Chapter (non-refereed)

Bailey-Watts, A.E.; Jones, D.H.; May, L.; Kirika, A.. 1983 The plankton ecology of Loch Leven. In: ***Annual Report of the Institute of Terrestrial Ecology 1982.*** **NERC/ITE, 14-19**

species produce adequate supplies of long-lived seeds, it is possible that their performance could be improved by replacing unimproved seed with blends of selected clones.

If negotiations are concluded successfully, this problem will be investigated by a Regional Project embracing Sierra Leone, Liberia, Ivory Coast, Ghana, Nigeria and Cameroon, a set of countries spanning many of the natural ranges of the species already mentioned. It is intended to have a phased programme of development in which the immediate implementation of existing knowledge about *T. scleroxylon* will be the focus of Phase 1, followed by a consideration of species of *Lovoa*, *Nauclea* and *Terminalia* in Phase 2, and species of *Khaya*, *Entandrophragma* and *Chlorophora* in Phase 3. However, in searching for superior clones, sometimes with tolerance to pests (eg to stem borers in *Entandrophragma* and *Khaya*), attention will not be diverted away from the development of more appropriate silvicultural practices than the oft-exploited methods of clear-felling. The conservation of trees should be linked with the conservation of water, soil, flora, and fauna, while retaining commercial advantages.

R R B Leakey and F T Last

Freshwater and marine ecology

THE PLANKTON ECOLOGY OF LOCH LEVEN

Why study plankton?

Populations of plankton are an important part of our natural environment. In energetic terms, the primary (photosynthetic) production of some lake ecosystems (Le Cren & Lowe-McConnell 1980) compares favourably with that of the most productive systems of all, tropical rain forests (see, for example, Odum 1971). Production at secondary and tertiary levels (herbivores, carnivores) is correspondingly high. Consequently, freshwater systems have considerable potential as a source of food for man, especially in Third World countries. To utilize this resource to the full, we need to understand the factors which control plankton species composition and abundance.

Man also depends on freshwater lakes for domestic water supply, power generation, irrigation, fisheries and tourism. As water quality is affected by the plankton it contains, it is, again, important that plankton be assessed and its behaviour understood.

The composition and abundance of plankton populations change rapidly. Plankton thus provides almost unlimited opportunities to study a wide range of ecological relationships over shorter periods than are possible with higher organisms with much longer life cycles.

Why study Loch Leven?

Until relatively recently, most of our limnological knowledge was based on deep stratifying lakes, and only in the last 15 years have shallow well-mixed water bodies received much attention. Nevertheless, these 2 types of lake are very different. Deeper lakes generally show a well-defined annual cycle of overturn and stratification, which tends to reduce variability within the system. In contrast, shallow exposed lakes respond rapidly to changing weather conditions, and are rather less predictable in their behaviour. Loch Leven is a good example of this type of lake.

The study of community ecology in Loch Leven has several advantages over similar studies in deeper stratifying systems. First, fewer samples need to be taken to obtain reasonable estimates of population densities, thus reducing the need for extensive, time-consuming spatial surveys and allowing sampling at more frequent intervals. Second, uniformity of the environment from which samples are collected simplifies data interpretation, particularly with respect to temperature and oxygen saturation. For example, it is almost impossible to estimate temperature-dependent rate coefficients for populations which constantly migrate through a temperature gradient. Finally, in deeper lakes, there are numerous problems in studying the population dynamics of organisms in an epilimnion which is periodically diluted by hypolimnetic water during storm conditions. These problems do not arise in shallow well-mixed lakes.

Loch Leven is also a valuable site for investigating the effects of eutrophication (nutrient enrichment). Enrichment has increased in recent years as a result of the more intensive use of agricultural fertilizers on surrounding farm land, and the increased discharge of treated sewage into the loch. Annual nutrient loadings of 2·0 g N and 0·2 g P per square metre of loch surface have been recorded. Such levels are classified as 'dangerous' for shallow lakes by Vollenweider (1968).

In Loch Leven, many biological changes have been recorded which appear to be associated with eutrophication. Walker (1970) and Johnson and Walker (1974) describe long term changes in the zooplankton, including the disappearance of the cladoceran *Daphnia hyalina* between the mid-1950's and 1970. Maitland and Hudspith (1974) comment on the decrease in species diversity of bottom-living invertebrates, especially insects, while Morgan (1974) notes the disappearance of one species of fish (the charr, *Salvelinus alpinus*), and Jupp *et al.* (1974) describe changes in the rooted vegetation. Concern over these changes and their possible effect on the world-famous brown trout fishery and wildfowl populations earned Loch Leven the status of National Nature Reserve in 1964.

In 1967, the loch was chosen for special study as a UK contribution to the International Biological Programme (Royal Society 1967). The research emphasized productivity measurements, with the main effort in plankton studies concentrating on phytoplankton, associated physical conditions, and water chemistry. Since then, the work has continued and a virtually unbroken record of 15 years' data is now available. Crustacean zooplankton records are less continuous, with only 2 short studies before 1974 (1969-70, 1972-73). Since then, however, the records are complete. A detailed study of the Rotifera was started in 1977.

Methods

In general, 2 fixed stations (Figure 5) have been sampled at more or less weekly intervals, as weather permits. However, in some years, the sampling has been fortnightly from November to February. This short interval sampling schedule is necessary because plankton communities change rapidly, especially at higher water temperatures.

To provide sufficient data for the detailed analysis of complex interactions within the plankton, an extensive sampling programme must be maintained. The meteorological, physical, chemical and biological parameters routinely measured are summarized in Table 5 with some notes on techniques. Further details of the methods can be found in the literature cited.

Results

In the long term, our sampling programme has revealed several important trends. One of the most striking examples concerns the disappearance of *Daphnia hyalina* (see above). The return of this species to the loch was marked by the collection of a single individual in 1970. In 1971 and in subsequent years, the species was abundant, and population maxima of 75-100 individuals l^{-1} were regularly recorded (Johnson & Walker 1974; D G George, D H Jones, unpublished data).

A general decline in phytoplankton abundance has also been recorded (Bailey-Watts 1978, 1982). Mean annual chlorophyll values of 35 mg m^{-3} from 1979-1982 contrast markedly with concentrations of 80 mg m^{-3} for the period 1968-1971 (Figure 6). In addition, certain chemical features have changed; nitrate levels have increased over the past 14 years, while phosphorus loadings have decreased significantly (Holden & Caines 1974; Holden 1976; L A Caines, R Harriman and A Kirika, unpublished data).

The changes in zooplankton, phytoplankton and chemistry described above are undoubtedly interrelated. For instance, it is likely that the long term decrease in algal biomass is due, at least in part, to reduced phosphorus

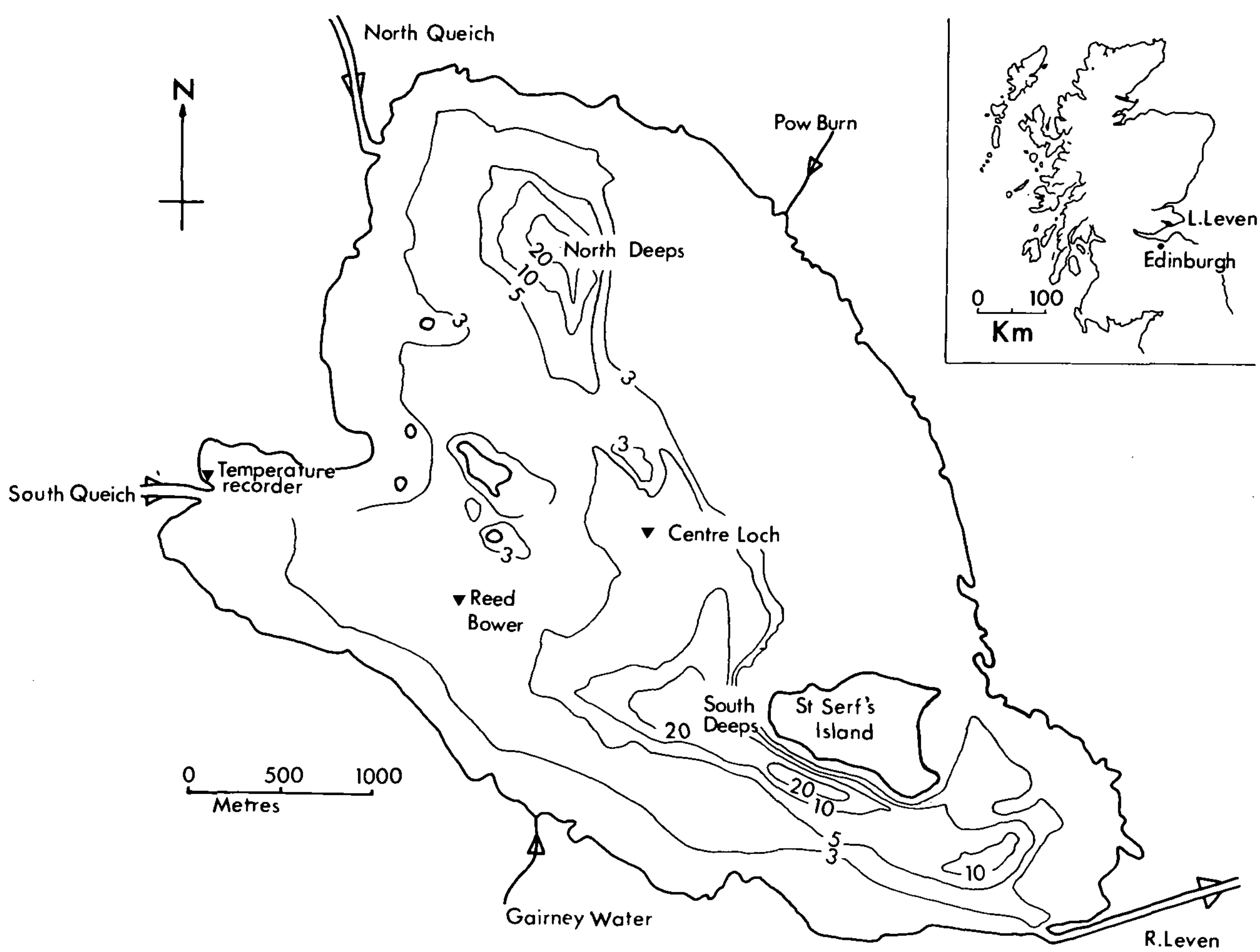

Figure 5 Map of Loch Leven showing the position of inflows, outflow, the 2 main sampling stations (▼) and major depth contours (in metres): inset shows the position of the loch in Scotland.

Table 5. Parameters measured and techniques used in the routine surveillance of Loch Leven plankton

	Parameter measured	Technique	Reference
Meteorological	Wind speed	(i) Continuously recording anemometer (ii) Visual assessment according to Beaufort scale	Smith 1973
Meteorological	Wind direction	Visual assessment	
Meteorological	Cloud cover	Visual assessment in accordance with Meteorological Office scale	
Meteorological	Solar radiation	Continuously recording solarimeter	
Meteorological	Hours of bright sunshine	Kinross weather station reports	
Meteorological	Daily min/max air temperature	Kinross weather station reports	
Physical	Loch level	Loch-side staff gauge	
Physical	Inflow	Continuous river level recorder	
Physical	Outflow	Forth River Purification Board gauging records	
Physical	Surface water movement	Visual assessment of wave conditions	
Physical	Ice cover	Continual visual mapping (Nature Conservancy Warden – G Wright)	Lyle 1981
Physical	Water temperature		
Physical	a) Sub-surface	Mercury-in-glass thermometer	
Physical	b) Depth profile	Submersible thermistor	Benham & George 1981
Physical	c) Harbour mouth	Continuously recording mercury-in-steel thermograph	
Chemical	Oxygen saturation	Mackereth type oxygen probe	Mackereth 1964 Benham & George 1981
Chemical	Conductivity	Platinum-in-glass electrode	Benham & George 1981
Chemical	Nitrate	Hydrazine reduction to nitrate and analysis on Technicon Autoanalyser II	Downes 1978
Chemical	Soluble reactive (ortho-) phosphorus (SRP)	Phospho-molybdate reaction with ascorbic acid	Murphy & Riley 1962
Chemical	Total phosphorus and total soluble phosphorus	As for SRP after acid digestion to convert all forms of phosphorus to ortho-phosphate	
Chemical	Soluble reactive silica	Silico-molybdate reduction with metol	Strickland & Parsons 1968
Biological	Phytoplankton		
Biological	a) Chlorophyll *a* and eopigments	Absorption spectroscopy on methanol and acetone extracts	Bailey-Watts 1973
Biological	b) Species composition and abundance	Tube sampling, sedimentation, identification & counting	Bailey-Watts 1978
Biological	c) Size	Vickers image-shearing module	Bailey-Watts & Kirika 1981
Biological	d) Total weight and C, N, P and opal content	Centrifugal concentration and analysis of dried slurry	Bailey Watts & Lund 1973, Bailey-Watts 1976
Biological	Zooplankton		
Biological	a) Rotifera	Collection with weighted tube, arcotization, preservation and counting of animals and eggs	May 1980a
Biological	b) Crustacea	Collection by tube sampler, identification, counts by instar or size groups. Egg counts	George & Owen 1978

availability, and increased grazing pressure by *Daphnia*; such considerations emphasize the need for integrated studies of the whole system, if we are to understand the factors regulating species composition and abundance of plankton communities.

Although plankton in Loch Leven varies from year to year, a certain underlying seasonal regularity in its behaviour has been identified in recent years. Data from 1981 are used here to illustrate this regularity. In early spring, when water temperatures are low (<6°C) and nutrients are abundant, algal growth is usually vigorous (Figure 7). Population doubling times of less than 3 days are not uncommon (Bailey-Watts 1974). The dominant organisms at this time are centric diatoms. These algae continue to grow rapidly until checked by a shortage of dissolved silica in mid-March. The diatoms are small (less than 20 μm in diameter), and appear to be a suitable food source for herbivorous zooplankton, but they escape heavy grazing and attain high population

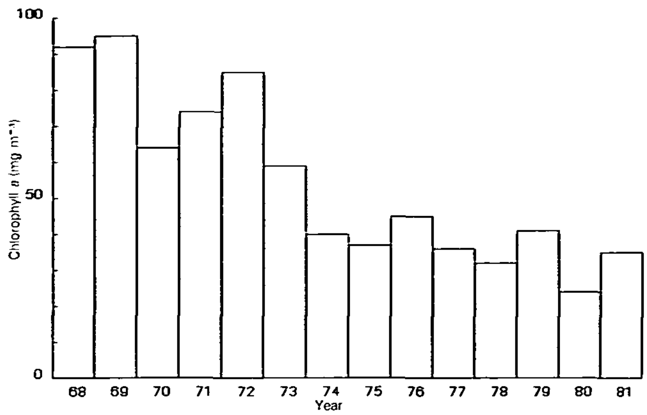

Figure 6 Bar chart showing the annual mean chlorophyll a concentrations in Loch Leven, 1968-1981.

densities because zooplankton reproduces slowly at this time of the year and its population densities remain low.

As the water temperature increases, the crustacean zooplankton becomes more abundant (Figure 8). These animals feed predominantly on phytoplankton, and it is possibly their grazing activity which prevents the accumulation of substantial algal populations from April to June.

Figure 8 shows that the crustacean population is in decline by mid-June, and total phytoplankton abundance begins to increase, followed closely by an increase in rotifer densities. It seems likely that, earlier

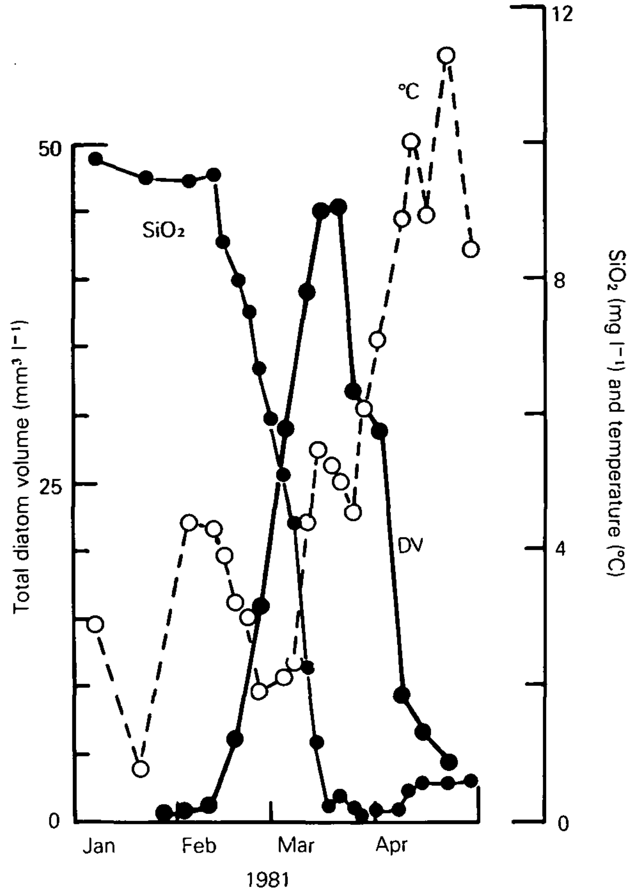

Figure 7 Fluctuations in water temperature (°C) and the concentrations of dissolved reactive silicate (SiO_2) and diatoms, expressed as total cell volume (DV) in Loch Leven during the first months of 1981.

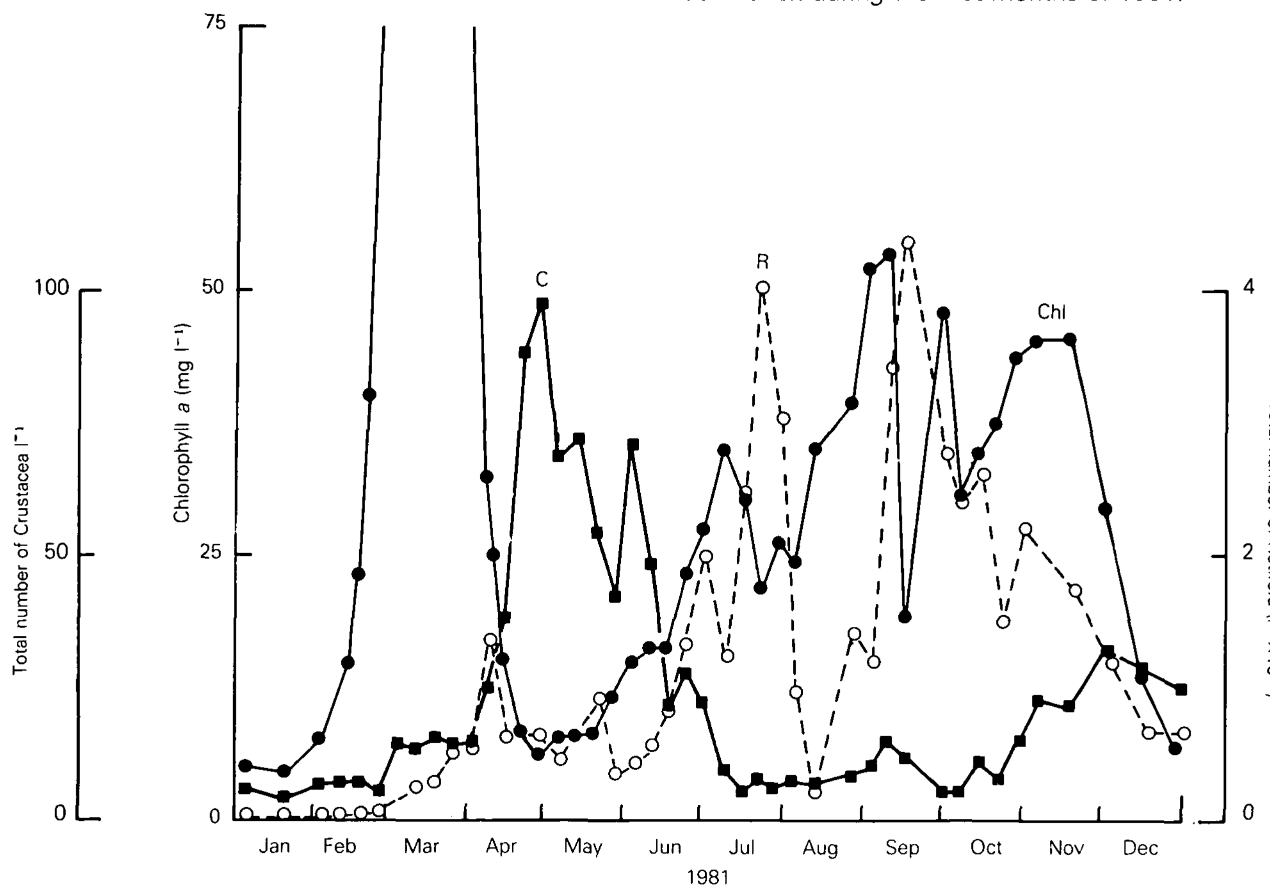

Figure 8 Seasonal changes in phytoplankton abundance (expressed as chlorophyll concentration—Chl), and the total numbers of crustacean (C) and rotifer (R) zooplankton in Loch Leven during 1981.

in the year, rotifers compete unsuccessfully with the Crustacea for food and only become abundant when crustacean densities are low. In addition, rotifers are also preyed upon by some Crustacea, particularly the cyclopoid copepod *Cyclops strenuus abyssorum* (Rutkowski 1980), which will also tend to reduce their population densities.

Rotifer numbers continue to increase until late July, when an abrupt decrease occurs, mainly as a result of the sudden reduction in abundance of the dominant species *Trichocerca pusilla*. Although chlorophyll tends to increase at this time, *Melosira granulata*, the food of this rotifer (May in press), is in decline. By the end of September, rotifer numbers are again high, and throughout the autumn their abundance tends to vary in a manner which reflects changes in algal abundance (Figure 8).

The causal relationships between variations in abundance are not easily explained by field studies alone.

For this reason, we intend to reduce our routine work to a monitoring watch, and increase laboratory studies to test hypotheses suggested by the field data. Experiments are planned to investigate the effects of physical and chemical conditions on the growth and development of plankton populations, and to evaluate biological interactions such as grazing, predation and competition.

An example of the way in which experimental data can increase our understanding of the field situation is described below. It concerns the relationship between water temperature, the rotifer *Notholca squamula*, and its food, the diatom *Asterionella formosa*. In spring and autumn 1981, dense crops of *A. formosa* were followed by an increased abundance of *N. squamula*. A simple grazing interaction seemed the most likely explanation. However, when high densities of the diatom were recorded in mid-summer, *N. squamula* did not reappear (Figure 9). Clearly, food availability was not the only environmental factor limiting the occurrence of this rotifer. Laboratory experiments showed that *N. squamula* is unable to reproduce successfully at temperatures above 10°C in culture (May 1980b). On re-examination, the field data confirmed that the abundance of *N. squamula* in the loch was related to that of *A. formosa* only at temperatures below 10°C. Above this temperature, the rotifer was absent irrespective of food availability.

Similar species-specific investigations are planned for the future. In addition, it is hoped that manipulation of natural plankton assemblages transferred to the laboratory, or enclosed *in situ* within Butylite containers, will provide an intermediate step between laboratory and field conditions.

Concluding remarks

It is evident from the above that a large amount of data describing the plankton and physical and chemical environment of Loch Leven has been compiled since 1968. This information is now held as a computer data bank. In the past, analyses have been restricted almost entirely to the comparison of time-abundance curves generated from the field results. In the future, the data will be subjected to a more rigorous and comprehensive statistical analysis and re-examined in the light of experimental results.

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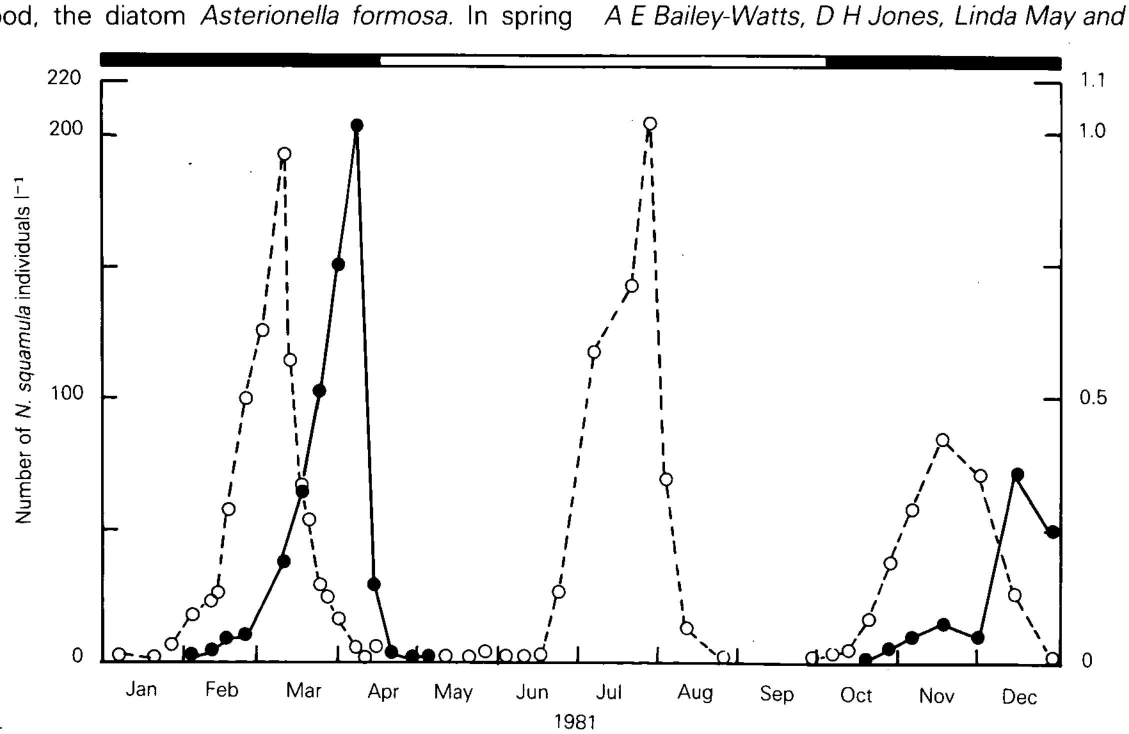

Figure 9 Seasonal variation in the abundance of Notholca squamula *(N) in relation to* Asterionella formosa *numbers (A) and water temperature (shaded area indicates periods during which the temperature was less than 10°C) in Loch Leven during 1981.*

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METALS IN FRESHWATER MUSSELS

Three species of freshwater mussel — *Anodonta anatina, Unio pictorum* and *Unio tumidus* — were collected for study from several sites along the river Great Ouse in the Cambridgeshire/Bedfordshire area. In particular, a large population of mussels from one area was sampled at about monthly intervals for 16 months. Concentrations of zinc, iron, cadmium and copper in the soft tissues of these animals were measured using atomic absorption spectrophotometry (Bull & Leach 1981).

Results indicate that copper concentrations are independent of size (or age) of mussel for *A. anatina* (Figure 10) at all times of the year sampled, and thus support the suggestion that copper may be 'regulated' in this species (Manley & George 1977). Seasonal changes of concentration do occur, however, and these are easily observed because copper concentrations are independent of size. Almost a 2-fold increase in copper concentrations occurs during the winter months (Figure 11), probably caused by weight changes in soft tissue, which also occur seasonally.

Zinc, iron and cadmium have a more complex pattern of accumulation in *A. anatina*. Concentrations of these metals show significant increases with size and age, at all times of the year. Furthermore, these increases are non-linear, even when plotted logarithmically (Figure 10). These metals do, however, follow similar accumulation patterns, and therefore show a highly significant correlation with one another (Figure 12).

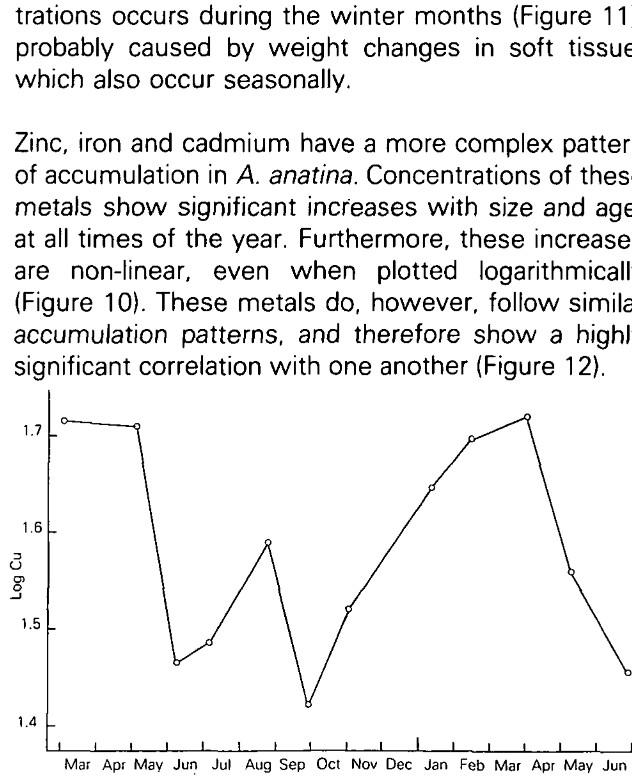

Figure 11 Mean log soft tissue copper concentrations (mg kg^{-1} dry weight) for A. anatina*—March 1979–June 1980.*