizations are possible.

In the context of the rather vague and very simplistic trophic-dynamic model of aquatic ecosystems that was the start of the I.B.P., rather little in the way of understanding will result. The model has been shown to be far too simple to be realistic, particularly in the secondary trophic levels where the complexity, variability and flexibility of the food *web* has been revealed as very much greater than hitherto imagined. This also means that statements about the general behaviour of such a system are often 'untestable' (Rigler 1975). This does not mean that some generalized conclusions have not resulted from the I.B.P.-P.F. observations. For example, a general order-of-magnitude fall in production at each successive link in the food chain has been confirmed (e.g. phytoplankton to fish in Loch Leven). Experiments in fish ponds produced very high correlations between rates of primary production and fish yield (Wolny & Grygierek 1972); an elegant experimental demonstration that the trophic dynamic-system works!

Attempts to simplify the system by eliminating all but the major components, or by re-classifying the taxa into functional groupings have been only partially successful. Species have a reality in the ecosystem as each has particular adaptations and thus particular parameters for its functional relationships with environmental factors. The consequence of this has been seen in the I.B.P.-P.F. attempts at ecosystem modelling. The simplest and crudest of these models have had considerable success in simulating in very broad terms the major features of quite different lake systems. They have not yet, however, been very revealing in explaining how the whole system functions. Very considerable elaboration of these models has not yielded a comparable increase in either accuracy of simulation or understanding. One particular aspect of this merits further comment. It is a feature of phytoplankton periodicity in lakes that a regular pattern of species and 'blooms' may be followed over a series of years, but then unexpectedly a new or rare species replaces one of the regular dominants and imparts quite a different character to that year's pattern. This phenomenon, understandably, cannot as yet be modelled. For example, it would have been very difficult to predict the behaviour of the phytoplankton in Loch Leven in 1968 when the early summer was dominated by a species new to science! These comments do not mean that all forms of models have proved unsuccessful. Some detailed models based on functions that describe fundamental processes have been developed and proved to work well. One example is Talling's (1957) model of photosynthesis in phytoplankton in relation to physical environmental factors, and this model has very widely proved its value.

What the attempts at modelling and much other I.B.P. work have shown, however, is that it is difficult in ecology to take short cuts and avoid the need for sound detailed basic information on taxonomy, life histories, ecological physiology, behaviour and population dynamics. There has also been ample demonstration that observation alone is not enough. Some of the most revealing results came from relatively simple experiments closely associated with field observations. An example of this is Dr Moriarty's work on the assimilation of algae by the fish in Lake George (Moriarty 1973).

This leads to one final comment in the context of the original concept of I.B.P.-P.F. This was the idea that a wide series of observations on the structure of the trophic system and its dynamics as measured by production at certain points would alone reveal how the system functioned and in particular (though this was never stated) its controlling mechanisms. In hindsight this was a quite unwarranted assumption; a much more experimental approach was needed to achieve this.

8. Some other features and achievements

No account of the I.B.P.-P.F. would be complete without mention of its organization, the meetings, symposium volumes and handbooks.

The full international sectional committee necessarily met rather rarely. After the initial planning meetings in the preparatory stage, much of the activity of the section was left to the initiatives of the individual teams actually doing the research. Central guidance and coordination was carried out by the Convenor, a small group of the more active members of the committee, and especially the very active Scientific Coordinator. This small, functional 'executive group' exercised control during the final stages of the programme, and, on the whole, worked relatively effectively. A vigorous full-time coordinator is obviously an essential for such a programme. I do not think that P.F. solved the problem of balancing efficient executive decision with democratic representation and individual initiative, particularly as some of the rather senior people who served on the international committee tended to be out of touch with both the latest ideas in their science and with the teams of rather young people actually doing the research.

This was, in some measure, remedied by the series of general meetings at most of which there was good representation of the active researchers. The first series of these meetings was convened to prepare methodological handbooks. Five of such handbooks were produced on primary, fish, secondary and microbial production and chemical methods. A sixth, rather different, handbook – *Project Aqua* – listed freshwater sites warranting conservation. These handbooks were written by one, two, or a group of authors. Three of them have had revised editions and have been the 'best sellers' in the I.B.P. Handbook series. Perhaps this is because they happened to meet a wide demand, but also I believe because they were well conceived, edited and coordinated and were the products of an effective combination of lively symposium meetings and good committee work followed by skilled editing. Some of these meetings also produced valuable symposium volumes which proved useful reviews of the 'state of the art', especially in relation to methodology.

The working meetings at Kazimierz Dolny and Reading were an essential part of the I.B.P.-P.F. programme. They provided opportunity at a moment in the latter part of the field programme and again in the 'writing up' period, for reporting, comparisons between preliminary results, free and unstructured discussion, and direct contact between the organizing committee and individual researchers. Their practical, formal and direct achievement was limited, but they served to bring more coherence to the whole programme and, above all, to transfer ideas, stimulus and enthusiasm by personal contact. They also demonstrated the particular skills in organization and communication needed at such meetings. It is appropriate here, in the context of a U.K. meeting, to emphasize the value of the support provided by the Royal Society, the hard work of the I.B.P.-P.F. central office, and the hospitality and skills in organization provided by Reading University at two of the largest I.B.P.-P.F. meetings.

In conclusion, what lessons have we learnt for future international exercises such as I.B.P.-P.F.?

There is little doubt that if it is viewed as a coordinated programme of scientific research aimed at answering specific scientific questions, I.B.P.-P.F. was inadequately conceived, planned, organized and controlled. The questions asked required much more careful formulation and definition. The methods needed more precise standardization and more rigorous checking and control. Much more sophisticated data collection, analysis and collation should have been organized and very much more time and effort should have been allowed for synthesis and writing up.

But, I have no doubt, either, that if such a well controlled programme had been followed, by the time it was completed the original scientific questions asked would have ceased to have much relevance. Further, many of the conclusions, because of the rigid framework in which they had been derived, would have been misleading. The I.B.P.-P.F. programme collected many irrelevant or inaccurate data but also a great many valuable ones. It generated new ideas and, above all, trained a new cohort of vigorous young scientists well versed in field work, team work, personal international friendship, and the spirit of original enquiry. It certainly expanded the horizons of limnology, and this science will never be the same again.

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Discussion

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referred to the somewhat drastic changes which had overcome the biology of Loch Leven during the period of investigation and asked whether similar changes had been observed in other shallow lakes such as the Neusiedler See which had been investigated under the I.B.P. He suggested that such changes were characteristic of shallow lakes rather than deep ones which maintained a higher degree of ecological stability. He enquired also whether there might be a relationship between the changes in Loch Leven, especially in phytoplankton, and the changes in pollution status of the affluent streams during the period of intensive observation.

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Several biological changes were observed in the study area of the River Thames during the I.B.P. Project. The substratum along the north bank altered; the submerged macrophytes *Nuphar lutea* and *Sparganium simplex* increased their distribution considerably; the composition of the benthic chironomid fauna changed; the population of roach (*Rutilus rutilus*) declined dramatically; and changes were recorded in the food taken by roach. The changes observed in Loch Leven and the River Thames demonstrate the need for long-term ecological studies. I.B.P. has achieved notable progress in describing the structure of aquatic ecosystems. It has started to investigate the functional relationships within the systems and the factors which influence them. If we are to progress to the next level of understanding we must ensure that research teams are able to carry out long-term investigations at suitable sites.