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Zooplankton of Loch Leven, Kinross-shire, Scotland.

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SUMMARY

Zooplankton samples collected from Loch Leven before and after the phosphorus (P) loading reduction of 1987/89 are compared. *Daphnia hyalina, Cyclops strenuus abyssorum* and *Diaptomus gracilis* continued to be the main species of crustacean zooplankton. The absolute and relative abundance of *Daphnia* and *Cyclops* were similar in 1979/82 and 1992, but *Diaptomus* abundance was slightly lower in 1992 than during the earlier period. The decrease in P loading seemed to have had little effect on these animals. Their overall species composition and abundance suggested that Loch Leven was still a very nutrient-rich environment.

In contrast, the rotifers, which are probably more sensitive indicators of environmental change, did seem to have been affected by P reduction. One of the 'new' species found in 1991/92 was *Kellicottia longispina,* first encountered in 1991. This species is generally considered to be an oligotrophic indicator and its arrival in Loch Leven may suggest that the loch is becoming a little less eutrophic. The overall reduction in rotifer numbers recorded in 1991/92, compared to 1987/92, also supports this view. However, the rotifer list for Loch Leven still contains many eutrophic indicator species suggesting that, on balance, the loch is still eutrophic.

Zooplankton grazing may significantly reduce algal biomass, especially when *Daphnia* numbers are high. However, this is unlikely to inhibit the growth of bloom forming blue-green algae because many of them form colonies which are too large for the zooplankton to ingest. If anything, grazing by zooplankton probably promotes the production of blue-green algal blooms by reducing the number of smaller, 'edible' algae which would otherwise compete for light and nutrients.

It is impossible to assess the impact of the resident brown trout population on the phytoplankton and zooplankton communities because too little is known about the feeding habits of these fish. The likely effects of introducing rainbow trout are also unknown. If both fish species feed primarily on benthic invertebrates, this introduction should have little impact on the zooplankton; if, however, competition led to the trout feeding on zooplankton, this could lead to an increase in the abundance of smaller phytoplankton, and a corresponding decrease in the biomass of larger, slower growing algae, such as the blue-greens.

CONTENTS

1. INTRODUCTION

Loch Leven was first chosen as a research site in the late 1960s in recognition of its conservation status. At that time, most of our understanding of the limnology of standing waters was based on studies of deep, stratifying lakes. In recent years, the research emphasis has centred around the problem of eutrophication and its effects on the loch, which include the formation of dense algal blooms. Algal blooms at Loch Leven were first documented in the late 1930s [Rosenberg, 1938], and may have occurred even earlier than this [see Wesenberg-Lund, 1905], but it was not until the late 1960s and early 1970s that concern about the problem developed. At this time, chlorophyll *a* concentrations often exceeded 150 $\mu g\ l^{-1}$ [Bailey-Watts, 1974, 1978].

As a result of this, and on the basis of crude estimates of phosphorus (P) loading [Holden & Caines, 1974], discharges of P-rich industrial effluent were reduced. A reduction in overall phytoplankton abundance followed, but it was difficult to attribute this to the fall in P inputs, alone, because the abundance of herbivorous zooplankton increased dramatically in 1971 [Johnson & Walker, 1974]. This, too, had a marked impact on chlorophyll *a* levels [Bailey-Watts, 1978].

Algal biomass increased again in the early 1980s and classic, bloom-forming blue-green algae (cyanobacteria) became more prominent once more. This led to a desk study which indicated that the P burdens to the loch had increased once again [Bailey-Watts, 1983], mostly due to effluent from a local woollen mill. A field survey in 1985 showed that of the 20 tonnes P per year entering the loch, 45% came from catchment runoff, 31% from the mill and 26% from local sewage treatment works [Bailey-Watts, Sargent, Kirika & Smith, 1987]. The mill was targeted for P reduction, in the first instance, and P levels in the effluent discharged began to fall in 1987, ceasing completely by the end of 1989 [Bailey-Watts, May & Kirika, 1991].

The effects of this reduction on the phytoplankton populations and water chemistry is being closely monitored [Bailey-Watts, May & Kirika, 1991, 1992; Bailey-Watts, Gunn & Kirika, 1993], but the effects on the zooplankton have been almost totally ignored. Nevertheless, as many are primary grazers, the abundance and species composition of the zooplankton is likely to be closely related to changes in phytoplankton production and, as potential indicators of environmental conditions, they may provide evidence of changes in the trophic status of Loch Leven.

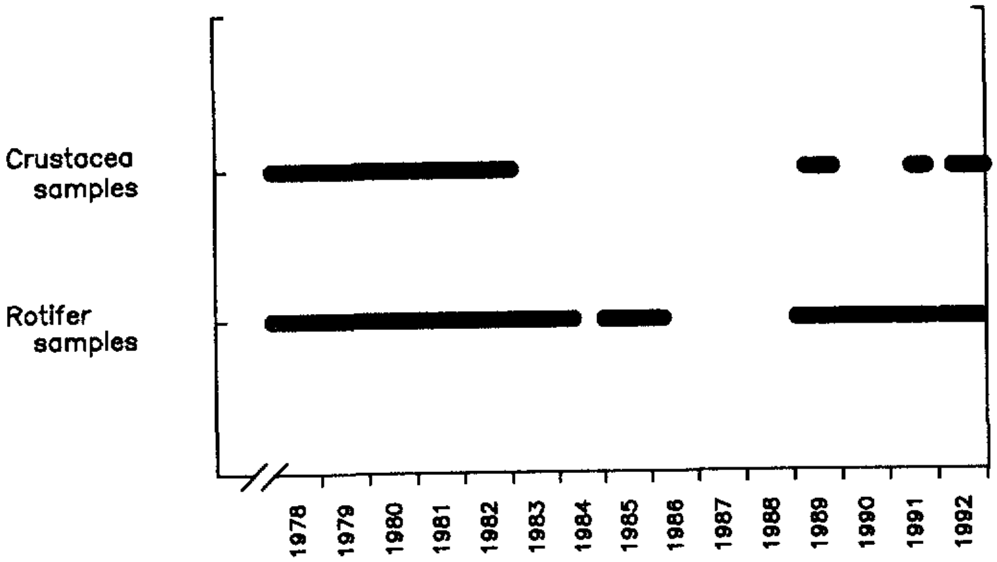


Figure 1. The frequency of sampling for rotifers and crustacea carried out between 1978 and 1992.

Zooplankton samples were collected on a fairly regular, routine basis, between 1977 and 1983 for the rotifers, and between 1968 and 1982 for the crustacea. Some of this work has been published [May, 1980b,c, 1983, 1986; May & Jones, 1989; Bailey-Watts *et al.*, 1990; May, *et al.*, 1993], but much of the data requires further analysis, especially with respect to identifying interactions between species. From 1984 onwards, little funding was available to continue the zooplankton sampling and samples were often collected on an *ad hoc* basis, usually when the loch was being visited for another purpose (eg. the P loading survey in 1985 which was part-funded by DAFS, NCC, SDD and TRC [Bailey-Watts, Sargent, Kirika & Smith, 1987]). The gaps in the long-term dataset which occurred as a result of this are only too obvious (**Figure 1**). The crustacea records were more seriously affected than the rotifer records because of the different sampling techniques involved. Rotifers, which are small and fairly randomly dispersed throughout the water column [May, 1980a], can easily be sampled from the loch edge e.g. the sluices outflow. However, sampling of the crustacea, which are much larger animals, and usually more unevenly distributed because of their tendency to swarm, requires the use of a boat to ensure loch-wide coverage.

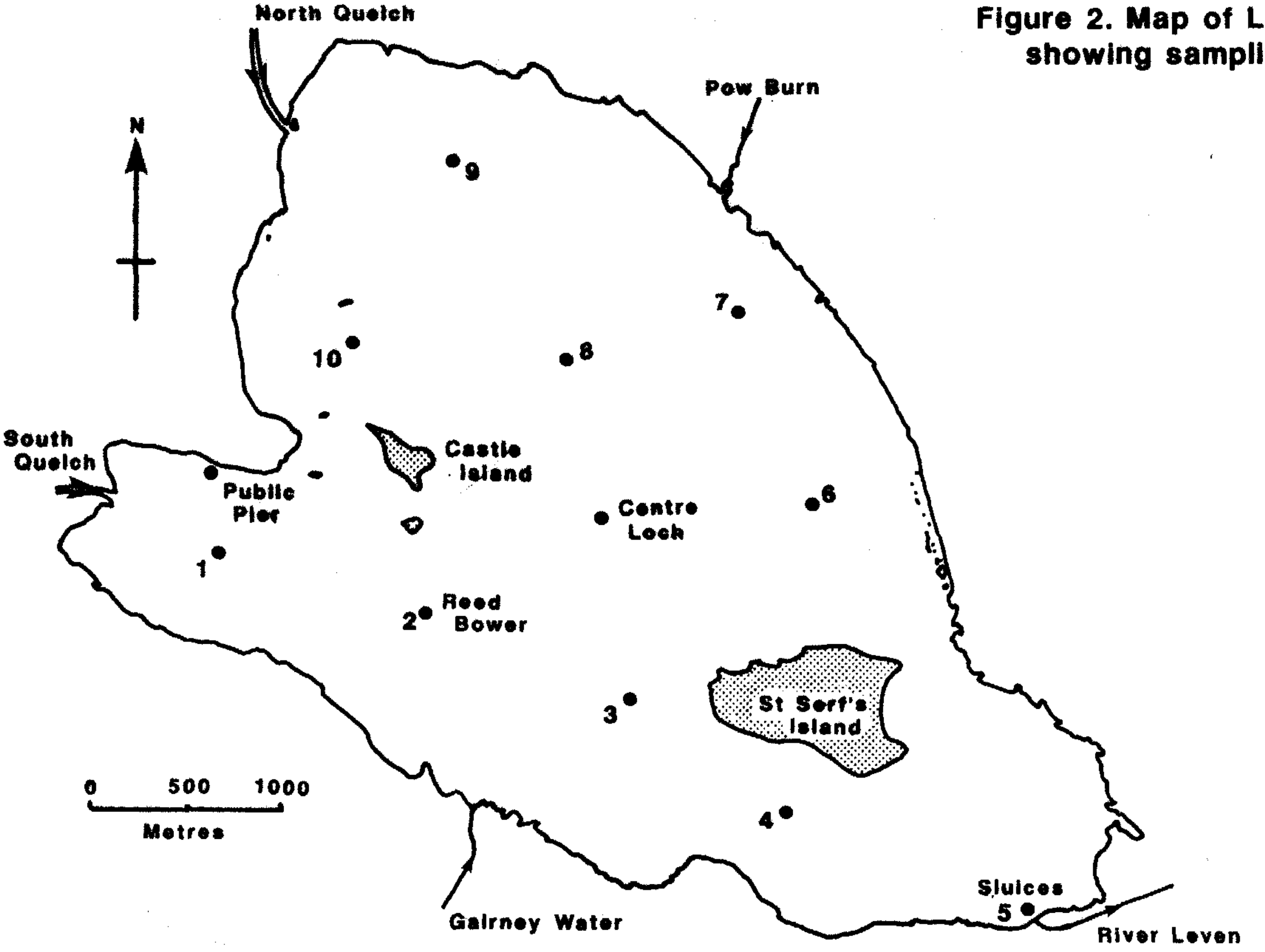
In spite of all these problems, a fairly extensive set of zooplankton samples has been secured and placed in storage since the end of 1983, and especially over the past few years. The present contract has provided the opportunity for some of the more recent samples to be analysed and the results compared to data collected earlier. Changes in species composition and abundance are discussed in relation to changes in water quality, the occurrence of phytoplankton blooms and the proposed introduction of rainbow trout (*Oncorhynchus mykiss* (Walbaum)).

2. SITE DESCRIPTION

Loch Leven (56°10'N, 3°30'W) is a shallow, eutrophic loch with a mean depth of 3.9 m and a surface area of 13.3 km^2 (**Figure 2**). The water column is generally unstratified due to wind-induced mixing, and its temperature (summer maximum approx. 21°C) closely parallels that of the air [Smith, 1974]. Details of the water chemistry and plankton ecology of the loch are given by Johnson & Walker [1974], Bailey-Watts [1978, 1982], May [1980a,b,c, 1983], Bailey-Watts & Kirika [1987], Bailey-Watts, Sargent, Kirika & Smith [1987], Bailey-Watts [1988], Bailey-Watts *et al.* [1990], Bailey-Watts, May & Kirika [1991], May *et al.* [1993], and the literature cited by these authors.

The inflows to the loch drain a catchment of 145 km^2. Agricultural lowland covers most of this area. As well as P in the runoff, P-rich industrial effluent and discharges from sewage treatment works have also contributed to the nutrient enrichment of this waterbody. P loading was reduced by 6.3 tonnes yr^{-1} between 1985 and 1989 [Bailey-Watts, May & Kirika, 1991]. The effects of this on the water chemistry and on the plankton communities are being monitored [Bailey-Watts, May & Kirika, 1991, 1992; Bailey-Watts, Gunn & Kirika, 1993; this report].

Figure 2. Map of Loch Leven showing sampling sites (●).



3. METHODS

3.1 Crustacean zooplankton

3.1.1 *Field sampling*

Crustacean zooplankton samples were taken at more or less weekly intervals between January 1979 and December 1982 and then not again until April 1989. Thereafter, samples were collected on an occasional basis until regular weekly sampling was resumed at the beginning of May 1992.

Between 1979 and 1982 samples were usually taken at the Reed Bower and Centre Loch sampling stations (**Figure 2**). During 1992, they were collected at Reed Bower only until mid-July, then alternately at sites 1, 2 and 5, and sites 1-10, from mid-July onwards. The 1979-1982 samples were collected either by vertical net haul (mesh size 100 μm) from 4 m to the surface, or with a tube sampler incorporating a filter (mesh size 125 μm - George & Owen, 1978) lowered to a depth of 4-5 m. During 1992, samples were again collected by vertical net haul, but a slightly coarser mesh (118 μm) was used compared to earlier samplings. The concentrated material was preserved in 4% formaldehyde.

3.1.2 *Laboratory analyses*

The preserved concentrates were placed in a glass vessel and made up to a final volume of 250 ml with distilled water. Each sample was then mixed thoroughly, to distribute the animals randomly, and subsampled with a Stempel pipette (volume 5 ml). The animals in each subsample were identified to species level [Scourfield & Harding, 1966; Harding & Smith, 1974] and counted with a low power microscope. Analysing crustacean zooplankton samples is a very time-consuming task and it was not possible to count all of the samples collected. Only samples from the Reed Bower site were counted routinely and these data, alone, are used here to compare zooplankton abundance in 1992 with that of earlier years. The data for April 1989 to April 1992 were unsuitable for inclusion in the analyses due to the long sampling intervals.

3.2 Rotifers

3.2.1 *Field sampling*

Rotifer samples were collected at more or less weekly intervals from 1979 to 1982, then at 10 or 12-day intervals in 1983. Only 2 samples were taken in 1984, a few at the beginning of 1986, and none at all during 1987 and 1988 due to lack of funding for the routine sampling programme. However, samples were secured at 8-day intervals during 1985 when the loch was being visited for the P loading survey [Bailey-Watts, Sargent, Kirika & Smith, 1987]. Regular sampling (*ca* 10-day intervals) was resumed in January 1989 until June 1992. Since then, samples have been collected weekly.

From 1979 until 1982, samples were taken with a weighted plastic tube [Lund, 1949]. In 1985, and between January 1989 and the end of June 1992, they were collected with a bucket from just below the water surface, either at the Public Pier or, more usually, at the Sluices (**Figure 2**). Open water sampling was resumed in July 1992 and, since then, samples have been collected at Reed Bower with a 2-m Marley® plastic drainpipe (5-cm internal diameter).

Whatever the collection method, each sample of water was mixed well and a 1-litre or 500-ml subsample was taken for counting. Procaine hydrochloride was added to each sample bottle to give a final concentration of approximately 0.04%. This relaxed the soft-bodied forms allowing easier identification of the specimens once preserved [May, 1985]. After 12 h, each subsample was preserved with 4% formaldehyde.

3.2.2 *Laboratory analyses*

The rotifer samples were concentrated by repeatedly settling the samples in glass measuring cylinders and siphoning off the overlying water. Plankton nets and sieves were not used in preparing the samples as these can lead to significant underestimates of abundance [Bottrell *et al.*, 1976; Orcutt & Pace, 1984]. The rotifers in each sample were identified according to Koste [1978] and counted with an inverted microscope. Particularly dense samples were randomly subsampled before counting. It was not possible to examine all of the samples which had been collected since the end of 1982. However, samples for 1991 and 1992 were counted and these data are compared to those from earlier years.

3.3 Phytoplankton abundance (chlorophyll *a* concentration)

3.3.1 *Field sampling techniques*

For the most part, phytoplankton samples were taken in parallel to the rotifer samples and the sampling sites and methods used are as detailed above for rotifers.

3.3.2 *Laboratory analyses*

Phytoplankton was concentrated by filtration onto Whatman® GF/C grade filters which were steeped in 90% methanol for *ca* 15 hours in the dark and at 4°C. Then, the chlorophyll *a* content, not corrected for degradation products, was determined using the spectrophotometric method proposed by Talling and Driver [1963]. The data collected between 1 January 1991 and 15 June 1992 were not suitable for inclusion in the report due to technical problems with the methods used. Approximate monthly figures for the period 1 January 1992 to 15 June 1992 were provided by the Forth River Purification Board.

4. RESULTS

4.1 Crustacean zooplankton

4.1.1 *Species List*

A complete species list of crustacean zooplankton collected from Loch Leven between January 1979 and December 1982, and during 1992 is shown in **Table 1**. All five species found in 1979-82 were also recorded in 1992. The only species collected in 1992 which was not found in the earlier samples was *Bosmina* sp. of which one specimen was noted in June 1992.

Table 1. A species list of crustacean zooplankton from Loch Leven.

	1979/1982	**1992**
Cladocera		
Daphnia hyalina var. *lacustris* Sars	✓	✓
Leptodora kindti (Focke)	✓(?)	✓
Bythotrephes longimanus Leydig	✓(?)	✓
Bosmina sp.	?	✓
Copepoda		
Diaptomus gracilis Sars	✓	✓
Cyclops strenuus abyssorum Sars	✓	✓

4.1.2 *Abundance*

Total crustacea densities, and the relative proportions of each of the five main species, were similar in the periods before and after the reduction in P loading. The cyclopoid copepod

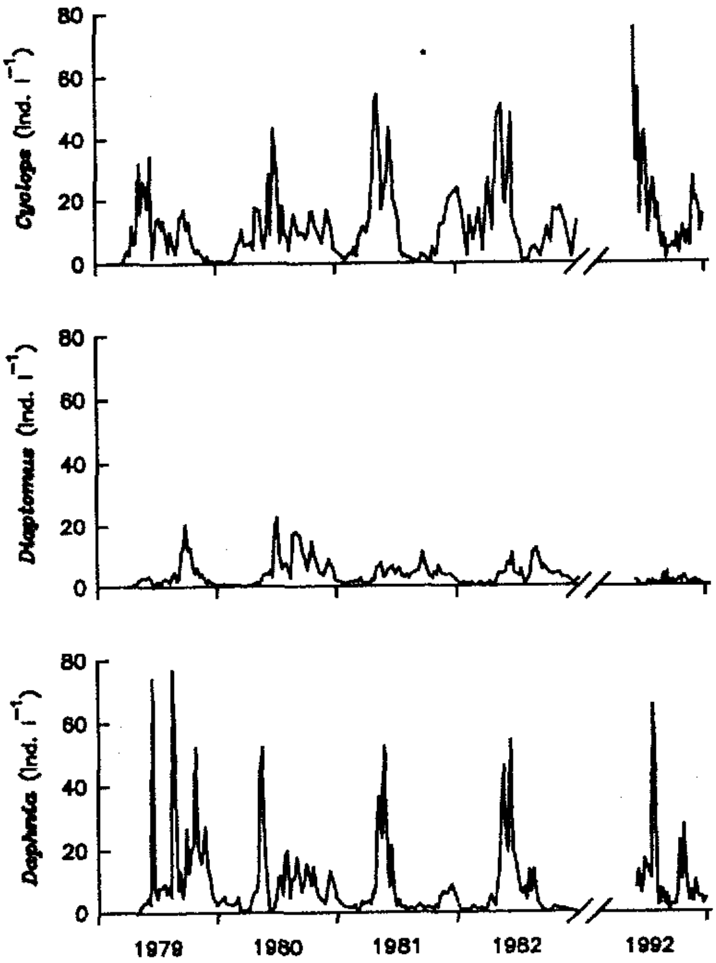


Figure 3. Total abundance of ***Cyclops*** (adults + copepodites I–V), ***Diaptomus*** (adults + copepodites I–V) and ***Daphnia*** in Loch Leven, 1979–1992

Cyclops strenuus abyssorum Sars and the cladoceran *Daphnia hyalina* var *lacustris* Sars remained co-dominant, with the calanoid copepod *Diaptomus gracilis* Sars occurring in smaller numbers (**Figure 3**). Both *Cyclops* and *Daphnia* numbers continued to peak in early summer, reaching maximum densities of 30-50 ind. l^{-1} and 50-80 ind. l^{-1}, respectively, with smaller secondary peaks in the autumn. In contrast, *Diaptomus* numbers showed a decrease in abundance in 1992 (maximum <5 ind l^{-1}) compared to the period 1979-1982 (maximum

22 ind. l^{-1}). *Leptodora kindti* (Focke) and *Bythotrephes longimanus* Leydig were minor constituents of the zooplankton and occurred only occasionally. This makes sense, as they are large predatory cladocerans.

4.2 **Rotifers**

4.2.1 *Species List*

A complete list of rotifer species collected from Loch Leven between January 1979 and December 1982, and between January 1991 and December 1992, is given in **Table 2**. Most of the species were found during both study periods, but a few were found only in the 1991/1992 samples. These were *Kellicottia longispina* (Kellicott), *Polyarthra euryptera* (Wierzejski), *Polyarthra vulgaris* Carlin, *Synchaeta oblonga* Ehrb., and *Synchaeta tremula* (Müller). Of these 'new' species, only *Kellicottia longispina* appeared in appreciable numbers (up to 430 ind. l^{-1}, **Figure 4**). The remainder were collected only occasionally and in very low

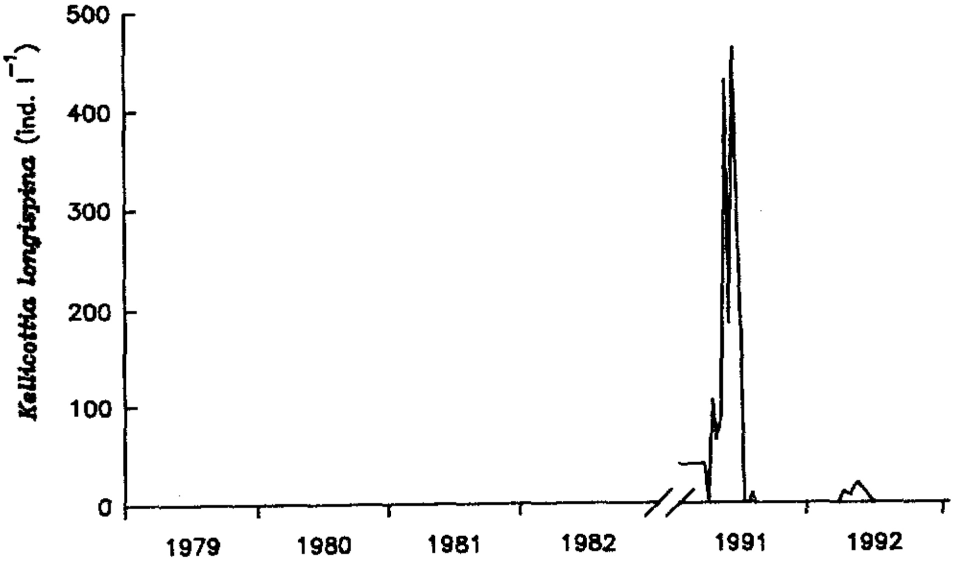


Figure 4. Abundance of ***Kellicottia longispina*** in Loch Leven, 1979–1992.

Table 2. A species list of rotifers collected from Loch Leven.
Eutrophic indicators are marked with an asterisk (*), oligotrophic indicators are marked with a cross (+). Species not found in 1979/82 samples are highlighted (bold).

Ploima

Brachionidae
* *Brachionus angularis* Gosse
Euchlanis dilatata Ehr.
Keratella cochlearis (Gosse)
* *Keratella tecta* (Gosse)
* *Keratella quadrata* (Müller)
+ ***Kellicottia longispina* (Kellicott)**
Notholca squamula (Müller)
Notholca labis (Gosse)
Colurella adriatica (Ehr.)

Lecanidae
Lecane lunaris (Ebr.)

Notommatidae
Cephalodella sp. Bory de St Vincent

Trichocercidae
* *Trichocerca pusilla* (Lauterborn)
Trichocerca sp. Lamarck

Asplanchnidae
Asplanchna priodonta Gosse

Synchaetidae
Polyarthra dolichoptera Idelson
* ***Polyarthra euryptera* (Wierzejski)**
Polyarthra major Burckhardt
***Polyarthra vulgaris* Carlin**
Synchaeta kitina Rousselet
Synchaeta grandis Zacharias
***Synchaeta oblonga* Ehrb.**
***Synchaeta tremula* Müller**

Flosculariacea

Testudinellidae
* *Pompholyx sulcata* Hudson
* *Filinia longiseta* (Ehr.)

Conochilidae
+ *Conochilus unicornis* Rousselet

Collothecacea

Collothecidae
Collotheca mutabilis (Hudson)

numbers. All of the species which had been recorded in the 1979/82 samples were also found in the 1991/92 samples.

4.2.2 *Abundance*

Total rotifer densities in Loch Leven were relatively high in 1979/82 with a maximum of 7150 ind. l^{-1} in 1979, 6734 ind. l^{-1} in 1980, 4390 ind. l^{-1} in 1980, and 10,620 ind. l^{-1} in 1982. In contrast, maximum abundances for 1991 and 1992 were only 1910 ind. l^{-1} and 2200 ind. l^{-1}, respectively (**Figure 5**). This reduction was not due to any one species in particular, but reflected an overall decline in rotifer numbers.

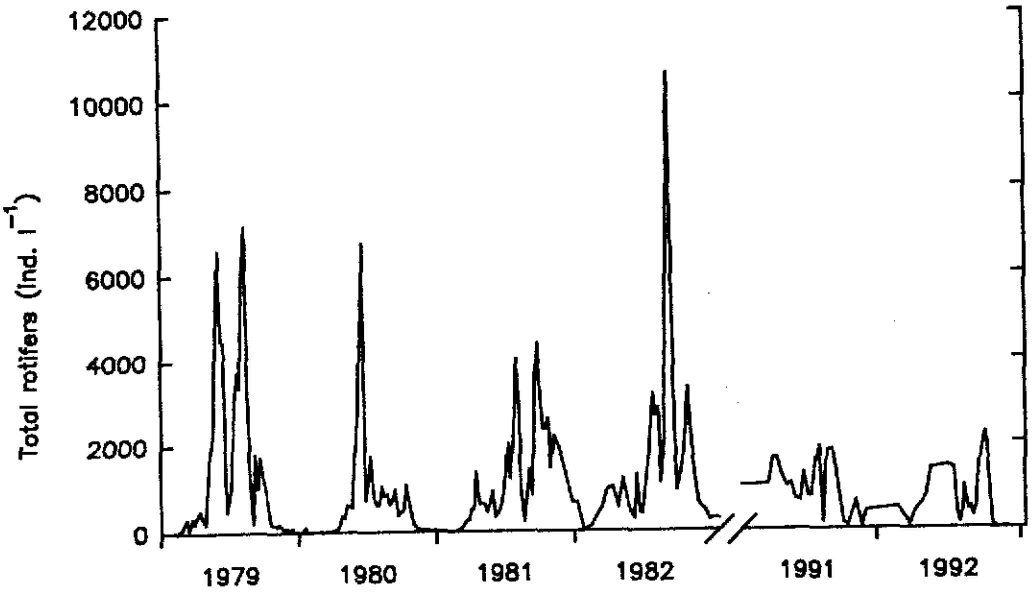


Figure 5. Total rotifer densities in Loch Leven, 1979–1992.

Rotifers are very seasonal in occurrence, so different species tend to dominate the rotifer community at different times of year. For the most part, the dominant rotifers are those which regularly achieve population densities of 1000 ind. l^{-1}, or more. These are *Keratella cochlearis, Keratella tecta, Trichocerca pusilla, Polyarthra dolichoptera, Synchaeta kitina,* *Pompholyx sulcata* and *Filinia longiseta*.

4.3 **Phytoplankton abundance (chlorophyll *a* concentration)**

Chlorophyll *a* levels in the loch varied considerably throughout the period 1979/1982 and 1992 (**Figure 6**). Mean values for each year show that, overall, the algal biomass in 1992 was no less than in the years before the recent reduction in P inputs (**Table 3**) - see also Bailey-Watts, May and Kirika [1991]. The relationship between *Daphnia* abundance and phytoplankton biomass during the period of study is shown in **Figure 7**. In general, phytoplankton abundance tended to be low when *Daphnia* densities were high, except when large inedible algae (such as *Anabaena*) were dominant.

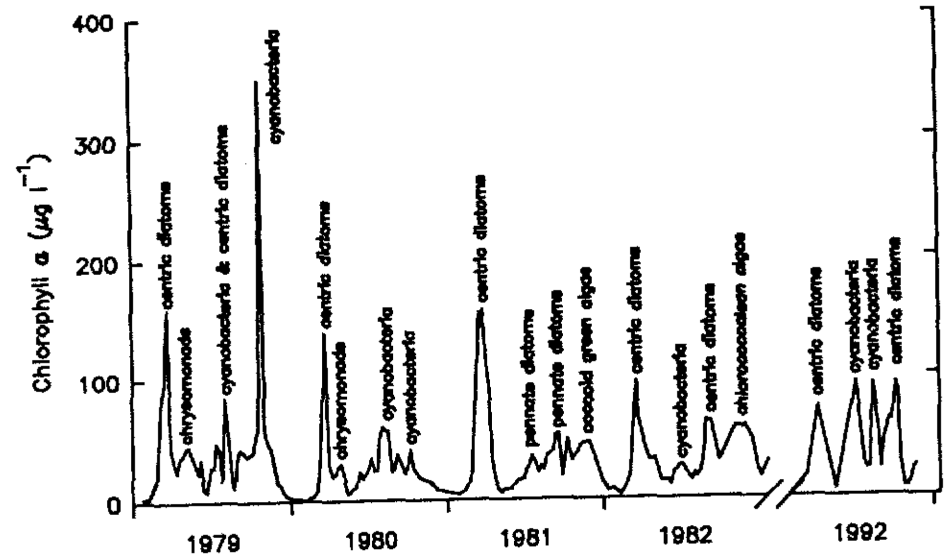


Figure 6. Fluctuations in chlorophyll *a* concentration 1979–1982 and 1992 showing dominant algae at crop maxima.

Table 3. Annual mean algal biomass levels (measured as chlorophyll *a*) in Loch Leven, 1979-1982 and 1992.

Year	chlorophyll *a* (µg l^{-1})
1979	44.3
1980	25.4
1981	43.5
1982	32.3
⋮	⋮
1992	42.5

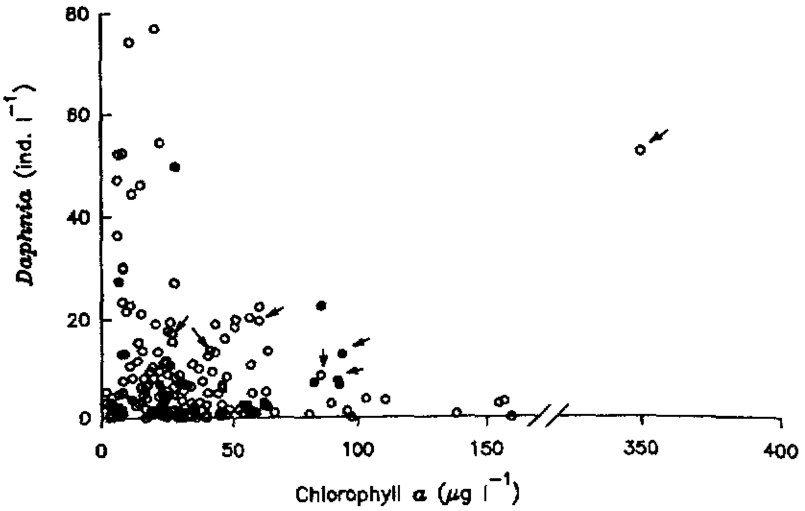


Figure 7. Relationship between ***Daphnia*** abundance and chlorophyll *a* concentration in Loch Leven, 1979–1982 (○) and 1992 (●). Values corresponding to a peak in blue–green algae are indicated (↙).

5. DISCUSSION

5.1 Zooplankton as environmental indicators

5.1.1 *Crustacea*

It has long been suggested that crustacean zooplankton could be used as environmental indicator species in freshwater communities. However, in his review on the effects of eutrophication on zooplankton, Ravera [1980] concludes that it is very difficult to classify waterbodies according to their trophic status on the basis of a list of zooplankton species alone, as many 'indicators' often occur in a range of waters other than their supposed characteristic type. In contrast, Maitland *et al.* [1981] in their survey of Scotland's five largest lochs (i.e. Awe, Lomond, Morar, Ness and Shiel), and Jones [1984] in his survey of five Tayside lochs (i.e. Earn, Laidon, Leven, Lintrathen and Lyon) found that it was possible to categorise each of these lochs satisfactorily, particularly in relation to their trophic status (evaluated by physical and chemical parameters), by examining species diversity and the absolute and relative abundance of each species.

Jones [1984] found that the following five zooplankton species were present in all of the five Tayside lochs in 1977: *Diaptomus gracilis*, *Cyclops strenuus abyssorum*, *Daphnia hyalina*, *Leptodora kindti* and *Bythotrephes longimanus.* However, these species differed in their relative importance among the sites. In Lochs Lyon and Laidon (oligotrophic) the crustacean zooplankton exhibited high species diversity with *D.gracilis* being dominant. The assemblages in Loch Earn (oligo-mesotrophic) and Loch of Lintrathen (mesotrophic) were less diverse and were dominated by *D.hyalina*. In Loch Leven (eutrophic) the crustacean zooplankton had a very low species diversity and was co-dominated by *C.strenuus abyssorum* and *D.hyalina,* two species which, by comparison, were only minor components of the zooplankton of oligotrophic Loch Laidon. The crustacean zooplankton was four times as abundant at Loch Leven as elsewhere, suggesting to Jones [1984] that absolute abundance could also be related to trophic status. In summary, he concluded that oligotrophic lochs would have a crustacean zooplankton characterised by relatively low abundance and a high species diversity tending to be dominated by *Diaptomus*, while eutrophic lochs would have a relatively high zooplankton abundance and a low species diversity dominated by *Cyclops/Daphnia*. McNaught [1975], in work on the Great Lakes of Canada, considered that Diaptomids were likely to be more successful in oligotrophic lakes than other crustacean zooplankton because of their superior filtering capacity and high ingestion rate at low algal densities.

Changes in the crustacean zooplankton at Loch Leven since the 1890's indicate a change in water quality. A total of 15 different species were recorded at the end of the last century, compared to only seven after the second world war and only five species since 1970 [Johnson & Walker, 1974]. This decrease in species diversity suggests that the loch has become more eutrophic over the last 100 years.

The most significant change recorded in recent years is probably the disappearance of *Daphnia* at some time between 1954 and 1966, and its subsequent re-appearance, in 1970 [Johnson & Walker, 1974]. However, this temporary loss of *Daphnia* has been attributed to possible poisoning by the organo-chlorine insecticide dieldrin, which was used as a moth-proofing agent by a local woollen mill during the late fifties/early sixties [Morgan, 1970; Burgis & Morris, 1987]; the loss is unlikely to indicate any change in the trophic status of the loch. The crustacean zooplankton community has remained fairly stable since 1971 and, in terms of species composition and relative abundance, indicates that Loch Leven is still eutrophic in spite of the various reductions in P loading.

5.1.2 *Rotifers*

Rotifers are thought to be much better indicators of environmental conditions than crustacea because they live for a very short time, only, reproducing very rapidly when conditions are favourable [Gannon & Stemberger, 1978], and disappearing into the sediments as resting eggs when conditions are unfavourable. In contrast, the Crustacea live longer and reproduce more slowly, so they must tolerate much greater fluctuations in environmental conditions if they are to survive.

Many of the species recorded in Loch Leven are thought to be indicators of eutrophy [Thunmarck, 1945; Berzins, 1949; Lillieroth, 1950; Järnefelt, 1952; Pejler, 1965; Gannon &

Stemberger, 1978; Berzins & Pejler, 1989]. The most notable exceptions are *Conochilus unicornis* and *Kellicottia longispina* (**Table 2**).

C. unicornis is usually found in oligotrophic lakes [Koste, 1978], although it has been found occasionally in eutrophic lakes [Berzins & Pejler, 1989]. It occurs regularly in Loch Leven and may be quite abundant in late spring/early summer (**Figure 8**), i.e. when chlorophyll levels are low due to heavy grazing pressure from *Daphnia* [Lampert & Schober, 1978]. Perhaps *C.unicornis* would be better thought of as an indicator of low algal biomass rather than of oligotrophy, a situation which occurs most of the time in oligotrophic lakes and only occasionally in eutrophic lakes. *C.unicornis* has been found here both before and after the P reduction and its presence does not seem to suggest any recent change in trophic conditions.

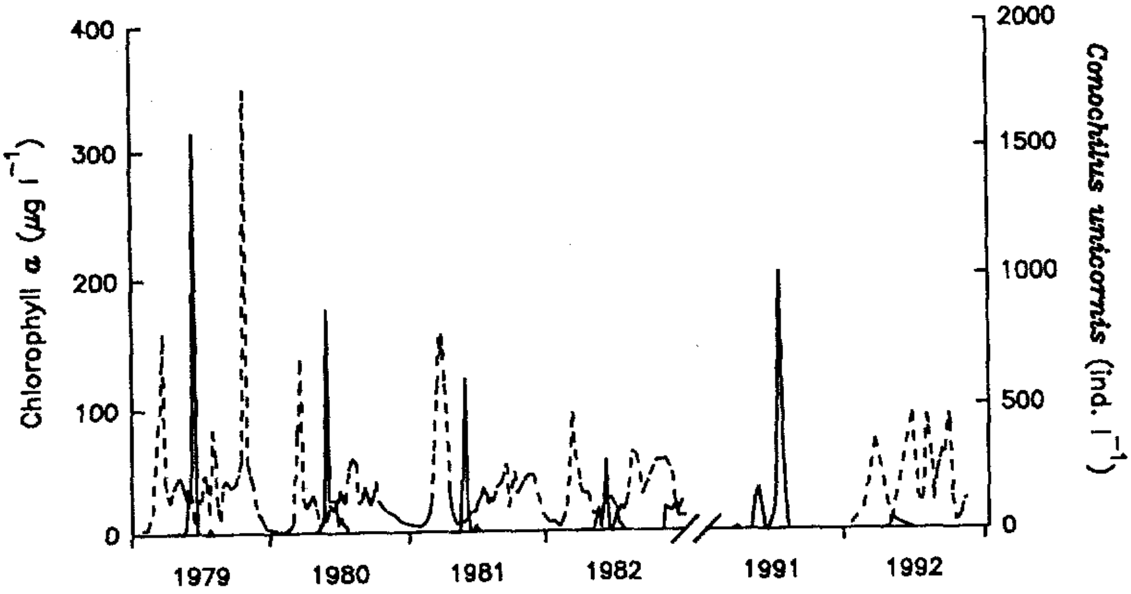


Figure 8. The relationship between abundance of the rotifer *Conochilus unicornis* (——) and chlorophyll *a* concentration (- - -) in Loch Leven, 1979–1992. No chlorophyll data were available for 1991.

The most notable change in rotifer species composition before and after P loading reduction was the rather sudden appearance, in 1991, of *Kellicottia longispina*. This species is considered by many authors to be an oligotrophic indicator [*e.g.* Pejler, 1989] and it is only rarely found in eutrophic lakes [Koste, 1978]. Its recent arrival in Loch Leven may well be one of the first indications that the loch is becoming a little less eutrophic.

The remainder of the rotifer community is typical of that found in eutrophic lakes. Berzins and Pejler [1989] assigned a trophic ranking number to each of the apparent indicators of trophic status in Sweden. This allowed them to be ordered as a continuous series ranging from oligotrophic indicators to eutrophic indicators (**Table 4**). Most of the species found in Loch Leven occupy the more eutrophic end of the series indicating that this site is a fairly rich environment.

Total rotifers, and annual maximum abundance in particular, are also thought to be good indicators of trophic status. Eutrophic systems generally have higher maximum rotifer densities than mesotrophic or oligotrophic waters (**Table 5**), reflecting the increased productivity of nutrient-enriched systems. The annual maximum densities recorded at Loch Leven for the period 1979-1982 are relatively high compared to many other lakes, confirming its eutrophic status. That said, however, annual maxima for 1991 (1910 ind.l^{-1}) and 1992 (2200 ind.l^{-1}) are much lower than for the earlier, pre-phosphorus loading reduction period. This, again, suggests that the loch may be becoming a little less eutrophic than it was.

5.2 Zooplankton grazing on phytoplankton with particular reference to the problem of phytoplankton blooms

A phytoplankton bloom can be defined as a population of algae which is so dense that it causes a visual discolouration of the water [Bailey-Watts, May & Kirika, 1991]. Such blooms can occur at Loch Leven at any time of year, but it is only in the summer that they seem to cause a nuisance. How troublesome an algal bloom becomes depends partly on the environment, and partly on our perception of it. For example, blooms of small, unicellular, centric diatoms develop in early spring virtually every year (**Figure 6**). These algae either remain suspended in the water column under windy conditions, or sink to the sediments when

Table 4. Rotifer indicator species ranked according to degree of trophy (after Berzins & Pejler 1989).

	Planktonic Indicators of Trophic Degree	Occurrence in Loch Leven	
		1979/82	1989/92
	Collotheca lie-pettersoni		
Oligotrophy	*Conochilus unicornis*	***	**
	Ascomorpha ecaudis		
	Gastropus stylifer		
	Postclausa hyptopus		
	Bipalpus hudsoni		
	Asplanchna herricki		
	Kellicottia longispina		**
	Polyarthra remata		
	Ascomorpha ovalis		
	Collotheca mutabilis		
	Keratella cochlearis robusta		
	Polyarthra major	**	**
	Trichocerca p. porcellus		
	Collotheca pelagica		
	Polyarthra vulgaris		
	Asplanchna priodonta	**	**
	Synchaeta stylata		
	Trichocerca rousseleti		
	Polyarthra dolichoptera	***	***
	Keratella c. cochlearis	****	***
	Polyarthra euryptera		
	Synchaeta oblonga		
	Synchaeta pectinata		
	Ascomorpha sultans		
	Keratella i. irregularis		
	Keratella i. wartmanni		
	Trichocerca birostris		
	Keratella tecta	****	***
	Pompholyx sulcata	****	**
	Brachionus a. angularis	*	*
	Keratella q. quadrata	**	**
Eutrophy	*Filinia longiseta*	***	*

* <50 ind l^{-1}

** 50 - <1000 ind l^{-1}

*** 1000 - <2,500 ind l^{-1}

**** >2,500 ind l^{-1}

Table 5. Maximum rotifer abundance in a range of lakes of different trophic status.

Lake	Trophic State	Rotifers (ind. l^{-1})	Reference
Attersee	oligotrophic	9	Müller, 1976
Titisee	mesotrophic	88	Szymanski-Bucarey, 1974
Delwart	mesotrophic	65	Bogaert & Dumont, 1989
Neusiedlersee	mesotrophic	784	Herzig, 1979
Warniak	eutrophic	1650	Hillbricht-Ilkowska & Weglenska, 1973
Mikolajskie	eutrophic	1800	Spodniewska *et al.*,1973
Piburgersee	eutrophic	2382	Schaber, 1976
Oglethorpe	eutrophic	7980	Orcutt & Pace, 1984
Leven	eutrophic	10,620	this study
Priest Pot	hypereutrophic	40,000	Hewitt & George, 1987

the weather is calm and never float to the surface causing scums. Although they turn the water brown, they are rarely noticed by the small number of people who visit the loch at this time of year. In contrast, many of the summer blooms are caused by large, blue-green algae (cyanobacteria) which are far more evident, even though, on a lake-wide basis, they are less abundant than the small diatoms. Colonies of these algae are often visible to the naked eye and they have gas vacuoles which buoy them to the surface during calm conditions, forming the classic, unsightly scums. They also produce a particularly unpleasant smell when they decay and may produce toxins. These factors, and the fact that they tend to occur at a time when there are many visitors and anglers in the area, generally arouses public concern. However, the perceived size of the problem often reflects the number of people affected by it. This is evidenced by the enormous public reaction to the blue-green algal bloom which occurred on 13 June 1992, on the day of the Natural Heritage Festival. Water-sports had to be cancelled because the bloom was found to be toxic, and the incident attracted unprecedented interest from the media and the public. Had the problem arisen a week later, or had the light breeze on that day blown east instead of west, even these blooms may have passed virtually unnoticed.

Massive algal blooms can occur only where nutrient levels are high and they are usually considered to be one of the main adverse effects of eutrophication, as they are in Loch Leven. It is well recognised that blooms of blue-green algae, in particular, are a feature of eutrophic lakes and this is thought to be due to a variety of factors [de Bernardi & Giussani, 1990] which include low N:P ratios (some blue-green species can fix atmospheric nitrogen) [Schindler, 1971], greater efficiency at using CO_2 in the high pH levels that these lakes often reach [King, 1970; Shapiro, 1973], low light availability [Mur *et al.*, 1978; Smith, 1986], and turbulence and dynamics of the water masses [Spigel & Imberger, 1987]. Although grazing by zooplankton is likely to be an important factor in reducing algal biomass in general, it may have little effect on the blue-greens [Brooks & Dodson, 1965; Shapiro *et al.*, 1975]. Many of these species are avoided by grazers, although there is some evidence that *Daphnia* can influence the size structure of blue-green algal populations by feeding on the smaller cells while avoiding the larger clumps [de Bernardi & Giussani, 1990]. *Daphnia* is the main grazer of phytoplankton in Loch Leven and when densities are high, the population may filter the algae from a volume equivalent to the entire loch in about 18 h [see May & Jones, 1989]. Even at the lower effective filtration rates[1] more usually recorded (approximately 10% of the loch volume per day) filter feeding by *Daphnia* tends to have a marked effect on overall phytoplankton biomass, as shown in **Figure 9.** The dramatic effect which the reappearance of *Daphnia* in 1970 had on chlorophyll *a* levels the following spring contrasts markedly with chlorophyll *a* levels in earlier years when *Daphnia* was absent. Data for 1979-82 and 1992 indicate that, in general, chlorophyll levels tended to be low when *Daphnia* were abundant, except when the high biomass was caused by a large inedible algae, such as *Anabaena* or *Microcystis* (**Figure** 7). This supports the hypothesis that *Daphnia* has little effect in controlling blue-green algal blooms in Loch Leven. Indeed, in many ways, *Daphnia* probably promote the growth of blue-green algal blooms because they feed on the other, smaller algae which would otherwise compete more successfully for nutrients. They also tend to feed on

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[1] Effective filtration rate is defined as the volume of ambient medium containing the number of cells eaten by the *Daphnia* population in a given time [see Jones, Lack & Jones, 1979].

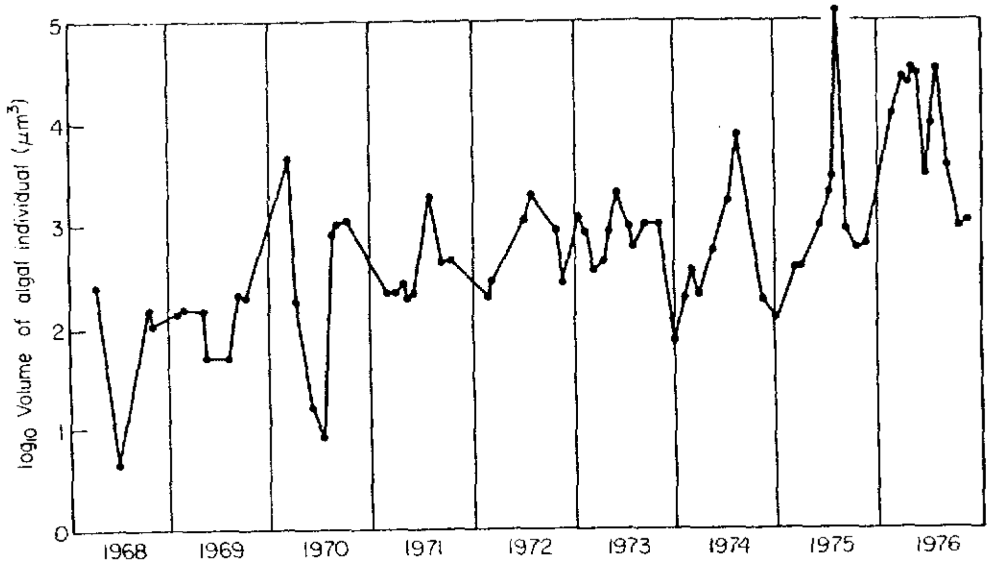

Figure 9. Mean volume of algae dominating the phytoplankton of Loch Leven, 1968-76, to illustrate the change in seasonality of algal size, particularly between the years prior to 1971 and those following it.

the smaller blue-green algal species, while leaving the larger species to proliferate. Bailey-Watts [1982, 1986] identified changes in the size structure of the phytoplankton at Loch Leven which he attributed to *Daphnia* grazing. For example, relatively small algae, including blue-greens, dominated the phytoplankton during the summers of 1968-1970, when *Daphnia* were rare or absent and the omnivorous copepod *Cyclops strenuus abyssorum* dominated the zooplankton, while relatively large forms became a feature of subsequent summers, when *Daphnia* was dominant (**Figure 10**).

It should not be forgotten that there are also other grazers among the zooplankton of Loch Leven which we know little about in terms of their grazing pressure, notably *Diaptomus* and *Cyclops* (especially their nauplii), and rotifers. These may also affect the size distribution of

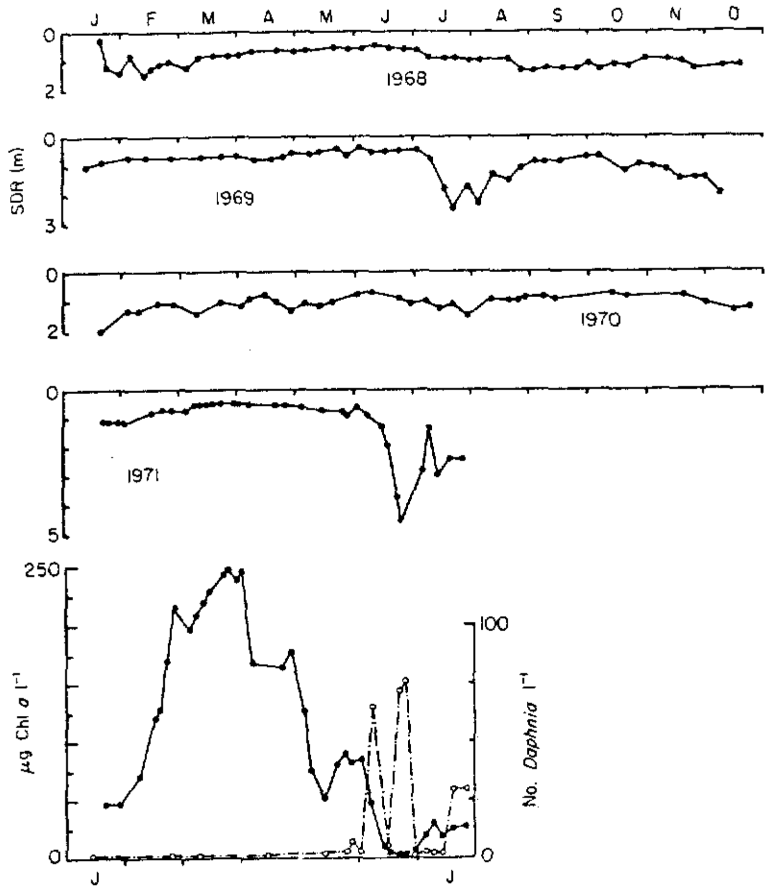

Figure 10. Lower panel: Marked increases in *Daphnia* numbers in Loch Leven, 1971 (—) with associated changes in total phytoplankton, expressed as chlorophyll *a* concentration (- -).
Upper panels: Water clarity (Secchi Disc Reading) records, 1968-71.

the algal population directly, by size selective grazing, or indirectly, by their predatory effect on *Daphnia* [Rutkowski, 1980; Bailey-Watts and Kirika, 1981]. Very little can be said about these complex interactions without further research in this area.

5.3 Possible effects of the introduction of rainbow trout to Loch Leven

The diet of brown trout (*Salmo trutta* L.) in Loch Leven has not been studied since the work of Thorpe [1974], so it is difficult to predict the effect that introducing rainbow trout (*Oncorhynchus mykiss* (Walbaum)) will have on the food-webs. Analysis of brown trout gut contents during the summer of 1971 showed that this species fed on mainly benthic invertebrates and perch fry. Only about 11% of the total food consumption was crustacean zooplankton, except in September when 35.5% of the food ration consisted of *Daphnia* [Thorpe, 1974]. In contrast, in the late 1960s when *Daphnia* was absent, chironomid larvae formed the main food item [Morgan, 1970]. In general, brown trout can have a very varied diet [Maitland & Campbell, 1992] and the example given above shows how opportunist they are in selecting their food.

None of the above authors mentions rotifers as being a significant part of trout diet. This is perhaps a reflection of the general use of low power microscopes for fish gut analyses, and a lack of expertise in detecting rotifers, rather than necessarily indicating that trout do not feed on them.

The introduction of the non-native rainbow trout into Loch Leven has been proposed on economic grounds in order to 'improve' the sport fishery there. It is difficult to predict what effect this will have on the zooplankton community without more information about the interactions between zooplankton and fish populations. However, work by Hunt and O'Hara [1973] on the stomach contents of rainbows taken from Llyn Alaw, Anglesey, showed that rainbow trout fed primarily on benthic invertebrates. According to Maitland and Campbell [1992], this fish has similar feeding habits and food preferences to native brown trout. If this is the case, brown and rainbow trout could become competitors for the same food resource. This is only likely to be a serious problem if food items become limiting.

Although fish predation can have a marked effect on zooplankton species composition [Brooks & Dodson, 1965; Wong & Ward, 1972; Hillbricht-Ilkowska & Weglenska, 1973; O'Brien, 1979; McQueen, Post & Mills, 1986], the research outlined above suggests that neither of these trout species is primarily planktivorous. So the zooplankton community in

Loch Leven will probably remain largely unaffected by the rainbow trout introduction, as long as there is a plentiful supply of benthic invertebrates to feed on. The fact that *Daphnia*, a relatively large zooplankter which is considered to be very vulnerable to fish predation pressures, co-dominates the Loch Leven zooplankton, suggests that fish predation has not had any appreciable effect on the zooplankton community, so far. Biomanipulation studies suggest that where fish predation is heavy, the zooplankton structure shifts from one where large cladocerans like *Daphnia* are dominant to a community where rotifers and small cladocerans predominate [Sondergard *et al.*, 1990].

It is impossible to predict what effect the proposed introduction of rainbow trout will have on the phytoplankton community until the effect on the zooplankton can be ascertained. If, as suspected, there is no discernible change, there will be little change in the phytoplankton community either, apart from those occurring as a result of changes in other factors such as nutrient availability and the weather. However, *if* fish predation does reduce the *Daphnia* population, this is likely to lead to less grazing pressure on the smaller phytoplankton. This, in turn, could reduce the level of nutrients available to the larger, slower growing algae, such as the large blue-greens, thus reducing their biomass.

6. FUTURE WORK

This study has identified 3 key areas which require further attention if we are to improve our understanding of the ecology of Loch Leven and strengthen our ability to predict the loch's response to environmental change. These are detailed below.

6.1 Regular monitoring of the plankton

Plankton (algae, protozoa, rotifers and micro-crustacea) is a very important part of the loch ecosystem. Firstly, it forms an integral part of the complex food webs which lead, ultimately, to fish. Secondly, its species composition and abundance can provide important clues to long-term changes in water quality. Thirdly, species interactions within the plankton, such as grazing, may determine whether nuisance algal blooms are likely to occur. Therefore, it is essential that the regular monitoring programme which has now been established is maintained in order to build up the basic long-term dataset which is needed for this type of analysis.

6.2 Fish feeding

Little is known about the diets of the various fish species in Loch Leven, or how these fish interact and compete for food. A study of fish feeding should be carried out as soon as possible so that the potential impact of introducing rainbow trout can be assessed, and the effects monitored. Detailed surveys of the distribution and abundance of all potential food items, including benthic and planktonic invertebrates, should be carried out in parallel to fish gut analyses, to provide information on food availability. This would allow food preferences to be determined and the degree of inter- and intra-specific competition for limited food resources to be assessed. Without this information it is impossible to say what the impact of introducing rainbow trout is likely to be on the resident fish populations.

6.3 Experimental research into species interactions

Species interactions at Loch Leven are not well understood, either within the plankton or elsewhere. It is necessary to identify and quantify grazing interactions (e.g. between zooplankton and phytoplankton) and predator-prey interactions (e.g. between fish and zooplankton) in order to interpret the field data that has been collected. This can only be achieved by a series of experimental studies under controlled environmental conditions.

7. CONCLUSIONS

1. The species composition, and absolute and relative abundance of the crustacean zooplankton have changed little since *Daphnia* re-appeared in 1970. This suggests that these animals have been unaffected by observed fluctuations in nutrient levels over this period.

2. Some changes in the rotifer community may indicate a slight reduction in nutrient levels and an associated improvement in water quality since the recent reduction in P loading. These are the appearance of *Kellicottia longispina* and an overall decrease in rotifer abundance.

3. Although grazing by *Daphnia* tends to reduce algal biomass, size selective grazing by this filter feeder may promote the growth of larger algae, including blue-green species, in summer.

4. The effects of other zooplankton grazers on the phytoplankton community is unknown and require further research.

5. Mechanisms whereby the introduction of rainbow trout could affect the zooplankton are discussed but, until sound data on the density, age structure and feeding habits of the resident brown trout population are obtained, these are speculative.

8. ACKNOWLEDGEMENTS

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