THE FRESHWATER BIOLOGICAL ASSOCIATION AND THE INTERNATIONAL BIOLOGICAL PROGRAMME (1961-1976)

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In 1962 I reviewed the primary productivity of the major types of vegetation in terms of tonnes of organic matter per hectare per year (Westlake 1963), and speculated that 'Comparative morphology was once the dominant form of biological investigation, and enabled great advances in knowledge to be made. Perhaps comparative productivity may become as important for the future of ecology'. At that time I was unaware that within the International Union of Biological Sciences discussions were taking place (Worthington 1975) which were to lead to fifteen years of activity and research on 'the biological basis of productivity and human welfare', stimulated and organized by the International Biological Programme (IBP). Aided by this programme, we now have a good idea of the magnitude of productivity in different types of ecosystem and much more knowledge of the ways in which energy flows within ecosystems from the sun, through green plants to bacteria, fungi and animals (Cooper 1975), but it is doubtful if we have yet achieved the kind of profound generalizations that developed from comparative morphology over a century ago.

The IBP operated in three phases: preparatory, operational and synthesis and the FBA has played a part in all three. This review will briefly consider the FBA's contribution to the preparatory and synthesis phases and then discuss in more detail the scientific results from the two projects on whole ecosystems with which it was directly involved, comparing these with two other projects where the involvement was indirect.

Preparatory phase.

This consisted of a great deal of consultation and committee work and members of the FBA took an active part in both national and international contexts. It was to be expected that their advice should be sought as the Association is one of the established and active freshwater research institutes. Moreover, at that time, the initial research programme of the River Laboratory was being planned around the production ecology of chalk streams, so there was naturally an interest within the FBA in one of the main themes of the IBP. The UK contributions to the IBP were organized by the Royal Society which set up a series of committees. The Productivity of Freshwaters (PF) Subcommittee was chaired first by Dr J. W. G. Lund and later by Mr E. D. Le Cren, and had several other members of the Council and staff of the FBA serving on it. There was also a committee to steer the joint UK-Ugandan project on Lake George (see below). Dr J. F. Talling was a member of this committee, which asked the FBA to administer the project on behalf of the Royal Society. The appointed members of the research team became temporary members of the FBA staff and received much of their training, and later guidance, from the Ferry House staff, especially Talling.

The preparation of manuals of methods was an important part of the preparatory phase, during which Le Cren jointly organized a conference with Reading University on methods for fish populations. Dr T. B. Bagenal contributed to the resulting 'best-selling' handbook and more recently has edited the third edition (Bagenal 1978). Dr A. F. H. Marker, Talling and Mr D. F. Westlake contributed to the manual on primary production, the two latter also assisting with the editing of both of its editions (Vollenweider 1974). Westlake contributed a paper to a symposium volume on methods for measuring the productivity of underground parts of plants (Ghilarov et al. 1968), and Dr G. Fryer, Dr M. Ladle, Mr H. Casey and Mr J. Heron helped in the preparation of the manuals on secondary production (Edmondson & Winberg 1971) and chemical methods (Golterman, Clymo & Ohnstad 1978). Throughout the IBP, discussions continued on terminology with FBA staff playing an active part, culminating in a working group chaired by Le Cren, which published recommendations (SCIBP 1975).

Operational phase.

The IBP/PF programme was divided, somewhat arbitrarily, into the 'main programme' and the 'supporting programme'. The main programme consisted of projects that had been planned specifically for the IBP, whereas the supporting programme was made up of research projects that would have taken place anyway, but which could be usefully linked into the IBP. Among the former the Lake George project in Uganda has already been mentioned. Another was carried out by the Nature Conservancy and Scottish Universities on Loch Leven. Lund was the chairman of the steering committee for this project and there were other informal links with the FBA. A third was organized by Reading University on the River Thames. This had several links with the River Laboratory and was supervised by Le Cren during a short interregnum after Dr K. Mann left and before Dr A. D. Berrie took over. Dr H. Golterman, a Council member, led a Netherlands project on Tjeukemeer, which became closely linked with the UK through a group of British zoologists.

Much of the work of the River Laboratory became part of the supporting programme. Apart from this and the Thames project, there were very few extensive studies of rivers in IBP/PF. Several of the research projects at The Ferry House became part of the supporting programme, notably the work on algae in Blelham Tarn and Esthwaite Water (e.g. Lund 1971; Talling 1971; Lund, Jaworski & Butterwick 1975), fish in Windermere (e.g. Bagenal 1977; Craig et al. 1979) and algae in the Shropshire Meres (e.g. Reynolds 1972, 1973, 1979). In addition Miss V. G. H. Collins, her research student Miss B. T. D'Sylva, and Dr J. H. Baker (before he joined the FBA staff) contributed to tundra microbiology as part of the Terrestrial Productivity programme (Holding et al. 1974; Collins, D'Sylva & Latter 1978).

During the operational phase several members of the FBA staff took part in international visits and discussions, which became more frequent as the synthesis phase approached. Some members participated in overseas research, e.g. Mr W. J. P. Smyly helped the IBP project on the Kličava Reservoir in Czechoslovakia.

Synthesis phase.

The IBP was planned to culminate in the editing and publication (by the Cambridge University Press) of a series of volumes which would bring together and 'synthesize' the information gained in all the projects, much of which was being published in detail in ordinary scientific papers. As a first step a series of international meetings were held. In the PF Section these were at Kazimierz Dolny (Poland) in 1970, Pallanza (Italy) in 1972 and Reading (England) also in 1972. At the last, which was organized largely by Dr Rzóska, Berrie and Le Cren, the basic information gained from nearly all the sites was summarized in a series of 'Data Reports' (the originals are now kept in the FBA library). After several editorial workshops the PF programme has been synthesized in a single volume (Le Cren & Lowe-McConnell, in press), to which several members of the FBA staff have contributed. In particular Marker and Westlake wrote several sections of the major chapter on primary production, the whole of which was edited by Westlake.

Talling edited and summarized the text on aquatic plants in a synthesis volume for the Production Processes (PP) section (Cooper 1975), which includes chapters on freshwater microphytes by Talling and on freshwater macrophytes by Westlake. In working on wetlands the PP and PF sections overlapped. Preliminary meetings at Tulcea (Romania) in 1970 and Mikołajki (Poland) in 1972 paved the way towards a synthesis volume on wetlands, for which Westlake is a joint editor and contributor.

Lake George.

The IBP investigations, summarized by Greenwood (1976), are compared with results from Loch Leven, which are summarized by Morgan & McLusky (1974).

Text-book descriptions of lake biology have been based largely on deep temperate lakes, so Loch Leven, which is shallow, and Lake George, which is shallow and in the tropics, were well chosen to upset conventional ideas. In the 'typical' deep temperate lake the long period of cold and low light in the winter, if accompanied by mixing, allows nutrients to be distributed throughout the water column. The annual productivity of the lake can often be related to the winter concentration of nutrients. In the

spring, light, warmth and the onset of stratification enable vigorous growth of algae which often exhausts the nutrients, a large proportion of which sediments into the hypolimnion and is unavailable until the winter mixing occurs. After the nutrient depletion there are sporadic growths of various algal species during the rest of the summer which may not show such regular patterns. The invertebrates, largely with short life cycles, are tied to these fluctuations in food supply, and the vertebrates, often carnivores, are correspondingly controlled by food shortages.

The contrasts with Lake George are great. Here the cycle of mixing, nutrient increase, growth, stratification and exhaustion is a daily event (Viner & Smith 1973). A high gross algal production and a moderately high net production are maintained all the year (see Tilzer et al., Fig. 5.8, in press; Hammer, Table 5.19, in press, for comparisons with other lakes), yet the concentrations of inorganic nitrogen and phosphorus are always very low (Ganf 1974). The high productivities appear to be attained by the continuous maintenance of a dense phytoplankton biomass (Ganf 1974), by some recycling of nutrients from the easily disturbed sediments (Viner 1975), and particularly by the rapid recycling of nutrients from dead and consumed phytoplankton as their organic matter is degraded by bacteria and zooplankton (Ganf & Blažka 1974). The phytoplankton biomass often approaches the theoretical maxima predicted by models that relate biomass and production to the incident irradiance, its attenuation by materials in the water, and self-shading by the phytoplankton. Starting from a low population, the denser the population the greater the production per unit area until an optimum population is reached. Further growth would increase the proportion of the population that is so shaded that net photosynthesis is not possible. This part of the population would continue to respire and the net production, and growth of the whole population would cease. The equilibrium population observed in Lake George fits well with that predicted by Talling's model (Ganf & Viner 1973). The predicted values depend on the observed ratio of gross photosynthesis to respiration, which can be affected by nutrient supply and light transmission through the water, both greatly influenced by sediment disturbances. These factors probably cause many of the observed fluctuations in phytoplankton biomass. In Loch Leven comparable, high phytoplankton populations occur occasionally, but there are great fluctuations in density and species composition from month to month and year to year (Bailey-Watts 1978). As in Lake George, mixing, disturbance of sediments and self-shading are important factors but temperature, silicon and phosphorus concentrations, parasites, protozoan grazing on sedimented algae and competition are also involved at times (e.g. Bailey-Watts & Lund 1973).

Like the phytoplankton, most of the planktonic and benthic populations of invertebrates and the fish populations in Lake George are remarkably constant, with all stages and sizes continually present (Burgis 1971; Dunn

1975; Darlington 1977). The productivity of these populations is fairly high but not exceptionally so (Burgis 1974; Gwahaba 1975), and invertebrate populations in Loch Leven often reach a higher biomass during the growing season.

Lake George lacks abundant submerged macrophytes (Lock 1973), as does Loch Leven. The explanation seems to be similar in both cases. Macrophytes are limited upwards by wave action and cannot survive at depths where there is insufficient light to support photosynthesis. Where a good supply of nutrients encourages a dense phytoplankton, and shallowness allows wind to disturb the sediment, the light transmission is so poor that these two limits leave no lake bottom suitable for macrophytes. The only difference is that in Lake George much of the nutrients comes from rapid recycling but in Loch Leven the inflow and annual recycling are more important.

It was expected that the phytoplankton would be only an indirect food source for the major invertebrate and vertebrate populations because it was originally assumed that these species could not digest blue-green algae. However a series of elegant studies (Moriarty et al. 1973) showed conclusively that, in Lake George, both the dominant zooplankter *Thermocyclops hyalinus* (a copepod), and the dominant fish *Sarotherodon (Tilapia) nilotica* and two species of *Haplochromis* (herbivorous cichlids), are capable of digesting the phytoplankton organisms, and that these form the major part of their diet. The supply of this food greatly exceeds the demand, so other factors limit their populations (Ganf & Viner 1973). In the case of *Thermocyclops* these factors are probably a shortage of algal species small enough to be eaten by their early developmental stages (Burgis et al. 1973)and predation by *Chaoborus* (Burgis 1971). Similarly the fish are likely to be limited by the scarcity of sufficient firm substrata suitable for spawning, but the intensive fishery, with ever-decreasing size limits, may also be important (Gwahaba 1975).

Loch Leven proved to be remarkably unstable. There are rapid and unaccountable changes in nitrogen and phosphorus. For a long time the macrophyte vegetation has decreased and the species have changed, yet there are now signs of recovery. The phytoplankton has fairly consistently become less dense, but from year to year and season to season a considerable variety of algal species dominate with little repeatable pattern. The zooplankton was initially dominated by *Cyclops strenuus abyssorum* but now *Daphnia hyalina* var. *lacustris*, a species absent since 1959, is codominant. *Endochironomus* disappeared from the fauna between 1967 and 1970 and many other benthic invertebrates changed in abundance. The brown trout catches fluctuate from year to year. This contrasts with the remarkable stability of species composition, population density and productivity in Lake George. However there are indications that this can be easily disturbed over short periods. Then deoxygenation and fish kills are widespread and even the algal populations are reduced (Ganf & Viner 1973). However, large changes in the environment, whether they are diurnal or prolonged for a few days, do not last longer than the generation time of the organisms. This means that the organisms that dominate are those specialized to resist large rapid fluctuations (Ganf 1974). In temperate lakes conditions generally change more slowly, giving time for a variety of organisms to build up populations suited to each range of conditions. Therefore the apparent biological stability of Lake George is very dependent on the special stability of the local climate and hydrology and could easily be changed by interference with the catchment. Historically, as determined from sediment studies (Viner 1977; Haworth 1977), the current stability seems to have been established for a long time and was preceded by a long sustained increase in fertility.

English Chalk Streams.

Westlake et al. (1972) have summarized the IBP studies at these sites. The findings of the project on the River Thames, described by Berrie (1972) and Mann et al. (1972), are compared with these results.

The chalk streams of southern England are also fertile. Their swift-flowing clear water has relatively high concentrations of nutrients, but since they are short the water stays in the river for only one to seven days and there is no time for phytoplankton to develop. Macrophytes and benthic algae are the dominant primary producers. By comparison the River Thames is slower, deeper, and much more turbid. When the water reaches Reading it has been in the river long enough for a phytoplankton to develop and at Reading the depth and turbidity restrict macrophytes to a narrow littoral band (Berrie 1972). Both rivers are subjected to extensive interference by man, including bank maintenance and some dredging. In the chalk streams the water plants are cut regularly, the sources are converted into water-cress beds (Crisp 1970), water is abstracted, the catchment is fertilized and some small effluents, largely organic in origin, are discharged (Casey & Newton 1973; Casey 1977). In many cases, fish for angling, especially trout and sometimes salmon, are stocked. The Thames is a navigable river with locks and receives the well-treated domestic and industrial effluents from several towns.

In the River Frome each of two weed-cuts every year removes up to 900 tonnes (fresh wt) of water plants, mostly water crowfoot (*Ranunculus penicillatus* var. *calcareus*) from 43 km of river (Westlake 1968). In the upper part of the Bere Stream the behaviour of this plant was studied when management was stopped. It was found that it dies down naturally soon after the time of the first main river cut, and does not regrow that summer. Furthermore, after several years the maximum biomass reached each year fell so low that it was unlikely that management would be needed again (Dawson 1976). The natural growth pattern of this plant is noteworthy; it makes appreciable growth in the autumn, overwinters as healthy green shoots and starts vigorous growth very early in the year. After flowering, which occurs progressively later downstream, it ceases growth and dies back (Dawson 1976). The annual production exceeds the seasonal maximum biomass by 16% as a result of autumn growth and losses of leaves and shoots before the maximum is reached. The growth pattern is crucial to many aspects of chalk-stream ecology, but its control is not yet clear. High temperatures and low flows seem to lead to poor growth, but an 'internal clock' appears to fix the time of flowering of different strains (Dawson, in press).

In the upper reaches emergent plants are often co-dominant, especially water cress *(Nasturtium aquaticum)*. Typically this becomes established only in late spring, when drifting fragments can become trapped on beds of *Ranunculus*, which reach the surface when the flow starts to fall. Once established it grows rapidly and smothers the *Ranunculus* as that dies back, so that healthy *Ranunculus* often survives only at the edges of the *Nasturtium* stands. Autumn floods wash away the *Nasturtium* and new *Ranunculus* beds develop at different sites. The two species and the hydrology interact so that in a sequence of average years, good years for their growth alternate with bad ones, but the timing of the autumn floods and the occurrence of late spring floods can switch the cycle into a new sequence (Ladle & Casey 1972; Dawson, Castellano & Ladle 1978). As *Nasturtium* spreads it soon achieves a stable biomass where it is established, because continuous growth is balanced by leaf and stem losses and very rapid decomposition. Hence the annual production is about three times the maximum biomass (Castellano 1977).

Nutrients appear to be unimportant as factors limiting plant growth in chalk streams. The amount supplied is nearly always far in excess of the plants' demands (Casey & Westlake 1975) and the internal concentrations exceed those required for optimum growth (Casey & Downing 1976).

The benthic algae also show a maximum biomass in spring, dominated by diatoms (Marker 1976a), with algal cover similar to that of productive lakes like Lake George (*c*.300 mg chl. *a* m^{-2}). During the summer the populations fluctuate and they are at a low level in the winter. Summer populations are often composed of green and blue-green algae, especially lime-encrusting forms, but occasional periods of high biomass of diatoms or filamentous algae are seen, especially of *Vaucheria* in the autumn. Thus there is a general pattern of biomass and community structure similar to that observed in many temperate lakes, including Loch Leven, yet the environmental conditions are very different. Certainly silicon deficiency is unlikely to terminate the spring diatom bloom, and similar patterns of growth occur near the springs where the temperature is almost constant. Productivity shows no great difference during and after the diatom bloom. There are indications that light limits net photosynthesis, and hence the rate

of accumulation of biomass in winter and early spring, and that grazing, especially by the larval chironomid populations that develop late in the diatom bloom, may keep the biomass low in the summer (Marker 1976b; Pinder 1977). Annual net production by benthic algae is probably similar to that of submerged macrophytes, but is very dependent on the area of gravel left exposed by macrophyte growth (Westlake et al. 1972). Nothing is known about the productivity of epiphytic algae, which may well be similar at some times of the year. In the Thames most of the bottom is too dark for algal growth but there is a vigorous phytoplankton of diatoms in the growing season that accounts for most of the primary production.

One of the outstanding features of both river projects is the enormous amounts of dead organic matter (detritus) involved, which may be dissolved, suspended or in mobile sediments. In the Bere Stream at Bere Heath, at any instant in midsummer, there are 2·3 kg org. wt m^{-2} of fine detritus (presumably including bacterial and fungal biomass) and dissolved organic material. This may be compared with a total biomass of plants and animals of about 0·4 kg m^{-2} and a total annual productivity of about 0·82 kg m^{-2} (Westlake et al. 1972). At the downstream end of the Bere Stream about 128 t of organic matter are exported every year, about 40% of this as dissolved material, and it was estimated that a further 30 t are lost in the system by respiration, making an estimated total input of 158 t. Primary production in the river itself can account for only a little over 10% of this input and leaf fall and other known sources outside the main river only add a further 25%. About 10% comes from dissolved material in the source water. The balance (55%) probably comes from a number of fairly small but concentrated sources, such as land drains and minor effluents, and this is a point of further investigation. However it appears that much of the material in large terrestrial inputs may be well decomposed by the time it reaches the river and that more readily decomposable local sources like tree leaves, algae and higher plants are the main sources of energy for secondary production. Similarly in the Thames the fish and invertebrates were estimated to use about 70 g m^{-2} yr^{-1} of organic material entering the Reading reach from the banks and about 500 g m^{-2} yr^{-1} of suspended material, including phytoplankton, while some 4000 t passed through the reach each year.

The invertebrate populations of chalk streams include oligochaetes, crustaceans, trichopterans, chironomids and simuliids. There is no zooplankton; the populations are benthic or epiphytic. At Bere Heath, in terms of biomass, in decreasing order of total population density, *Rorippa* beds are dominated by *Gammarus pulex*, a small oligochaete *(Stylaria lacustris)* and chironomid larvae; mud contains mostly tubificid worms (especially *Limnodrilus hoffmeisteri*); *Ranunculus* stands have chironomid and simuliid larvae, and exposed gravel is dominated by *Gammarus* with trichopteran larvae (Westlake et al. 1972; see also Pinder 1977). Hence the total invertebrate populations of stretches of chalk stream are very dependent on plant growth, which controls the size and distribution of the different habitats. As is typical in temperate waters, many species have several short-lived generations during the warm season, but there are some longer-lived species that reproduce for much of the year.

Most species appear to be detritus feeders, though some, especially some of the chironomids, probably graze diatoms. Total invertebrate productivity is estimated to exceed algal productivity (Westlake et al. 1972). The *Ranunculus* beds provide a large surface area which supports drift-feeding larvae, especially *Simulium equinum* and *ornatum*, and enables them to exploit the suspended organic matter. It was estimated that in the summer these larvae would ingest nearly 1 g C m^{-2} d^{-1} to grow at only 15 mg C m^{-2} d^{-1} (Ladle et al. 1972); this low conversion rate is further evidence that suspended organic material is not a good food source. The peak population is estimated to be able to remove all the suspended matter in 0·6 km, if there were no inputs and no resuspension of faecal pellets. In the River Thames the suspended organic matter is exploited by a very different population, composed of long-lived bivalves, Porifera and Polyzoa, which dominate the biomass and production of the whole invertebrate fauna.

Chalk streams are regarded as brown-trout waters *(Salmo trutta)* but small fish are often more important in terms of biomass and production, especially *Cottus gobio*, *Phoxinus phoxinus* and *Noemacheilus barbatulus*. Thus, at the Bere Stream IBP site, the trout present are nearly all in their first year and account for only 7% of the total fish production, while over 80% of the production is by bullheads *(Cottus)* (Mann 1971). At a deeper site, not far downstream, the proportions are 37% *Salmo* first to third year fish and 43% *Cottus* first and second year fish, and generally there are considerable differences between sites and rivers. Although growth occurs throughout the year it is much slower in the winter months.

Further downstream larger coarse fish, including roach, dace and pike are found. Successful year classes are very prominent. The roach *(Rutilus rutilus)* and dace *(Leuciscus leuciscus)* have low populations, but grow well, feeding on the rich invertebrate fauna (Mann 1973; 1974). As in Lake George the lack of suitable spawning sites and shelter for young fish, rather than food, are probably the main limiting factors. The pike *(Esox lucius)* also grow well (Mann 1976) feeding mainly on cyprinid fish, especially the abundant minnows *(Phoxinus phoxinus)* and dace. The mild climate of chalk streams, especially their relative warmth in winter, favours the growth of pike, and probably the other fish as well.

Although the Thames would be called a coarse fish river and the populations of roach, dace, perch *(Perca fluviatilis)* and bleak *(Alburnus alburnus)* are extremely high, size and growth are less than might be expected, except for the bleak. Successful spawning, and no pressure from fisheries, lead to

intense competition for food. More than 10% of the food of bleak is contributed by anglers' bait.

More than eighty FBA publications are related to these contributions to the International Biological Programme, culminating in the volume synthesizing freshwater productivity edited by Le Cren & Lowe-McConnell (in press). As in much IBP research, these projects have emphasized the importance of dynamic phenomena in understanding aquatic ecology, such as weather, flow, throughput, metabolic responses, nutrient recycling, competition and population variability.

It is encouraging that in some of these projects, and in many others in the programme, models have provided satisfactory quantitative accounts of the behaviour of specific parts of the ecosystem. However more general models have been less successful, usually being unable to cope with the prediction of change in species and of the size, distribution and variation of niches favouring particular species. The studies of rivers have emphasized the predominance of organic matter originating outside the system and our lack of knowledge about the use made of this material. They have also drawn attention to the need to look at water bodies, even large lakes, as part of their catchment. The work of IBP has shown the value of co-operation between scientists of different nations and of organized teams tackling all levels of ecosystems, producing results that fit together and which can be compared with similar results. These cross-comparisons might have been easier if standardized methods and concepts had been enforced, but it is also clear that such an approach would have inhibited originality in recognizing and investigating the many important topics which were under-emphasized or unrecognized when IBP started.

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