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Title

Long-term trends in Loch Leven invertebrate communities

Authors

I. D. M. Gunn[1], M. T. O'Hare[1], P. S. Maitland[2] and L. May[1]

[1]Centre for Ecology & Hydrology, Edinburgh, Bush Estate, Penicuik, Midlothian EH26 0QB, UK.

[2]Fish Conservation Centre, Gladshot, Haddington, East Lothian, EH41 4NR, UK.

Corresponding author: Iain Gunn Email idmg@ceh.ac.uk; telephone +44 (0)131 445 8538; fax +44 (0)131 445 3943

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This paper has not been submitted elsewhere in identical or similar form, nor will it be during the first three months after its submission to Hydrobiologia.

Abstract

Detailed studies of the macroinvertebrate benthos and zooplankton communities in Loch Leven, the largest shallow lowland lake in Scotland, UK, were carried out from 1966 to 1973 as part of the International Biological Programme (IBP). The results revealed a reduction in species diversity that was attributed to increasing eutrophication. This work provides a baseline against which the response of the invertebrate communities to subsequent changes in management can be assessed. This paper compares macroinvertebrate benthos and zooplankton data from the IBP study with the post-IBP *era* during which changes at Loch Leven included a 60% reduction in the phosphorus input from external sources and variations in fish stocking rates. Only in recent years has there been evidence of ecological recovery by the invertebrate communities: the number of macroinvertebrate and zooplankton taxa has increased (including taxa considered to be sensitive to nutrient enrichment) and invertebrate abundances have declined. These changes appear to reflect the improvements in water quality and habitat conditions at Loch Leven that have occurred as a result of the recent reduction in nutrient loads, albeit with a substantial delay before any ecological response could be detected. This time lag in recovery has important implications for assessing improvements in the ecological status of other lake systems, as is required by the EU Water Framework Directive.

Introduction

As a group, freshwater invertebrates are generally regarded as good indicators of the biological integrity of aquatic habitats and they play a key role in lake productivity, nutrient cycling and decomposition (Jones & Sayer 2003; Jónasson, 2004; Brönmark & Hansson, 2005). It has been suggested that they have a wide range of environmental sensitivities and relatively rapid life cycles that can respond quickly to changes in lake processes (Williams & Feltmate, 1992; Rosenberg & Resh, 1993). In recognition of this, the EU Water Framework Directive (WFD) has included macroinvertebrate communities as one of the biological elements to be used for assessing the ecological status of lakes (European Parliament, 2000).

Historically, profundal and sub-littoral macroinvertebrates have been widely used as indicators of the trophic status of lake ecosystems (e.g. Cairns & Pratt, 1993; Brinkhurst, 2002), while the use of the littoral fauna for ecological monitoring has proven more challenging. Pressure and state relationships for littoral invertebrate communities are generally poorly understood (Håkanson, 2001) and they have a high temporal and spatial patchiness that may vary with lake type (White & Irvine, 2003). However, if sampling is limited to clearly defined meso-habitats, then littoral macroinvertebrates do seem to have the potential to be used to monitor lake responses to eutrophication and other pressures (O'Hare et al., 2007). Although zooplankton have been omitted from the WFD, many species are primary grazers, and thus their abundance and species composition are likely to be closely linked to changes in phytoplankton production and, as potential indicators of environmental conditions, they may also provide evidence of changes in the trophic status of lakes

Within a lake, water quality and productivity change over time in response to variations in external drivers such as nutrient input and climate. A freshwater site that has been strongly affected by such changes over the last 40 years is Loch Leven, a large and shallow lake in Scotland, UK where long-term monitoring data has been collected since the late 1960s (Carvalho et al, this volume; Dudley et al., this volume; May & Spears, this volume; May et al., this volume;). Between 1966 and 1973, Loch Leven formed part of the International Biological Programme (IBP), a study of 43 lakes and 12 reservoirs located across a range of geographical regions from the tropics to the arctic, which aimed to take a whole ecosystem approach to understanding lake ecology (Brylinski & Mann, 1973).

The IBP project included studies of both of the macroinvertebrate benthos and zooplankton communities in Loch Leven (Royal Society of Edinburgh, 1974). By the late 1960s, the macroinvertebrate biomass had become dominated by Oligochaeta and Chironomidae. Given the pivotal role of Chironomidae in the benthic community as consumers of algal primary production, and as food for tertiary feeders such as the brown trout, the latter part of the IBP project focused on detailed studies of chironomid productivity (Maitland et al., 1972; Charles et al., 1974a, 1974b, 1975; Maitland & Hudspith, 1974; Charles & East, 1977; Maitland, 1979). Overall, the benthos was found to be relatively poor in terms of species diversity compared with the late 19th century and the first half of the 20th century when Coleoptera, Ephemeroptera, Gastropoda and Trichoptera species were abundant (historical records summarised by Maitland & Hudspith, 1974). Similarly, the crustacean zooplankton had declined from 15 different species recorded at the end of the 19th century to only five species by the early 1970s (Johnson & Walker, 1974). This decline in species richness was attributed to the increasing eutrophication of the loch since the turn of the century (Morgan, 1970, 1974).

In recent years, attempts have been made to improve water quality at Loch Leven by reducing the inputs of nutrients from the catchment (e.g. Bailey-Watts & Kirika 1987, 1999; LLCMP, 1999; May et al., this volume). Recent evidence suggests that this has resulted in an improvement in water quality (D'Arcy et al., 2006; Fergusson et al, 2008). Cyanobacterial blooms have reduced in frequency (Carvalho, pers comm.), spring water clarity has increased (Carvalho et al., this volume) and underwater plants have begun to thrive again in deeper water (Dudley et al., this volume; May & Carvalho, 2010). With the recovery of Loch Leven from eutrophication, comes a rare opportunity to investigate how the invertebrate communities have responded to this change using the IBP data (Royal Society of Edinburgh, 1974) as an historical baseline. Since the IBP project finished in the early 1970s, invertebrate monitoring, including that conducted under the auspices of the UK Environmental Change Network (ECN), has continued in Loch Leven (e.g., Fozzard, 1993; Lowery & Morrison, 1994, 1995, 1996; Morrison, 1997; Long, 1999, 2000), although, apart from work on rotifer ecology (May, 1980a, 1980b, 1983, 1985, 1987a, 1987b, 1989; May & Jones, 1989; May et al., 1992, 2001), most of this has not been published. Our study, therefore, aims to improve our understanding of the impact of eutrophication and recovery at Loch Leven on invertebrate communities and, more generally, to investigate the effectiveness of using invertebrates for the bio-monitoring of shallow lakes that are recovering from eutrophication. This issue is of increasing relevance given the current drive, under the WFD, to restore lakes to good ecological status.

Materials and methods

Study site

Loch Leven (56^{0}10'N, 3^0 30'W) is a large, shallow, lowland, eutrophic lake, situated near Kinross in Scotland, UK. It lies in a predominantly agricultural catchment. The sediments of Loch Leven are composed of 42% sand, 57% mud and <1% stones (Maitland & Hudspith, 1974). The lake is described in detail in May & Spears (this volume).

Field Sampling

Zooplankton

Crustacean zooplankton were sampled at weekly intervals between January 1975 and December 1982 at the Reed Bower and Centre Loch sampling stations (Figure 1) and then not again until April 1989. Thereafter, samples were collected on an occasional basis until regular sampling was resumed in May 1992. Between 1975-1982, samples were collected either by vertical net haul (mesh size 100 µm) from 4 m depth to the surface, or with a tube sampler incorporating a filter of mesh size 125 µm (George & Owen, 1978) that was lowered to a depth of 4 m to 5 m. From 1992 onwards, samples were collected by vertical net haul (mesh size 118 µm). In the laboratory, crustacean zooplankton samples were sub-sampled, and the animals were identified and counted.

Rotifer zooplankton samples were taken with a weighted plastic tube (Lund, 1949) at weekly intervals from 1977 to 1982 and, thereafter, sporadically collected with a bucket from just below the water surface throughout the rest of the 1980s. Regular sampling by bucket resumed from January 1989 and to June 1992, with most samples being taken at the Sluices sampling site (Figure 1). Open water sampling (weekly to fortnightly) restarted in July 1992 and, since then, samples have been collected either using a 2 m plastic drainpipe (5 cm internal diameter) or an integrated tube sampler (3.00 m – 3.75 m) at the Reed Bower sampling location, although samples collected from 1999 onwards have yet to be analysed. The rotifer samples were concentrated by repeatedly settling the samples in glass measuring cylinders and siphoning off the overlying water. The concentrated rotifer samples were counted with an inverted microscope (see May 1980a,b, for details).

<u>Macroinvertebrate benthos</u>

The macroinvertebrate benthos in Loch Leven occurs in two main zones, the sub-littoral and the littoral. The mean depth of Loch Leven is 3.9 m and, although for much of the last 40 years mean Secchi depth transparency measurements have been less than this (Carvalho et al., this volume), the majority of the lake bed is potentially within the zone of effective light penetration, as demonstrated by macrophytes growing at depths in excess of 4 m (Dudley et al., this volume; May & Carvalho, 2010) when water quality is good. Following the definition of Solimini et al. (2006), i.e. that the sub-littoral is the bottom area of a lake that is covered by submerged macrophytes and algal vegetation, the majority of the Loch Leven 'open-water' benthos is classified as 'sub-littoral' rather than 'profundal'. The littoral zone, itself, is defined as the near-shore areas where emergent macrophytes grow (Solimini et al., 2006).

Summary data for the sub-littoral benthos from May and October 1970 was derived from chironomid production studies in the sandy areas undertaken by Maitland & Hudspith (1974). In addition, a spatially comprehensive 'snapshot' survey of 60 samples of the sub-littoral benthos (32 in sand and 28 in mud) of Loch Leven was carried out in May 1994. This survey used the same methodology (i.e. a Maitland corer over sand and a Jenkin surface sediment sampler over mud) as was used in 1968 (Maitland et al, 1972; Maitland, 1979).

The macroinvertebrate communities from three representative stony littoral sites, i.e. Castle Island, Kirkgate and either St Serf's Island (pre-2002) or the shore near the Sluices (post-2002) (Figure 1), were sampled three times a year from 1998 to 2008, using a standard 3-minute kick-sampling technique as part of the routine monitoring for the UK Environmental Change Network (ECN) (Sykes et al., 1999). Additional data from other surveys of the littoral benthos of the loch were compiled from the available literature (Maitland & Hudspith, 1974; Fozzard, 1993; Long, 1999, 2000).

Data Analysis

Recent and older data sets were compared, where possible, using statistical analyses. However, this approach could not be used for survey data that was available in summary form, only. Regression analyses and a t-test were used to test for significant trends over time and for consistency of results across sites. In all cases, the data were tested for normality prior to analysis, using Anderson – Darling tests; it was found that no transformations were required. Minitab Version 13 was used for parametric analysis. Detrended Correspondence Analysis using the computer programme CANOCO (for Windows version 4.5) tested for seasonal, spatial or annual patterns in the ECN littoral benthos data.

Results

The Loch Leven planktonic and littoral benthic invertebrate communities, monitored regularly since 1992 and 1998, respectively, have both undergone substantial changes since the IBP studies of the late 1960s and early 1970s. Both groups have become more species rich and show signs of a decline in total abundance.

Crustacean zooplankton – species composition

The taxon richness of the crustacean zooplankton community between 1975 and 2007 was greater than in the IBP study that was undertaken in the late 1960s (Table 1). In this early study, the crustacean zooplankton was almost entirely composed of the copepod *Cyclops abyssorum*, although small numbers of *Bythotrephes longimanus*, *Leptodora kindti* and *Eudiaptomus gracilis* were also found (Johnson & Walker, 1974). In 1970, the *Daphnia hyalina* species complex was detected for the first time after an absence of 15-20 years (Johnson & Walker, 1974), the last published record being from August 1954 when it was found amongst the stomach contents of four trout (Morgan, 1970). From then onwards, the species composition of the crustacean zooplankton remained fairly stable with *Daphnia* and *C. abyssorum* co-dominating the community, the copepod *E. gracilis* occurring in smaller numbers, and the predatory cladocerans *L. kindti* and *B. longimanus* occurring occasionally and in very low numbers in summer (May et al., 1993; Gunn et al., 1994; Gunn & May, 1995, 1996, 1997, 1998, 1999). The community composition changed again in the 2000s, with *Cyclops vicinus* returning after a long period of absence (Carvalho et al., 2002, 2007, 2008) and *Bosmina longirostris* being recorded in large numbers for the first time in 2007 (Carvalho et al., 2008).

Crustacean zooplankton – abundance

Typically, the crustacean zooplankton in Loch Leven has been co-dominated by *Daphnia* and *Cyclops* populations since the early 1990s, with population maxima occurring in late spring/early summer followed by smaller secondary peaks in the autumn (e.g. Gunn et al., 1999). Carvalho et al. (this volume) examined the data for evidence of long-term trends in *Daphnia* densities by comparing four seasonal population means with a range of water quality variables over the period 1975 to 2007, but found no trends to be significant. However, it became apparent that, over the last two decades, *Daphnia* densities had increased markedly in May (though not quite significantly) in response to warmer spring temperatures and that there was a general decline in *Daphnia* numbers between July & October. This is reflected in the statistically significant decline in the recorded mean summer (June to August) monthly maxima (Figure 2, upper panel). *Daphnia* numbers build up in spring peaking in May and June. They then decrease but remain at higher densities throughout the rest of the summer than in the early months of spring. Overall, summer *Daphnia* numbers tend to reflect the spring phytoplankton bloom and continuing productivity during the summer period.

Rotifer zooplankton – species composition

Nine rotifer species were recorded from samples collected between 1969 and 1970 (Johnson & Walker, 1974), whilst samples collected between 1977 and 1982 contained 14 species (May, 1980a) and those collected between 1991 and 1998, 21 species (Table 2). Samples collected between 1977 and 1982 and between 1991 and 1998 are directly comparable, having been collected over a similar period and with comparable sampling effort. When compared, it was found that all of the species present in the earlier period were also recorded in the later period. However, a 50% increase in species was noted in the latter period, with new records for: *Collotheca mutabilis*, *Conochilus hippocrepis*, *Kellicottia longispina*, *Polyarthra vulgaris*, *Synchaeta oblonga*, *Synchaeta pectinata* and *Synchaeta tremula*. Although most of these additional species can be found in many types of lake across the trophic gradient, it is interesting to note that *C. hippocrepis* and *K. longispina* are usually associated with oligotrophic systems (Ruttner-Kolisko, 1974), suggesting an improvement in water quality in the 1990s compared with 1977-1982. The appearance of *S. tremula* in the 1990s probably reflects an increase in macrophyte coverage (Dudley et al., this volume; May & Carvalho, 2010), as this species tends to live in the littoral zone (Ruttner-Kolisko, 1974).

Rotifer zooplankton – abundance

Total rotifer abundance was relatively low during the 1990s compared with 1977-82, t-test, t value 3.79, d.f. = 7, $p < 0.01$ (Figure 2). This suggests that the reduction in nutrient input to the loch, which began in the late 1980s, strongly influenced rotifer abundance, probably through its impact on food availability. Gunn & May (1997; 1998; 1999) examined the relationship between *Daphnia* numbers and total rotifer abundance in Loch Leven over several years in the 1990s and found that short-term variations in total rotifer abundance were inversely related to *Daphnia* densities. It was concluded that, when *Daphnia* numbers were low, rotifer abundance increased due to decreased competition for their preferred phytoplankton food. It is unlikely that this effect was caused by interference competition (i.e. from physical damage to the rotifer population from *Daphnia* filtering), as has been suggested for other sites (e.g. Burns & Gilbert, 1986), because experimental studies showed that this does not affect the population dynamics of rotifers and *Daphnia* in Loch Leven (May & Jones, 1989).

Littoral benthos - species composition

The littoral community is now dominated numerically by Crustacea (*Asellus aquaticus* and *Gammarus pulex*), Oligochaeta (Tubificidae & Lumbriculidae), Chironomidae, Trichoptera (*Tinodes waeneri*, *Agraylea multipunctata)* and Ephemeroptera (*Caenis luctuosa*). The full list of macroinvertebrate species recorded from Loch Leven's littoral zone is given in Appendix 1. Changes in the total number of macroinvertebrate taxa recorded in the littoral area of Loch Leven over the study period are shown in Figure 3. Ninety-six taxa were recorded pre-1966, 41 taxa between 1966 and 1973 (IBP studies), and 153 taxa between 1993 and 2006. Of these, 24 of the taxa recorded pre-1966 were not recorded again and 48 of the taxa recorded in 1993-2006 were recorded for the first time. All of the taxa collected in 1966-1973 were also found on, at least, one more occasion. As sampling effort and collection method differed among the studies, the opportunities for direct comparisons of these records are limited. However, it is noteworthy that the numbers of Plecoptera, Ephemeroptera, Coleoptera and Trichoptera species recorded during the ECN monitoring (1998-2006) were much higher than those recorded in earlier surveys (Figure 4). In the later surveys, the species recorded included pollution intolerant species such as *Diura bicaudata* and *Ecdyonurus dispar*.

Littoral benthos – abundance /species richness at ECN sites

There was little change in relative total sample abundance or species richness, over time, either at Castle Island or Kirkgate (Figure 5). However, from 2006-2008, abundance and species richness (all seasons combined) were lower than previously recorded at both of these ECN sites. .

Littoral benthos - spatial & temporal patterns at ECN sites

The ordination analysis revealed that the biggest difference in community composition within the ECN samples was not related to location or year, but the season in which the samples were collected. Spring samples were distinct from summer samples, with autumn values overlapping to some extent with both spring and summer (Figure 6).

Sub-littoral benthos – species composition and distribution

The species composition, mean densities and spatial distribution of the sub-littoral benthos recorded in May 1994 (Table 3; Appendix 2) were broadly similar to that found in the IBP studies (Maitland & Hudspith, 1974; Charles et al., 1974a). The most abundant macroinvertebrate groups were Nematoda, Oligochaeta (mainly Tubificidae), Diptera (mainly Chironomidae) and Mollusca (mainly *Pisidium* spp. and *Valvata piscinalis*). New species records included a chironomid genus, *Paracladopelma*, considered to be a genera relatively tolerant of organic pollution (Wilson & Ruse, 2005), and three oligochaete species: the naid *Uncinais ucinata* and the tubificids *Psammoryctides barbatus* and *Limnodrilus claparedeianus*, which have also been recorded in other eutrophic lakes in the UK (Carter & Murphy, 1993; Potter & Learner, 1974). The chironomid *Endochironomus,* a taxa considered tolerant of organic pollution (Wilson & Ruse, 2005), which had not been recorded post-1969 in the IBP chironomid production studies (Charles et al., 1974a), re-appeared in 1994. A number of taxa found during the IBP studies were not recorded in the May 1994 survey. These included a number of chironomid genera including *Diamesa, Microtendipes, Harnischia, Micropsectra, Pentaneura, Psilotanypus* and several naid species, i.e. *Stylaria lacustris, Nais paradalis* and *Nais variables*.

Sub-littoral benthos – abundance (1968, 1970 vs. 1994)

Summary abundance data were available for the major groups of sub-littoral benthos recorded in the sandy areas for some of 1968 and 1970 (Maitland & Hudspith, 1974). These were compared to the May 1994 survey data. Total abundance was substantially higher in May 1994 than in May 1970. *Pisidium*, Oligochaeta, and Nematoda were all more abundant in 1994 than in the earlier years, although Chironomidae numbers were lower (Table 3). The Oligochaete to Chironomid ratio, often used in applied limnology as an indicator of trophic conditions, with higher ratios indicating increased enrichment (e.g. Saether, 1979), was also higher in 1994 than during an equivalent period in 1970. This suggested that water quality was poorer in 1994 than 1970, although better than that recorded for October 1968.

Discussion

Loch Leven is a shallow lake in central Scotland, UK, that has a well documented history of increasing and then decreasing nutrient inputs over the last 100 years (May et al., this volume). When exceptionally high phosphorus inputs to the loch were recorded in 1985, a programme of nutrient reduction was put in place through targeted catchment management (LLCMP, 1999). This resulted in a 60 per cent decrease in the phosphorus (P) input to the loch between 1985 and 1995 (May et al., this volume). Although recycling of P from the sediments prevented an immediate improvement in water quality (Carvalho et al., this volume; Spears et al., this volume), there are clear signs that the water quality is now improving (Carvalho et al., this volume), with macrophytes returning to deeper water (Dudley et al., this volume; May & Carvalho, 2010). Between the periods 1968 - 1977 and 1998 - 2007 the average annual means of total phosphorus (TP) and chlorophyll *a* concentrations declined in Loch Leven from 81 μg l^{-1} and 60 μg l^{-1} to 59 μg l^{-1} and 37 μg l^{-1}, respectively (Carvalho et al., this volume). Carvalho et al. (this volume) also showed, that over this study period, there was a highly significant, increasing linear trend in spring air temperatures.

Lakes that are undergoing eutrophication are normally characterised by increases in nutrient concentrations and phytoplankton production (often including increased frequencies and intensities of toxic cyanobacterial blooms). These changes have the potential to reduce water clarity and increase the supply of organic matter to the sediments which, in turn, may lower oxygen availability and reduce structural complexity within the benthic zone resulting in an impact on phytobenthos production (Heiskanen & Solimini, 2005). Metrics of the likely ecological impacts of eutrophication on benthic and pelagic invertebrate communities are increased absolute levels of abundance (reflecting the increased productivity of nutrient-enriched systems) and reduced species diversity (indicating a reduction in suitable physiological conditions for many species to thrive in).

Detailed sampling of the invertebrate community only commenced when Loch Leven was already impacted, making it difficult to set targets and assess recovery. However, evidence for their being a time lag in the expected recovery of some components of the fauna, after the implementation of pollution controls enacted in the late 1980s, is provided by the results of the 1994 “snap-shot” study of the sub-littoral benthos. It showed that the fauna was still indicative of eutrophic conditions and was comparable with that found in the IBP studies in the 1960s and early 1970s. Although the rest of the Loch Leven invertebrate dataset is patchy post-IBP with, for example, some large gaps in the zooplankton data, some encouraging trends pointing towards ecological recovery from eutrophication are discernible. In the years after the restoration programme began, species diversity (including species known to be less tolerant of eutrophication) increased in both the zooplankton and the littoral benthos communities and total abundance declined, especially in the rotifer zooplankton community.

It should be noted, however, that the most significant change in the crustacean zooplankton community occurred in 1970, when *Daphnia* was detected after a temporary absence of some 15-20 years. This occurred before the restoration programme began and is believed to have been a response to reductions in the discharge of dieldrin by a local mill (D'Arcy et al., 2006; May & Spears, this volume) rather than to any change in nutrient input. The re-appearance of *Daphnia* had a major impact on zooplankton (Johnson & Walker, 1974) and phytoplankton communities (Bailey-Watts, 1974) in the early 1970s as well as on the macroinvertebrate benthos, with the latter shifting from detrital/phytoplankton feeding species to benthic algal feeding species (Johnson & Walker, 1974; Maitland & Hudspith, 1974). Carvalho et al. (this volume) carried out a detailed examination of trends in *Daphnia* numbers at Loch Leven in relation to changing water quality and concluded that, in the early 1970s, TP and chlorophyll *a* concentrations dropped abruptly as a result of the re-appearance of *Daphnia* in the lake. However, since 1988 the lower densities of *Daphnia* observed in summer cannot be explained by phytoplankton biomass, as summer chlorophyll *a* trends show no significant decline over the same period. Carvalho et al. (this volume) suggest that the decline in mean and maxima *Daphnia* densities over the last decade may, therefore, be as a result of either an increased proportion of poorer quality food (e.g. inedible or toxic algae) in the *Daphnia* diet or increased predation from zooplanktivorous fish.

Fish predation on *Daphnia* in Loch Leven may have increased because due to stocking with brown trout (*Salmo trutta*, L.) and rainbow trout (*Oncorhynchus mykiss* Walbaum) in 1983-2006 and 1993-2004, respectively, to boost angling catches (Duncan, 1994; May & Spears, this volume; Winfield et al., this volume). The proportion of macroinvertebrates and zooplankton in the diets of brown trout (*Salmo trutta* L.) collected between 1993 and 1995 (Lowery & Morrison, 1994, 1995, 1996; Morrison, 1997) has been compared to Nature Conservancy data collected over the period 1967-1970 (Maitland, unpublished data). This analysis showed that, by the 1990s, chironomid larvae, although still the dominant food item, had become less important as a food source, with Mollusca and Crustacea (including zooplanktonic microcrustacea) making up a greater proportion of the diet. Although detailed information on prey availability is not available for the two study periods, it is known that chironomids were present in Loch Leven in high numbers in the late 1960s, which may explain their dominance in the diet of trout at the time. In a separate study, Yang et al. (1999) showed that the densities and size frequency of the *Daphnia* population in Loch Leven changed little over the period 1992-95, suggesting that stocking with rainbow trout which began in 1993 was less important than other factors, such as food resources and water temperature, in controlling *Daphnia* numbers at that time. Overall, improvements in water quality seem to have resulted in a general decline in crustacean zooplankton abundance coupled with a small increase in species diversity over the period of restoration. Changes in species composition and total abundance were more marked in the rotifer community than in the crustacean zooplankton community, suggesting that rotifers respond more readily to changes in nutrient inputs and, subsequently, water quality than their crustacean counterparts. Further analysis of the rotifer samples collected from 1999 onwards would be instructive in seeing whether this trend of declining total abundance and increased species diversity has continued into the last decade.

Classification and monitoring schemes based on macroinvertebrates have, traditionally, focused on the profundal fauna of deep lakes (e.g. Saether 1979; Wiederholm 1981), where more uniform environmental conditions prevail. In general, macroinvertebrates from the littoral areas of lakes such as Loch Leven, where a sub-littoral zone predominates, have received relatively little attention as potential environmental indicators. Solimini et al. (2006) hypothesised that benthic invertebrate communities in this zone would be less affected by eutrophication than the benthos in the profundal region and Moss et al. (2003) concluded that metric indicators based on functional status might be the most reliable way of assessing ecological condition in this area. Such metrics include the ratio of oligochaetes to chironomids (O:C) in soft sediment samples. The data from Loch Leven seem to support the use of the O:C ratio and the sub-littoral benthos, in general, as a measure of environmental conditions in these areas, and is in agreement with similar findings from other systems (e.g. Lang & Reymond, 1992).

Solimni et al. (2006) speculated further that littoral invertebrate communities would be affected even less by eutrophication than the sub-littoral benthos. It has been suggested that the heterogeneity of shallow lake habitats causes differences within the benthos that would mask any changes associated with changes in nutrient status (Moss et al, 2003). However, because the ECN littoral benthos sampling method used in this study is limited to a single type of shoreline (i.e. stony) and the same sites are used each year, the differences caused by habitat heterogeneity should be minimised and sensitivity to other types of change, such as lake wide eutrophication, maximised (Brauns et al., 2007; O'Hare et al, 2007; White & Irvine, 2003). The value of the Loch Leven system is that it is one of only a few lakes that have long term records over a period of recovery from eutrophication with which this hypothesis can be tested. The results of this study only partially support these assertions. Regression analysis of metrics recorded at two separate sampling sites did show that different locations can produce comparable results year-on-year for eutrophication sensitive metrics such as total abundance. However, temporal variation in species richness differed at the two sites. This may have been caused by changes in local conditions, such as variations in water level, which can expose different combinations of meso-habitat at different sites to sampling. Hence, macroinvertebrates at individual sites may respond more to changes in local, rather than lake-wide, conditions in some cases. Therefore, care should be taken when interpreting littoral invertebrate data as it may not be indicative of water quality, alone.

Conclusions

All of the available macroinvertebrate and zooplankton data collected in Loch Leven since the baseline IBP study in the late 1960s/early 1970s have been compiled. Results from detailed analysis of the trends in all of the different components of the invertebrate community, despite large gaps in the data, have shown, overall, a positive response, in terms of increased species diversity and reduction in total abundance (Table 4). There was, however, a substantial delay in the ecological recovery of some elements of the fauna in response to changes in management practices and reductions in nutrient input at Loch Leven. This time lag has important implications for assessing improvements in the ecological status of other lake systems under the EU Water Framework Directive.

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Tables

Table 1 Crustacean zooplankton species in Loch Leven, late 1960s to 2007. Chydoridae and miscellaneous copepods associated with the sediments and aquatic vegetation, which are occasionally found in the plankton, are not included.

	Late 1960s	**Early 1970s**	**1990s**	**2000s**
Cladocera				
Daphnia hyalina species complex	-	X	X	X
Bosmina longirostris (O.F.Müller)	-	-	-	X
Bythotrephes longimanus Leydig	X	X	X	X
Leptodora kindti (Focke)	X	X	X	X
Copepoda				
Eudiaptomus gracilis (Sars)	X	X	X	X
Cyclops abyssorum Sars	X	X	X	X
Cyclops vicinus Uljanin	-	-	-	X

Table 2 Planktonic rotifer species in Loch Leven, late 1960s to 1998.

Species	1969-1970	1977-1982	1991-1998
Asplanchna priodonta Gosse 1850	X	X	X
Brachionus angularis Gosse 1851	-	X	X
Brachionus rubens (Ehrenberg)	X	-	
Collotheca mutabilis (Hudson 1885)	-	-	X
Colurella adriatica Ehrenberg 1831	-	X	X
Conochilus hippocrepis (Schrank 1830)	-	-	X
Conochilus unicornis Rousselet 1892	X	X	X
Filinia longiseta (Ehrenberg 1834)	X	X	X
Kellicottia longispina (Kellicott 1879)	-	-	X
Keratella cochlearis (Gosse 1851)	X	X	X
Keratella quadrata (Müller 1786)	X	X	X
Notholca squamula Müller 1786	-	X	X
Polyarthra dolichoptera Idelson 1925	X	X	X
Polyarthra euryptera (Wierzejski 1893)	-	X	X
Polyarthra major (Burckhardt 1900)	-	-	X
Polyarthra vulgaris (Carlin 1943)	-	-	X
Pompholyx sulcata Hudson 1885	X	X	X
Synchaeta grandis Zacharias 1893	-	X	X
Synchaeta kitina Rousselet 1892	-	X	X
Synchaeta oblonga (Ehrenberg 1832)	-	-	X
Synchaeta pectinata Ehrenberg	X	-	
Synchaeta tremula (Müller 1786)	-	-	X
Trichocerca pusilla Lauterborn 1898	-	X	X

Table 3 Density (individuals m^{-2}) of the major taxonomic groups of macroinvertebrates found in the sand area of Loch Leven in 1968, 1970 and 1994; the ratio of Oligochaeta to Chironomidae is also shown.

Macroinvertebrate taxonomic group	**October**		**May**	
	1968	**1970**	**1970**	**1994**
Hirudinea	158	109	29	93
Gastropoda	255	206	177	77
Pisidium	995	840	199	1,635
Chironomidae	21,411	23,039	16,784	14,414
Oligochaeta	25,934	3,729	3,330	6,876
Nematoda	34,953	243	227	8,176
Total	**83,706**	**28,166**	**20,746**	**31,271**
Oligochaeta /Chironomidae ratio	*1.21*	*0.16*	*0.20*	*0.48*

Table 4 Summary of biotic signals, by invertebrate group, indicative of ecological recovery in Loch Leven since the IBP baseline studies of 1966-1973.

Invertebrate Group	**Species Composition**	**Abundance**
Crustacean zooplankton	Increased species diversity	Increased *Daphnia* densities in May; lower mean summer monthly maxima
Rotifer zooplankton	Increased species diversity	Total rotifer abundance significantly declined in 1990s
Littoral benthos	Increased species diversity	Unclear - insufficient data to draw conclusions
Sub-littoral benthos	Unclear - no data since 1994	Unclear - no data since 1994

Figure captions

Fig. 1 Map of Loch Leven showing macroinvertebrate and zooplankton sampling sites

Fig. 2 Trends in abundance of zooplankton in Loch Leven over the study period. Regression parameters for *Daphnia* are: $F = 9.25$, $n = 24$, $P < 0.01$, Rsq. Adj. 24.8%. Summer mean rotifer numbers were significantly higher in the earlier sampling period (1977-1982) than in the later period (1991, 1992, 1994-1998). T-test: t value of 3.79, d.f. = 7, $p<0.01$)

Fig. 3 Total number of macroinvertebrate taxa recorded in studies of the littoral area of Loch Leven over time; the black shaded areas show the number of taxa that were unique to one time period, only

Fig. 4 The number of species in selected major insect groups recorded during the IBP (1966 – 1973; cross hatching) and ECN (1998 – 2006; black shading) time periods; the pre-1973 data are taken from (Maitland & Hudspith, 1974).

Fig. 5 Comparison of metrics calculated from macroinvertebrate data collected at two Environmental Change Network (ECN) littoral sites, Kirkgate and Castle Island, in Loch Leven between 1998-2008.

Fig. 6 Detrended Correspondence Analysis (DCA) of the three season Environmental Change Network (ECN) macroinvertebrate data from 1998 to 2006.

Figure 1

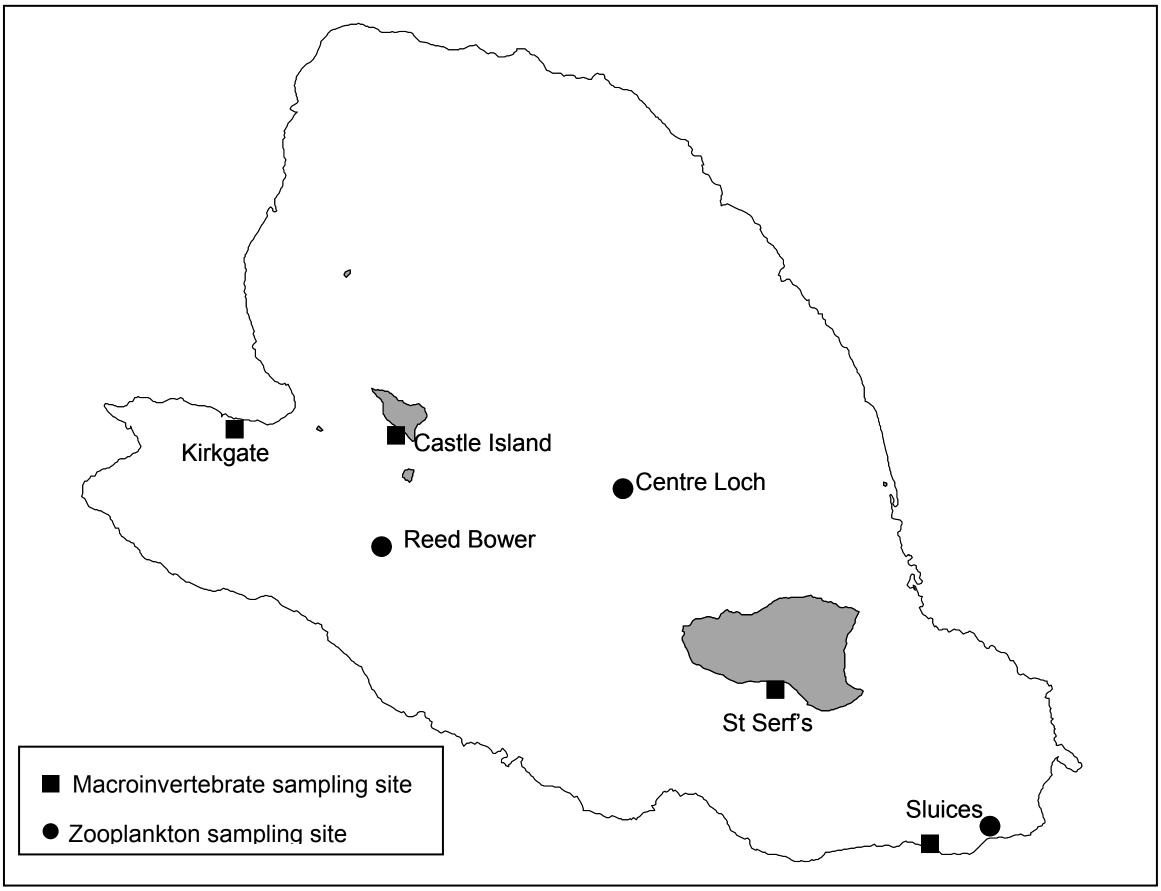
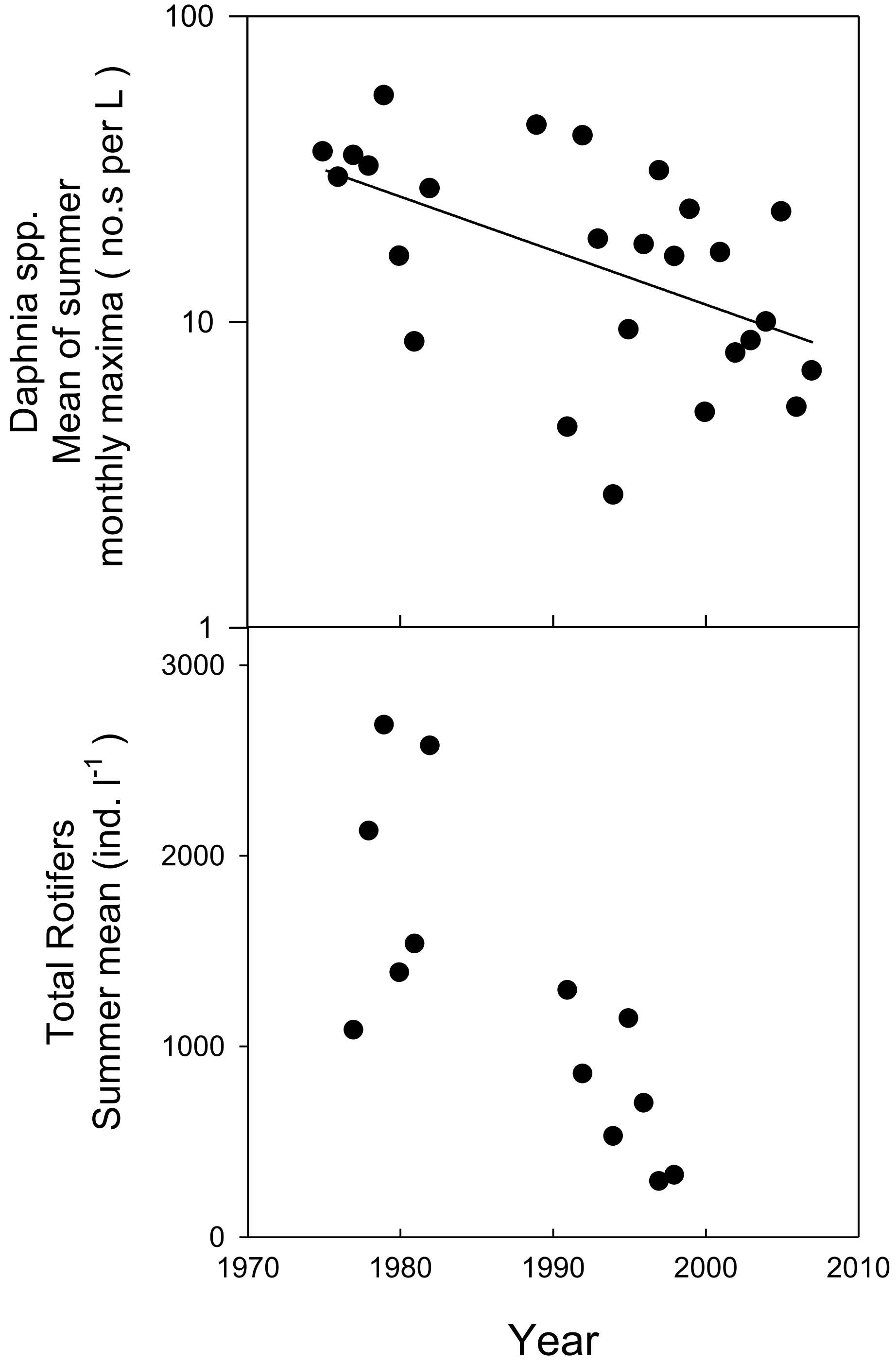
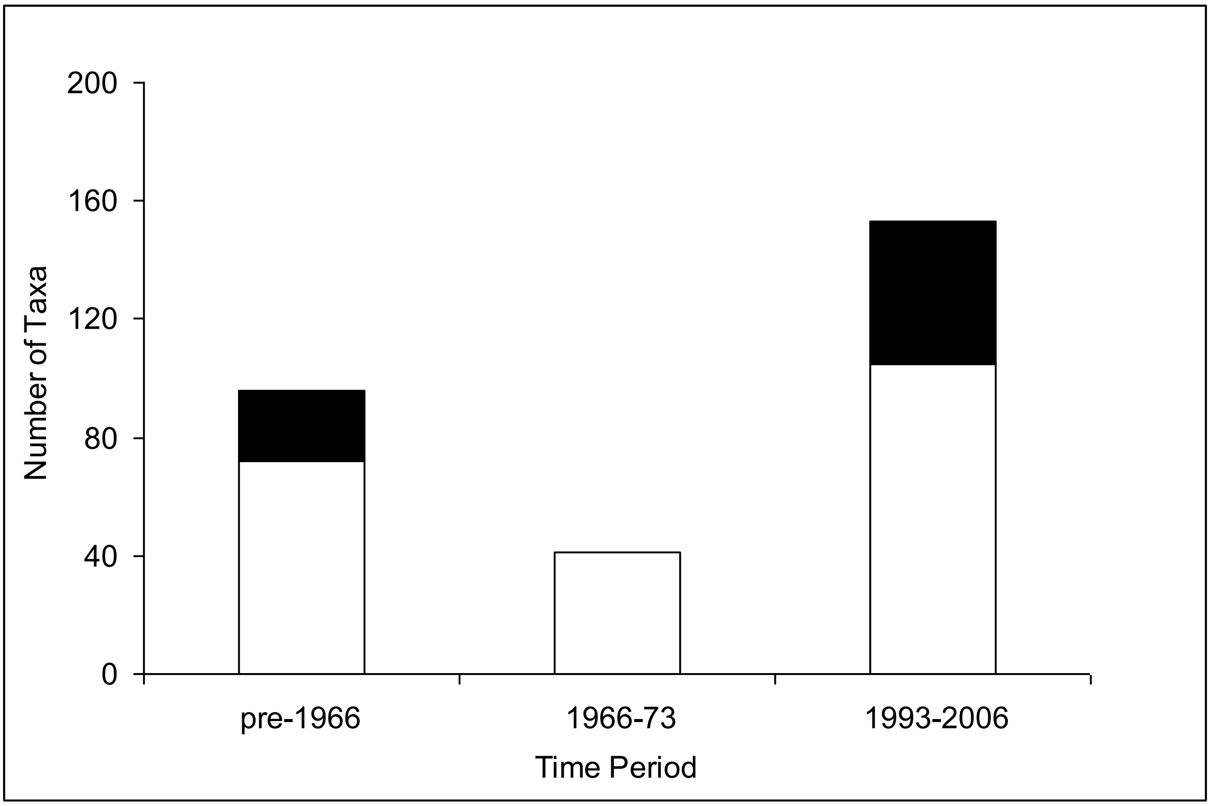

Kirkgate
Castle Island
Centre Loch
Reed Bower
St Serf's
Sluices
Macroinvertebrate sampling site
Zooplankton sampling site

Figure 2



Daphnia spp.
Mean of summer
monthly maxima (no.s per L)
100
10
1
Total Rotifers
Summer mean (ind. l-1)
3000
2000
1000
0
1970
1980
1990
2000
2010
Year

Figure 3



200
160
120
80
40
0
Number of Taxa
pre-1966
1966-73
1993-2006
Time Period

Figure 4

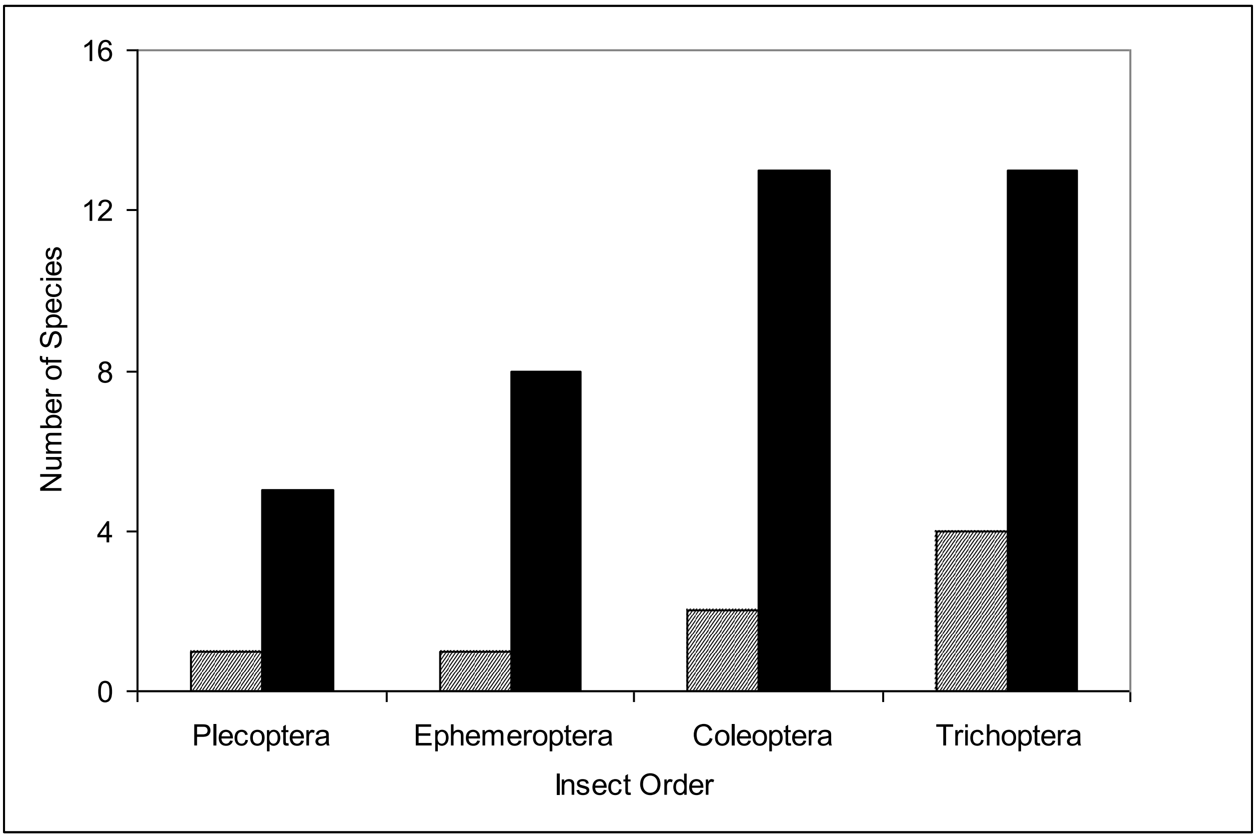

16
12
8
4
0
Number of Species
Plecoptera
Ephemeroptera
Coleoptera
Trichoptera
Insect Order

Figure 5

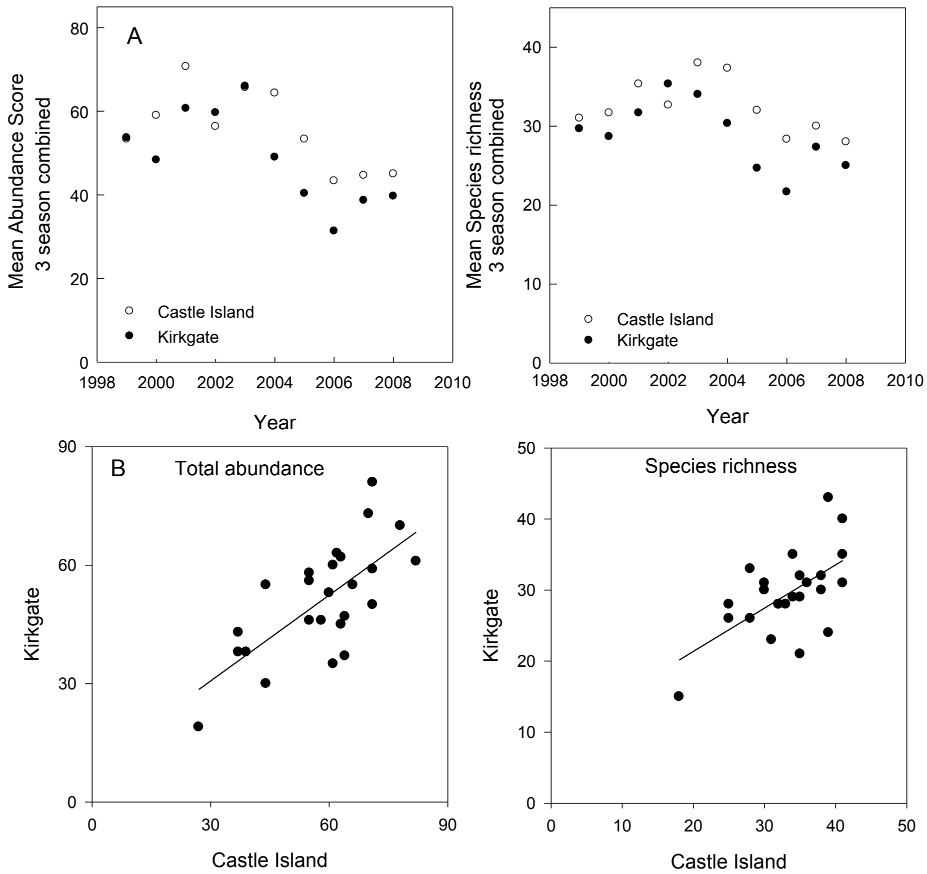
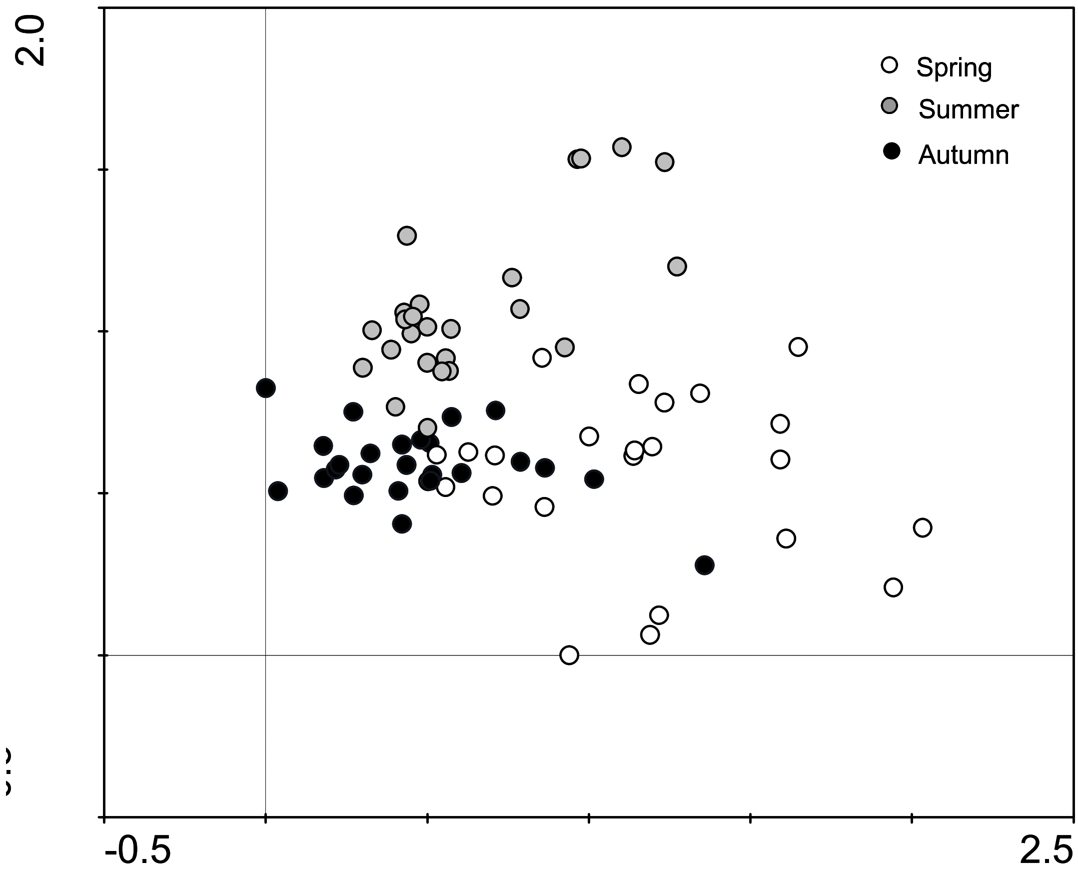

A
Mean Abundance Score
3 season combined
Castle Island
Kirkgate
Year
Mean Species richness
3 season combined
B
Total abundance
Kirkgate
Castle Island
Species richness

Figure 6



Appendix 1 Macroinvertebrate species recorded from the littoral zone in Loch Leven

Family/Class	**Species/Genus**	**Pre-1966**	**IBP 1966-73**	**FRPB/SEPA 1993-1999**	**ECN 1998-2006**
Planariidae	*Polycelis* spp. *(nigra (*Muller*)/tenuis* (Ijima))	X	X	X	X
Nematoda		X	X		X
Valvatidae	*Valvata cristata* Muller	X			
	*Valvata piscinalis (*Muller)	X	X	X	X
	Valvata macrostoma Morch			X	
Hydrobiidae	*Potamopyrgus antipodarum* (Gray)	X	X	X	X
Physidae	*Physa fontinalis* (L.)	X	X	X	X
Lymnaeidae	*Radix balthica* (L.)	X	X	X	X
	Stagnicola palustris (Muller)	X			
	Radix auricularia (L.)	X			
	Galba truntcatula (Muller)	X		X	X
	Lymnaea stagnalis (L.)				X
	Lymnaea sp.				X
Planorbidae	*Bathyomphalus contortus* (L.)	X			X
	Gyraulus albus (Muller)	X	X	X	X
	Planorbis carinatus Muller	X		X	X
	Gyraulus laevis (Alder)			X	
	Planorbis planorbis (L.)	X		X	
	Gyaulus crista (L.)	X			X
Ancylidae	*Ancylus fluviatilis* Muller	X	X	X	X
Unionidae	*Anodonta anatina* (L.)	X	X		X
Sphaeriidae	*Pisidium* spp & *Sphaerium* spp	X	X	X	X
Oligochaeta		X	X	X	X
Hydridae			X		X
Piscicolidae	*Piscicola geometra* (L.)				X
Glossiphoniidae	*Glossiphonia complanata* (L.)	X	X	X	X
	Abloglossiphonia heteroclita (L.)		X	X	X

Family/Class	Species/Genus	Pre-1966	IBP 1966-73	FRPB/SEPA 1993-1999	ECN 1998-2006
	Helobdella stagnalis (L.)	X	X	X	X
	Theromyzon tessulatum (Muller)	X	X	X	X
	Hemiclepsis marginata (Muller)			X	
Erpobdellidae	*Erpobdella octoculata* (L.)	X	X	X	X
	Erpobdella testacea (Savigny)			X	
	Dina lineata (Muller)				X
Hydracarina			X	X	X
Ostracoda		X	X	X	X
Cladocera		X	X	X	X
Copepoda		X	X	X	X
Asellidae	*Asellus aquaticus* L.	X	X	X	X
Gammaridae	*Gammarus pulex* (L.)	X	X	X	X
Baetidae	*Baetis scambus* Eaton				X
	Cloeon simile Eaton	X		X	X
	Centroptilum luteolum (Muller)	X			
Siphlonuridae	*Siphlonurus lacustris* Eaton			X	X
Heptgeniidae	*Ecdyonurus dispar* (Curtis)			X	X
Leptophlebiidae	*Habrophlebia fusca* (Curtis)				X
Ephemerellidae	*Serratella ignita* (Poda)				X
Caenidae	*Caenis horaria* (L.)	X	X	X	X
	Caenis luctuosa (Burmeister)			X	X
Nemouridae	*Nemoura cinerea* (Retzius)			X	
Leuctridae	*Leuctra* sp.			X	
	Luectra fusca (L.)				X
	Leuctra hippopus (Kempny)			X	
	Leuctra geniculata (Stephens)				X
Capniidae	*Capnia bifrons* (Newman)			X	
Perlodidae	*Diura bicaudata* (L.)			X	X
	Isoperla grammatica (Poda)				X
Chloroperlidae	*Siphonoperla torrentium* (Pictet)		X		X

Family/Class	Species/Genus	Pre-1966	IBP 1966-73	FRPB/SEPA 1993-1999	ECN 1998-2006
Coenagriidae		X		X	
Gerridae		X	X		X
Corixidae		X	X	X	X
	Corixa punctata (Illiger)			X	
	Callicorixa praeusta (Fieber)	X	X		X
	*Callicorixa wollastoni (*Douglas & Scott)	X	X		
	Arctocorisa germari (Fieber)	X			X
	Micronecta poweri (Douglas & Scott)	X	X		X
	Paracorixa concinna (Fieber)	X		X	
	Sigara semistriata (Fieber)	X			
	Sigara distincta (Fieber)	X			
	Sigara dorsalis (Leach)	X	X	X	X
	*Sigara falleni (*Fieber)	X	X	X	X
Haliplidae	*Haliplus lineolatus* Mannerheim	X		X	X
	*Haliplus lineatocollis (*Marsham)	X			
	Haliplus confinis Stephens	X		X	X
	Haliplus ruficollis (Degeer)	X	X		
	Haliplus immaculatus Gerhardt	X			
	Haliplus wehnckei Gerhardt	X			
	Halplus fulvus (Fabricius)	X			
	Haliplus spp.		X	X	X
Dytiscidae		X	X	X	X
	Hygrotus inaequalis (Fabricius)	X			
	*Coelambus novemlineatus (*Stephens)	X			
	Ilybius fuliginosa (Fabricius)	X	X	X	
	Nebrioporus depressus/elegans	X		X	X
	Agabus sturmii (Gyllenhal)	X			
	Agabus chalconatus (Panzer)	X			
	Agabus bipustulatus (L.)	X			
	Platambus maculatus (L.)	X			X

Family/Class	**Species/Genus**	**Pre-1966**	**IBP 1966-73**	**FRPB/SEPA 1993-1999**	**ECN 1998-2006**
	Rantus exsoletus (Forster)	X			
	Ranthus frontalis (Marsham)	X			
	Colymbetes fuscus (L.)	X			
	Dytiscus marginalis L.	X			
	Gyrinus natator (L.)	X			
	Oreodytes sanmarkii (Sahlberg)	X			X
	Oreodytes septentrionalis (Gyllenhal)	X			X
	Hydroporus striola (Gyllenhal)	X			
	Hydroporus palustris (L.)	X			
	Hydroporus planus (Fabricius)	X			
Hydrophilidae		X			X
Elmidae	*Elmis aenea* (Muller)				X
	*Limnius volckmari (*Panzer)		X		X
	Oulimnius tuberculatus (Muller)		X	X	X
	Esolus parallelepipedus (Muller)				X
Dryopidae					X
Sialidae	*Sialis lutaria* (L.)			X	
Rhyacophilidae	*Rhyacophila dorsalis* (Curtis)			X	
Hydroptilidae	*Agraylea multipunctata* Curtis			X	X
Psychomyiidae	*Tinodes waeneri* (L.)		X	X	X
Polycentropopdidae	*Cyrnus trimaculatus* (Curtis)				X
	Polycentropus flavomaculatus (Pictet)			X	X
	Holocentropus sp.			X	
Limnephilidae				X	X
	Anabolia nervosa (Curtis)			X	X
	Chaeopteryx villosa (Fabricius)				X
	Limnephilus centralis Curtis			X	X
	Limnephilus lunatus Curtis			X	X
	Limnephilus vittatus (Fabricius)			X	X
Goeridae	*Goera pilosa* (Fabricius)				X

Family/Class	Species/Genus	Pre-1966	IBP 1966-73	FRPB/SEPA 1993-1999	ECN 1998-2006
Leptoceridae	*Athripsodes cinereus* (Curtis)			X	X
	Mystacides sp.			X	X
	Mystacides longicornis (L.)			X	
	Oecetis ochracea (Curtis)		X		X
Pyralidae				X	
Tipulidae				X	X
Psychodidae					X
Ceratopogonidae			X	X	X
Simuliidae					X
Chironomidae		X	X	X	X
Empididae					X
Dolichopodidae					X
Sciomyzidae					X
Muscidae					X

Appendix 2 Mean densities (individuals m^{-2}) of macroinvertebrate taxa recorded in sandy and muddy sediments in Loch Leven, May 1994; immature specimens are denoted by an asterisk (*) while 'P' indicates a taxon that was present in the family level count but was not counted separately.

Taxa	**Sand**	**Mud**
Nematoda	8,176	42
Mollusca		
Gastropoda		
Valvata piscinalis (Muller)	34	188
Potamoprygus antipodorum (Gray)	25	0
Radix balthica (L.)	8	0
Bivalvia		
Sphaerium spp.	0	18
Pisidium spp.	1,635	592
Annelida		
Oligochaeta		
Naididae	662	0
Uncinais ucinata*(*Orsted)	-	-
Tubificidae	5,149	5,182
Aulodrilus pluriseta (Piguet)	-	P
Potamothrix hammoniensis (Michaelsen)	-	P
Limnodrilus claparedeianus Ratzel	-	P
Limnodrilus hoffmeistrei Claperède	P	-
Psammoryctides barbatus (Grube)	P	P
Potamothrix/Tubifex group*	P	P
Limnodrilus/P.moldaviensis group*	P	-
Enchytraeidae	419	0
Lumbriculidae	587	9
Lumbriculus variegatus (Muller)	-	-
Hydracarina	0	9
Hirudinea		
Glossiphonia complanata (L.)	0	9
Helobdella stagnalis (L.)	34	99
Erpobdella octoculata (L.)	59	0
Arthropoda		
Crustacea		
Ostracoda	0	18
Malacostraca		
Asellus aquaticus L.	0	9
Insecta		
Ephermoptera		
Caenis horaria (L.) & C. *luctuosa* (Burmeister)	0	18
Trichoptera		
Oecetis ochracea Curtis	25	18
Diptera		

Chironomidae		
Tanypodinae		
Procladius sp.	59	4,106
Orthocladiiinae		
Psectorocladius sp.	75	0
Chironominae		
Chironomus sp.	8	583
Cladotanytarsus sp.	11,086	0
Cryptochironomus sp.	176	9
Dicrotendipes sp.	75	63
Endochironomus sp.	17	9
Glyptotendipes sp.	8	9
Paracladopelma sp.	84	0
Polypedilum sp.	8	0
Stictochironomus sp.	2,818	0
Tanytarsus sp.	0	1,219
Ceratopogonidae	143	18