Hydrobiologia
DOI 10.1007/s10750-011-0925-8

LOCH LEVEN RESEARCH

Changes in the fish community of Loch Leven: untangling anthropogenic pressures

I. J. Winfield · C. E. Adams · J. D. Armstrong · R. Gardiner · A. Kirika · J. Montgomery · B. M. Spears · D. C. Stewart · J. E. Thorpe · W. Wilson

Abstract Loch Leven, U.K., contains brown trout (*Salmo trutta*), eel (*Anguilla anguilla*), minnow (*Phoxinus phoxinus*), perch (*Perca fluviatilis*), pike (*Esox lucius*) and three-spined stickleback (*Gasterosteus aculeatus*), with brook lamprey (*Lampetra planeri*) and stone loach (*Barbatula barbatula*) also present in its tributaries. Arctic charr (*Salvelinus alpinus*), Atlantic salmon (*Salmo salar*) and flounder (*Platichthys flesus*) are now extinct. The brown trout population has supported a world-renowned recreational fishery for over a century, although a decline in fishery performance led to extensive stocking between 1983 and 2006, including with non-native rainbow trout (*Oncorhynchus mykiss*). This review combines historical information with contemporary gill-net and hydroacoustic surveys. In 2008, brown trout, perch and three-spined sticklebacks were abundant, but pike and stone loach were rare. The obstruction of migratory routes was probably responsible for the loss of Atlantic salmon and flounder, while a lowering of water level likely caused the extinction of Arctic charr and contributed to a reduction in pike abundance. Perch abundance has fluctuated markedly, being influenced by disease and eutrophication, although a reduction in nutrients and associated recovery of macrophytes are likely to have benefitted this species. Although the brown trout population has undoubtedly shown a long-term decline, individuals are currently in excellent condition.

Keywords Population · Eutrophication · Lake level · Fishery · Brown trout (*Salmo trutta*) · Rainbow trout (*Oncorhynchus mykiss*) · Perch (*Perca fluviatilis*) · Cormorant (*Phalacrocorax carbo*)

Guest editors: L. May & B. M. Spears / Loch Leven: 40 years of scientific research

I. J. Winfield (✉)
Centre for Ecology & Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster LA1 4AP, UK
e-mail: ijw@ceh.ac.uk

C. E. Adams
Scottish Centre for Ecology and the Natural Environment, University of Glasgow, Glasgow G12 8QQ, UK

J. D. Armstrong · R. Gardiner · D. C. Stewart · J. E. Thorpe
Freshwater Laboratory, Marine Scotland, Faskally, Pitlochry PH16 5LB, UK

A. Kirika · B. M. Spears
Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK

J. Montgomery · W. Wilson
Kinross Estate Office, Kinross KY13 8AS, UK

Introduction

Along with phytoplankton, which may periodically appear to colour an entire lake vivid green, and birds,

Published online: 15 November 2011

which at certain times of year teem on its water surface, terrestrial margins and in the skies above it, a lake's fish populations commonly enjoy the highest public profiles of all of its flora and fauna. However, in contrast to phytoplankton, which are easy to sample, and birds, which are easy to count, the assessment and monitoring of lake fish communities is technically difficult and presents a number of continuing methodological challenges (Kubečka et al., 2009). When the complexities and uncertainties of fisheries socio-economics within a multi-use landscape (e.g. Arlinghaus et al., 2002) are added to this situation, objective and confident understanding and management of lake fish communities become extremely difficult to achieve.

The history and contemporary state of the fish community of Loch Leven in east-central Scotland, U.K., is a good example of this complexity, even though a total of only 12 resident and migratory fish species has been recorded in this large, shallow and eutrophic lake (see below). Amongst these species, the local population of brown trout (*Salmo trutta*) has received by far the greatest attention in terms of research effort and fisheries exploitation, with commercial netting having been practised here from 1314 to 1873 and recreational fly fishing from 1844 onwards (Thorpe, 1974a; Munro, 1994). The latter, at its height, supported 52 hire boats (W. W., unpublished data). Management activities in support of angling activity have been documented by Montgomery (1994), including an early example of the use of hatchery and rearing ponds in 1882 when 60,000 fry and 4,000 2-year-old brown trout of unrecorded origin were placed in inflowing streams, a practice that was expanded from the 1920s to 1936 resulting in up to 300,000 fry being hatched each year. Subsequently, the hatchery was closed during the Second World War and only reopened in the early 1980s using 'home-bred' stock of exclusively local origin (Montgomery, 1994). The Loch Leven trout fishery persists to the present with 13 boats available for hire (W. W., unpublished data) and a national and international reputation such that it was included as a venue for the 29th FIPS-Mouche World Fly Fishing Championships in June 2009. In recent years, however, it has experienced turbulent fortunes with various anthropogenic pressures (e.g. Duncan, 1994), the socio-economic vagaries of the angling community (e.g. Montgomery, 1994) and predation by cormorants (*Phalacrocorax carbo*) (e.g. Stewart et al., 2005) all potentially involved. Many of these influential factors have a long local history (May & Spears, 2011) and so an understanding of the contemporary fish community requires a correspondingly long-term perspective.

This article reviews historical published and unpublished information in combination with contemporary gill net and hydroacoustic surveys to describe long-term changes in the fish community of Loch Leven. Observed alterations in the fish community are then interpreted in the context of historical and current anthropogenic pressures.

Materials and methods

Study site

Loch Leven is a large (surface area approximately 13.3 km^2) but relatively shallow (mean depth 3.9 m, maximum depth 25.5 m) lake located in east-central Scotland, U.K. (56° 12′N, 3° 22′W; altitude 107 m). This culturally eutrophicated water body drains a catchment of 145 km^2 and discharges into the Forth Estuary via the River Leven. Further details of its bathymetry (Kirby, 1971), water quality history (Carvalho et al., 2011; May et al., 2011; Spears et al., 2011), phytoplankton (Bailey-Watts, 1982; Bailey-Watts et al., 1990), zooplankton (Gunn et al., 2011), macrophytes (Dudley et al., 2011), macroinvertrbrates (Gunn et al., 2011) and birds (Carss et al., 2011) are reported elsewhere.

Historical published and unpublished information

Published and unpublished information relevant to an understanding of the fish community of Loch Leven was collated by searches of the published and grey literature, combined with unpublished data held by the authors who collectively have been directly responsible for, or involved with, almost all fish research and all fisheries operations on the loch. This resulted in the identification of over 30 publications and reports including, or supplemented with, data on fish populations from the 1960s, 1970s, 1980s, 1990s and 2000s and fisheries data from 1900 to the 2000s.

Contemporary hydroacoustic and gill net surveys

Before this study, the most recent sampling of the fish populations of Loch Leven had been undertaken using survey gill nets during March and December 2001 (Stewart et al., 2005). Consequently, a community sampling programme using a combination of hydroacoustics and survey gill nets as used on a series of other lochs by Winfield et al. (2009a) was begun in late 2007.

On 10 October 2007, day- and night-time hydroacoustic surveys were performed where water depth exceeded approximately 5 m in the southern area of the loch using a BioSonics DT6000 echo sounder (BioSonics Inc., Seattle, U.S.A.) with a 200 kHz split-beam vertical transducer following the approach described by Winfield et al. (2009a). The transducer was positioned approximately 0.5 m below the surface of the water and data were recorded starting from a range of 2 m. Following a standard hydroacoustic analysis employed extensively elsewhere in the U.K. by Winfield et al. (in press), the resulting data were used to produce densities of 'small' (i.e. −52 to −45 dB, length 40–99 mm), 'medium' (−44 to −37 dB, length 100–249 mm) and 'large' (greater than −37 dB, length greater than 250 mm) fish along each of 18 transects.

Gill netting was undertaken using benthic and pelagic versions of the Norden survey gill net as described by Appelberg (2000). The benthic version is bottom-set and is approximately 1.5 m deep and 30 m long, with 12 panels of equal length having bar-mesh sizes 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm, respectively. The pelagic version, which is set floating from the water surface, is approximately 6.0 m deep and 27.5 m long, with 11 panels of equal length having bar-mesh sizes 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm, respectively. A total of nine such nets was set overnight to sample three inshore-bottom sites, three offshore-bottom sites and three offshore-surface sites on 17 March, 20 August and 6 October 2008. Upon lifting, all fish were removed from the nets and killed before being identified, counted and then frozen at −20°C for future processing in the laboratory. The latter comprised measurements of individual length (fork length, mm) and weight (g) and the removal of materials for age and diet determination.

For comparison purposes, corresponding individual data were assembled from brown trout and perch taken from a total of seven other lochs sampled using the same gill-netting methodology in 2007 and 2008 by Winfield et al. (2008a, b, 2009b), and from Loch Leven perch sampled in March 2001 (D. C. S., unpublished data from gill netting) and August 1968 (J. E. T., unpublished data from trawling).

Results

Historical fish community

A total of 11 native fish species has been recorded in Loch Leven, i.e. Arctic charr (*Salvelinus alpinus*), Atlantic salmon (*Salmo salar*), brook lamprey (*Lampetra planeri*), brown trout, eel (*Anguilla anguilla*), flounder (*Platichthys flesus*), minnow (*Phoxinus phoxinus*), perch (*Perca fluviatilis*), pike (*Esox lucius*), stone loach (*Barbatula barbatula*) and three-spined stickleback (*Gasterosteus aculeatus*). However, brook lamprey and stone loach have always been largely restricted to tributary streams and flounder was probably only an occasional visitor (Day, 1887).

Three of the above species became locally extinct during historical times. The Atlantic salmon and flounder, which both used to migrate along the outflowing River Leven to and from the Forth Estuary, were lost during the eighteenth century (Day, 1887), while Arctic charr have not been recorded since 1837 (Burns-Begg, 1874).

Only one fish species has subsequently been added to the Loch Leven fish community, i.e. the non-native rainbow trout (*Oncorhynchus mykiss*), which was stocked for fishery purposes from 1993 to 2004.

Brown and rainbow trout fishery

The performance of the Loch Leven brown trout rod fishery from 1900 to 2002 is given in Fig. 1a; after 2002, catch records collected by the fishery became less reliable as an indicator of fishery performance as a result of anglers releasing fish that they could have retained. Between 1900 and 1970, the annual catch frequently exceeded 40,000 brown trout with less than 20,000 fish landed in only a very few years. After 1970, however, catches declined markedly and rarely exceeded 20,000 fish. Furthermore, this level of brown trout catch was last surpassed in 1990. The post-1970 decline in absolute catch of brown trout was

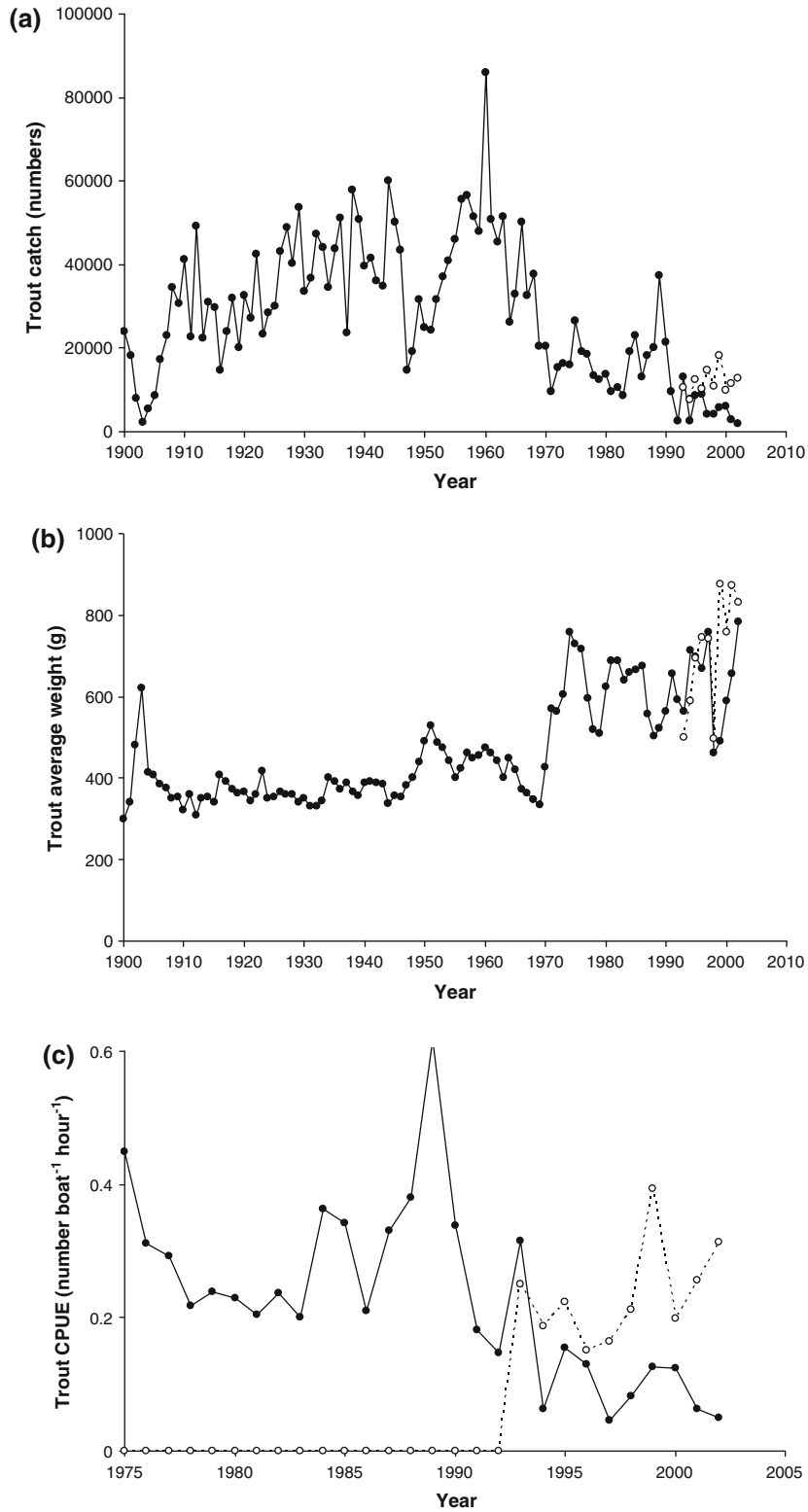

Fig. 1 Loch Leven fishery **a** absolute catch for brown trout (*closed circles*, *continuous line*) and rainbow trout (*open circles*, *broken line*) from 1900 to 2002, **b** average weight for brown trout (*closed circles*, *continuous line*) and rainbow trout (*open circles*, *broken line*) from 1900 to 2002 and **c** catch-per-unit-effort (CPUE) for brown trout (*closed circles*, *continuous line*) and rainbow trout (*open circles*, *broken line*) from 1975 to 2002

accompanied by a marked increase in individual weight (Fig. 1b).

This dramatic decline in fishery performance led to the reintroduction, in 1983, of brown trout stocking directly into the loch using 5,000 fish of local origin from the re-opened hatchery and rearing-ponds (Montgomery, 1994). The number of brown trout stocked each year steadily increased until 1988, when 166,000 fish were introduced. Stocking in excess of 100,000 brown trout continued in most years until 2004, when the number was reduced to 5,000 and stocking was discontinued in 2006. Unlike the earlier period when the stocked fish consisted mainly of fry introduced to tributary streams, from 1983 onwards the stocked fish were released directly into the loch, generally as yearlings of 120–180 mm in length (Montgomery, 1994). However, from 2004 to 2006, the emphasis was on introducing older fish of approximately 280 mm in length (W.W., unpublished data) which were already large enough to be taken by anglers.

During the 1980s component of the stocking programme, the performance of the brown trout fishery in terms of catch-per-unit-effort (CPUE, calculated from fishery returns from all anglers as the number of brown trout caught per boat-hour) was relatively stable but then decreased again in the 1990s (Fig. 1c). This further deterioration in brown trout fishery performance, coupled with poor environmental conditions (in terms of low oxygen availability and low water clarity) and changing angler preferences, led the fishery to stock with rainbow trout from 1993 to 2004. During this period at least 30,000 fish were stocked each year. This stocking dramatically changed the nature of the Loch Leven fishery such that the absolute catch (Fig. 1a) and CPUE of rainbow trout (calculated as for brown trout, Fig. 1c) almost equalled that of brown trout in the first year of stocking of the latter species, and then greatly exceeded it in all subsequent years with stocking and for which catch data are available.

Perch population

Sampling in 2008 produced a total of 641 perch, of which 45 individuals were taken in March when they ranged between 83 and 251 mm in length and 6 and 292 g in weight. The length frequency distribution of these fish contained only one individual above 180 mm in length (Fig. 2a), which amounted to 2% of individuals and contrasted with corresponding data from March 2001 (Fig. 2b) and August 1968 (Fig. 2c) when 43% of 67 individuals and 48% of 180 individuals, respectively, exceeded this length. This currently truncated length frequency distribution was also evident when the 2008 Loch Leven length and weight data were compared with corresponding data from perch populations in two other lochs sampled using identical methodology although, on the basis of their relatively high weights at lengths, individual fish were in good condition (Fig. 2d).

Brown trout population

Sampling in 2008 produced a total of 163 brown trout, of which 25 individuals were taken in March when they ranged between 135 and 577 mm in length and 27 and 2,317 g in weight. The length frequency distribution of the latter individuals contained relatively high numbers of large fish (Fig. 3a), with a length-weight relationship indicative of excellent individual condition and with markedly higher weights-at-lengths for individuals greater than 400 mm when compared with similar data from several other lochs (Fig. 3b).

Contemporary fish community

The population density of all fish recorded by hydroacoustics in the deeper (i.e. water depth 5 m and greater) areas of Loch Leven during October 2007 was 72.7 fish ha^{-1} (geometric mean with lower and upper 95% confidence limits of 21.8 and 242.5 fish ha^{-1}, respectively). Note that these results were subject to a near-surface blind zone of approximately 2.5 m within which fish could not be detected. A breakdown by fish length classes is given in Fig. 4a.

Gill-net sampling in 2008 produced a total of 1,139 individuals of five fish species, i.e. brown trout, perch, pike, three-spined stickleback and stone loach (Fig. 4b). However, catches were numerically dominated by brown trout (14% by numbers), perch (56%) and three-spined sticklebacks (29%), with pike (less than 1%) and stone loach (less than 1%) represented by only single individuals.

Discussion

The fish community of Loch Leven is relatively simple in terms of species number, with a cumulative total of

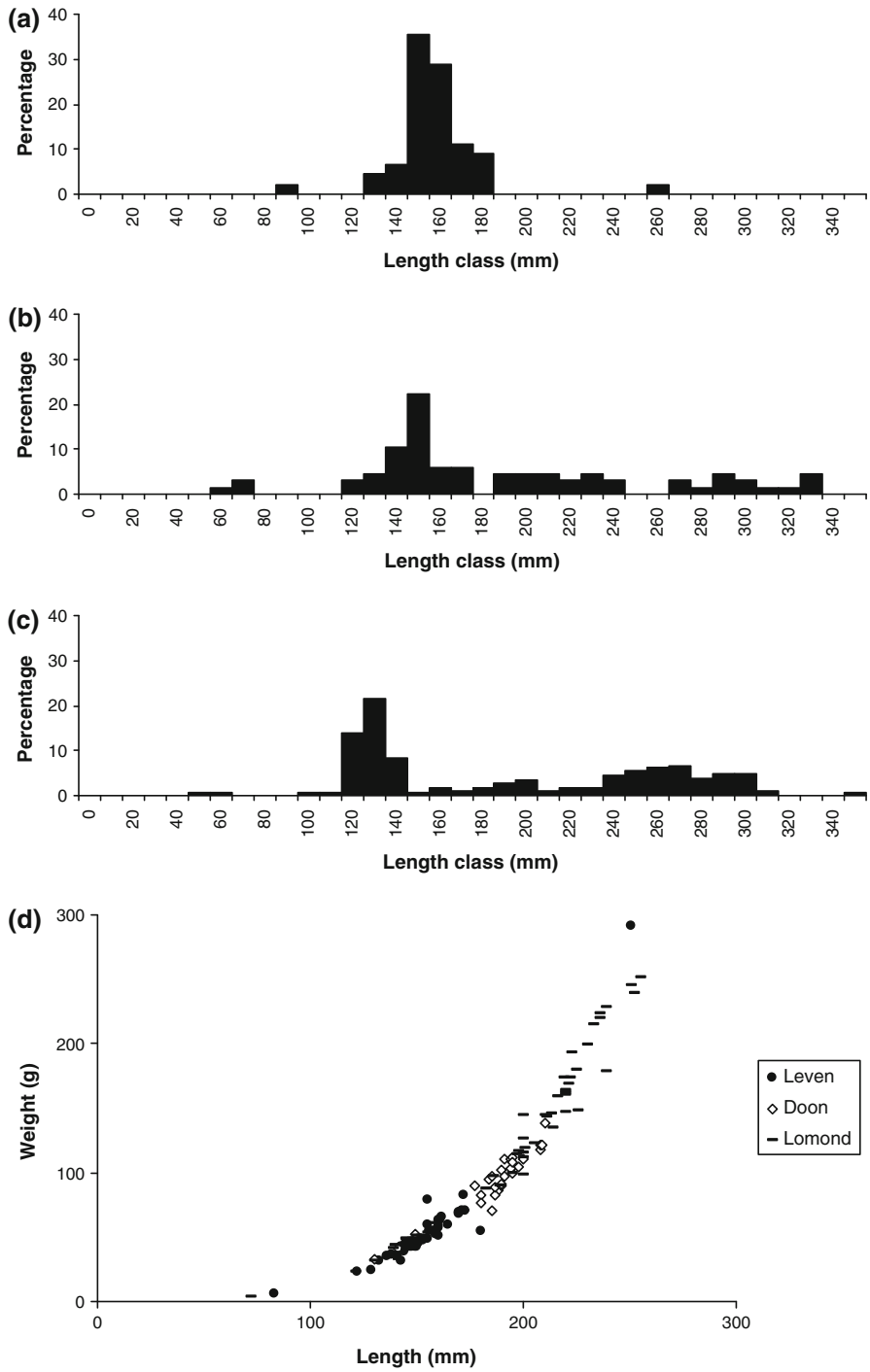

Fig. 2 Length frequency distributions of perch sampled from Loch Leven **a** 45 perch in March 2008, **b** 67 perch in March 2001, **c** 180 perch in August 1968 and **d** length-weight relationship of 45 perch sampled from Loch Leven in March 2008. For comparison, the latter also shows corresponding data from Loch Doon and Loch Lomond

only 12 species including the rainbow trout which is non-native to the U.K. and was introduced for fishery purposes. However, it has displayed a number of major changes over the long-term and the extensive 2008 sampling recorded only five species, i.e. brown trout, perch, pike, three-spined stickleback and stone loach. Furthermore, in numerical terms, the community is now dominated by just three species, i.e. brown trout, perch and three-spined stickleback, with a total abundance of 72.7 fish ha^{-1} as measured by the initial

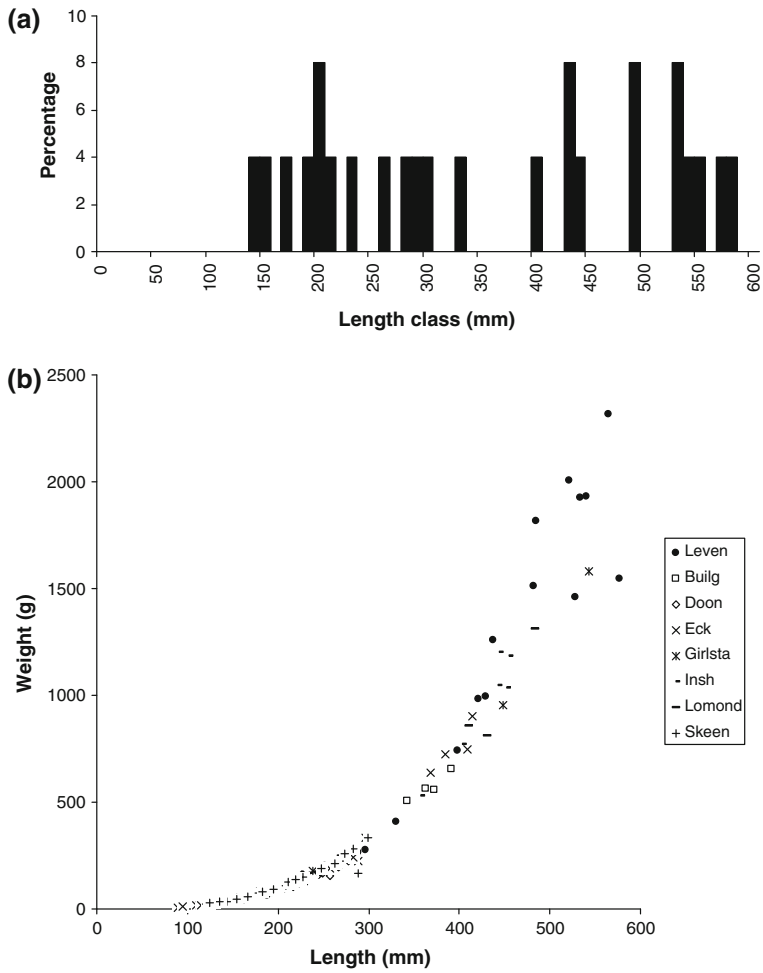

Fig. 3 **a** Length frequency distribution and **b** length-weight relationship of 25 brown trout sampled from Loch Leven in March 2008. For comparison, the latter also shows corresponding data from Lochs Builg, Doon, Eck, Insh, Lomond and Skeen, and Loch of Girlsta

extensive hydroacoustic survey of October 2007 being near the middle of the range observed for 17 other U.K. water bodies by Winfield et al. (in press).

The present absence of brook lamprey and rarity of stone loach probably reflect the local distribution patterns of these two riverine species, with their populations primarily inhabiting the loch's tributary streams, and so are not of any significance in terms of long-term changes. However, the current apparent absence of Arctic charr, Atlantic salmon, eel (although this species is poorly sampled by gill nets), flounder, minnow and rainbow trout and the great scarcity of pike are worthy of further discussion where data allow, as are the observed changes in the perch and brown trout populations. Unfortunately, most previous assessments of the loch's fish including Thorpe (1974a, b), O'Grady et al. (1993) and Alexander et al. (1999) have not attempted to sample the minnow and three-spined stickleback populations. Consequently, while our 2008 sampling has shown that these two species are, respectively, now apparently absent and relatively abundant, nothing can be concluded concerning their long-term population dynamics.

The present Loch Leven fish community composition is also noteworthy in the context of absent species. First, it appears that most or all of the 370,000 rainbow trout stocked into the loch between 1993 and 2004 have now either died or been removed and that no local reproduction has occurred. Although an extremely small number of juvenile and adult rainbow trout have recently been caught by anglers, these are thought to have entered the system from one or more of several newly opened fisheries on the loch's tributaries (B. M. S. and W. W., personal observations). Second, a number of other major lakes in the

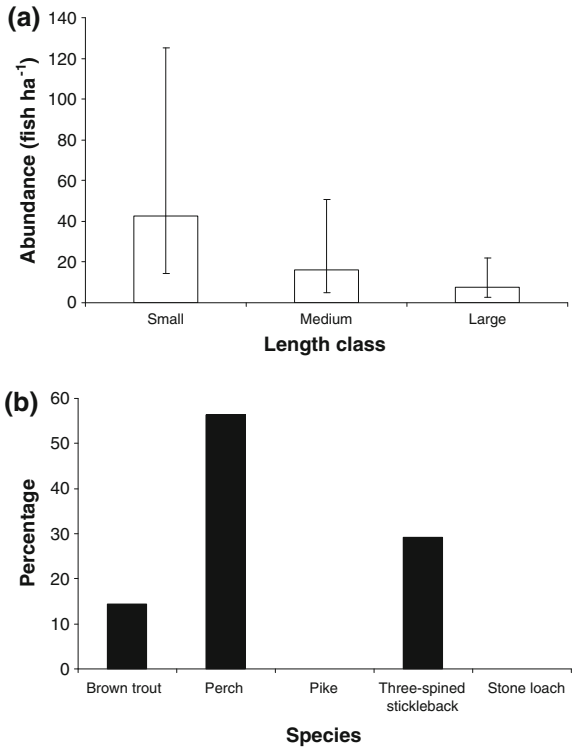

Fig. 4 **a** Abundance estimates (geometric means with 95% confidence limits) by length class for small (length 40–99 mm), medium (length 100–249 mm) and large (length equal to or greater than 250 mm) fish recorded at Loch Leven on 10 October 2007, **b** Composition by numbers of the contemporary fish community of Loch Leven based on sampling in March, August and October 2008. Total sample size was 1,139 fish. Note that single pike and stone loach were sampled, although they are not visible on the figure at this scale

U.K. have recently experienced unconsented introductions of several fish species, most notably roach (*Rutilus rutilus*) and ruffe (*Gymnocephalus cernuus*), as a result of anglers fishing for pike using fish as live baits (Winfield & Durie, 2004). Although there is thus a potential for such unwanted introductions to Loch Leven, with potential implications for the native fish community, the extensive sampling of 2008 did not record any new arrivals.

The three apparent local extinctions of fish species, i.e. Arctic charr, Atlantic salmon and flounder, all occurred before scientific studies of Loch Leven began, so their causes can only be speculated upon. However, Burns-Begg (1874) noted that the Arctic charr was lost only a few years after the marked lowering of the loch level in 1830, which is strong circumstantial evidence that this was the major factor behind its extinction. This potential pressure has parallels with more recent and better-studied effects of falls in lake levels on Arctic charr and other members of the fish community of Haweswater, U.K. (Winfield et al., 1998), and elsewhere (Maitland et al., 2007). Furthermore, even if the Arctic charr had survived this pressure, it would then have faced a significant pressure from subsequent eutrophication which currently stresses other U.K. populations such as those in Windermere (Winfield et al., 2008c). The local extinctions of Atlantic salmon and flounder occurred even earlier in the eighteenth century and may have been due to the obstruction of migratory routes by river pollution, although increasing physical difficulty of passage due to sluice construction associated with the subsequent lowering of the loch in 1830 and the construction of weirs further downstream would probably have formed additional factors.

The above local anthropogenic pressures together with more widespread factors (Bonhommeau et al., 2008) are also likely to have contributed to a decline in the eel population of Loch Leven. The catches of commercial eel fishings at the outflow from the loch declined through the nineteenth century and these operations finally came to an end in 1901 (Munro, 1994). Furthermore, this species was not recorded during extensive sampling from 1968 to 1973 (J. E. T., personal observation). Even allowing for the inefficient sampling of eels by gill nets, it is remarkable that the survey of O'Grady et al. (1993) and the present sampling also failed to record any individuals of this once ubiquitous species. However, recent very infrequent captures by anglers, the sighting of a dead eel in the harbour at Kinross and very occasional captures of eels in survey work in the Gairney Burn, a tributary of Loch Leven, (B. M. S., W. W. and R. G., personal observations) confirm the presence of at least a few eels. It is possible that the eels now present may have accessed the catchment via the River Devon, which runs independently into the Firth of Forth, and is linked with the Gairney Burn by the Pow Burn which drains into both catchments.

The pike population of the loch has also declined markedly since historic times, with the surveys of O'Grady et al. (1993) and this study recording 0 and 1 individuals, respectively. Duncan (1994) considered that a long-term pike removal programme operated by the fishery was probably responsible for this decline, although a reduction in macrophytes associated with

eutrophication over the same period (Dudley et al., 2011), which are used as spawning and nursery habitat by pike (Craig, 1996), may also have been involved. In addition, the earlier lowering of water levels may also have had a negative effect on pike recruitment through reducing spawning and nursery habitat.

The reduction in macrophyte abundance mentioned above is also likely to have had a negative effect on the perch population of Loch Leven because this species uses their physical complexity for spawning and nursery habitat and it also influences competitive interactions involving adult members of the population (Craig, 2000). In addition, Duncan (1994) considered that a perch disease that he reported as first observed in Loch Leven in 1983 may also have contributed to a marked decline, although the first signs of this disease were actually observed over a decade earlier in 1971 (J. E. T., personal observation). Long-standing and marked fluctuations in the perch population are evident from abundance estimates of 968,000 individuals and 253,000 individuals in 1970 and 1971, respectively (Thorpe, 1974a), by the scarcity of perch in the 1993 sampling of O'Grady et al. (1993), and by their limited size distribution in the present sampling of 2008. Even allowing for the substantial natural variation in abundance of perch observed in relatively undisturbed habitats such as that of the north basin of Windermere (Paxton et al., 2004), the decline of the perch population in the eutrophicated Loch Leven has been particularly marked. However, some recovery of the perch population might now be expected as the loch's level of eutrophication reduces (Carvalho et al., 2011) and its macrophytes increase in abundance (Dudley et al., 2011; May & Carvalho, 2010). As adult perch consume over 6% of their body weight per day during the summer (Thorpe, 1977) and young perch are probably a major planktivore within the Loch Leven system, such population changes are likely to have important implications for the loch's food web through impacts on their prey populations.

The brown trout population has undoubtedly received by far the most research attention of all of Loch Leven's fish species, driven in large part by its fishery importance and thus high public profile. Although documented and undocumented changes over time in fishing practices and equipment mean that trends in fishery performance must be interpreted with caution, the decline of the Loch Leven trout fishery has been so marked that it undoubtedly reflects an actual decline in the local brown trout population. This problem was widely acknowledged by the early 1990s and led to much previous research being presented or reviewed during a dedicated conference on the trout fishery reported by Hutchinson & Walker (1994). Consequently, this earlier research will not be revisited here in any detail.

Brown trout spawn in flowing water and the streams that feed the loch are therefore a vital component of the habitat for this species. Despite heavy impacts of agriculture and some localised gravel abstraction on parts of the catchment, the streams entering Loch Leven are highly productive of brown trout. Surveys conducted in the early 1990s (Armstrong et al., 1994; Armstrong & Gardiner, 1995) assessed the strength and aspects of the demographics of trout in the streams. Strong relationships were evident with key components of the habitat such that the degree of bank overhangs (which correlated strongly with bankside vegetation) together with coarse in-stream substratum explained 76% of the variation in trout densities in winter. Trout densities in autumn were strongly influenced by the degree of overhead cover together with densities of trout in May/June. Trout older than 1+ in autumn were scarce in the sampled sites. These results were consistent with a possible limitation of spawning on production, through one or a combination of low numbers of eggs, or insufficient distribution of spawning substratum. There was no evidence of trout tending to remain in the streams as older fish rather than migrating to the loch, as observed also in an earlier study (Thorpe, 1974a). Despite this potential limitation of recruitment on production, densities of trout were high in Loch Leven streams compared with other populations and at least as high as those determined by Thorpe (1974a). The presence of the remnants of yolk sacs and a wide range of lengths in samples collected in May/June were consistent with the occurrence of a wide range of spawning times and may facilitate high levels of production through heterogeneous advantage (Griffiths & Armstrong, 2001) due to young fish of different sizes using different local niches and therefore competing little with one another. Further examination of the streams would be enhanced by trapping of trout migrating to and from the loch to measure production of smolts and migrant fry directly, to assess the numbers of spawners, and to derive indices of stock size.

Estimates of the brown trout population within Loch Leven have been undertaken during three different periods, including an examination of the effect of an aeromonad epidemic on the spawning population (Thorpe & Roberts, 1972). However, caution is urged with respect to the interpretation of long-term dynamics because outside of the population estimates by Thorpe (1974a), which themselves ranged from 127,000 fish in 1968 to 52,000 fish in 1971, later assessments by O'Grady et al. (1993) and Alexander et al. (1999) were undertaken using different techniques, for different components of the population and for different times of the year. Consequently, their assembly into a single time series cannot be performed robustly.

These latter data have subsequently been used by both Wright (2003) and Stewart et al. (2005) to assess the controversial subject of the impact of cormorants overwintering at Loch Leven. In common with other inland locations across the U.K., the number of cormorants wintering at Loch Leven increased substantially in the late 1980s (Wright, 2003). By comparing CPUE for gill-net and angling catches before and after the arrival of wintering cormorants, Wright (2003) concluded that cormorants had no effect on brown trout abundance or fishery performance. Using diet analysis coupled with a consumption model, Stewart et al. (2005) estimated that cormorants consumed 80,803 brown and 5,213 rainbow trout over a 7 month period and concluded that there was a high potential for competition between the birds and the fishery for available fish. Stewart et al. (2005) also found a link between brown trout stocking level in spring and cormorant abundance the following winter, suggesting that increased stocking could have attracted more cormorants to the site and that the subsequent increase in predation would cancel out any benefits of stocking on the fishery yield.

The numbers of brown and rainbow trout estimated to have been removed by cormorants (Stewart et al., 2005) suggested high levels of impact relative to any of the estimates of the trout populations that have been attempted (Wright, 2003). However, even in Loch Leven, which has been more intensively studied than most other large water bodies in the U.K., there is considerable uncertainty regarding the size of the trout populations such that precise estimates of the impacts of piscivorous birds on them are not possible.

A clear feature of the brown trout population is that the length frequency distribution and length-weight relationship observed in 2008 indicates that those individuals present are in excellent individual condition. This observation is consistent with the marked increase in the average weight of brown trout in the fishery, which accompanied the decline in their apparent abundance in the 1970s. This relationship is consistent with density-dependent increase in size rather than reduction in density due to mortality associated with poor average condition.

Conclusion

The fish community of Loch Leven is relatively simple with a cumulative total of 12 species, but it has undergone a number of extinctions and major changes over historical and recent times and is currently dominated by just brown trout, perch and three-spined stickleback. A lowering of water level probably caused the local extinction of Arctic charr and contributed to the deterioration of the pike population, while the obstruction of migratory routes was likely responsible for the loss of Atlantic salmon and flounder. The perch population has shown marked fluctuations in abundance typical of this species, although its local dynamics have also probably been influenced by a perch-specific disease outbreak and increasing eutrophication. The present lowering of nutrient levels in the loch and associated recovery of macrophytes are likely to benefit this species, which, given its position as a major planktivore within the system, is likely to have important implications for the loch's food web. The size of the brown trout population was initially estimated by application of mark and recapture methodology on an unusually large scale. However, differences in methodologies applied subsequently make it difficult to compare the size of the population over time and this has hampered robust analysis of the factors that may be involved in the demise of the trout fishery. Nonetheless, the decline has been so marked that it undoubtedly reflects an actual decline in the local brown trout population.

Acknowledgments We would like to thank Janice Fletcher, Ben James and other colleagues at the Centre for Ecology & Hydrology for help in the field and laboratory during the recent study of the fish community of Loch Leven. Colin Bean of Scottish Natural Heritage kindly allowed the use of individual

brown trout and perch data collected under contract at a number of other locations. We also gratefully acknowledge appropriate sampling permissions from the Kinross Estates, Scottish Natural Heritage and The Scottish Government. The preparation of this review was primarily funded by the Natural Environment Research Council. Loch Leven is part of the UK Environmental Change Network (http://www.ecn.ac.uk/).

References

Alexander, G., C. E. Adams, J. Devine, J. Drummond & C. W. Bean, 1999. Loch Leven: hydroacoustic technique development and fish population estimation. University of Glasgow Report to Scottish Natural Heritage. Scottish Natural Heritage, Edinburgh.

Appelberg, M., 2000. Swedish standard methods for sampling freshwater fish with multi-mesh gillnets. Fiskeriverket Information 1: 3–32.

Arlinghaus, R., T. Mehner & I. G. Cowx, 2002. Reconciling traditional inland fisheries management in industrialized countries, with emphasis on Europe. Fish and Fisheries 3: 261–316.

Armstrong, J. D. & W. R. Gardiner, 1995. Juvenile trout populations in the Loch Leven catchment. Fisheries Research Services Report 13/95.

Armstrong, J. D., W. R. Gardiner & A. F. Walker, 1994. Juvenile brown trout production in the Loch Leven catchment. Fisheries Research Services Report 07/94.

Bailey-Watts, A. E., 1982. The composition and abundance of phytoplankton in Loch Leven (Scotland) 1977–1979 and a comparison with the succession in earlier years. Internationale Revue der Gesamten Hydrobiologie 67: 1–25.

Bailey-Watts, A. E., A. Kirika, L. May & D. H. Jones, 1990. Changes in phytoplankton over various time scales in a shallow eutrophic lake: the Loch Leven experience with special reference to the influence of flushing rate. Freshwater Biology 23: 85–111.

Bonhommeau, S., E. Chassot, B. Planque, E. Rivot, A. H. Knap & O. Le Pape, 2008. Impact of climate on eel populations of the Northern hemisphere. Marine Ecology Progress Series 373: 71–80.

Burns-Begg, R., 1874. The Loch Leven angler. Barnett, Kinross.

Carvalho, L., C. Ferguson, B. M. Spears, I. D. M.Gunn, H. Bennion, A. Kirika & L. May, 2011. Water quality of Loch Leven: responses to enrichment, restoration and climate change. Hydrobiologia. doi:10.1007/s10750-011-0923-x.

Carss, D., B. M. Spears, L. Quinn & R. Cooper, 2011. Long-term variations in waterfowl populations in Loch Leven: identifying discontinuities between local and national trends. Hydrobiologia. doi:10.1007/s10750-011-0927-6.

Craig, J. F., 1996. Pike: biology and exploitation. Chapman & Hall Fish and Fisheries Series 19. Chapman & Hall, London.

Craig, J. F., 2000. Percid fishes: systematics, ecology and exploitation. Blackwells, Oxford.

Day, F., 1887. On the Loch-Leven trout (*Salmo levenensis*). Journal of the Linnaean Society of London, Zoology 20: 71–90.

Dudley, B., I. D. M. Gunn, L. Carvalho, I. Proctor, M. T. O'Hare, K. J. Murphy, A. Milligan, 2011. Changes in aquatic macrophyte communities in Loch Leven—evidence of recovery from eutrophication? Hydrobiologia. doi:10.1007/s10750-011-0924-9.

Duncan, W., 1994. The fish community in Loch Leven. In Hutchinson, P. & A. Walker (eds), The Loch Leven trout fishery—its future. Institute of Fisheries Management, Pitlochry: 29–38.

Griffiths, S. W. & J. D. Armstrong, 2001. The benefits of genetic diversity outweigh those of kin association in a territorial animal. Proceedings of the Royal Society London, Series B 268: 1293–1296.

Gunn, I. D. M., M. T. O'Hare, P. S. Maitland & L. May, 2011. Long-term trends in Loch Leven invertebrate communities. Hydrobiologia. doi:10.1007/s10750-011-0926-7

Hutchinson, P. & A. Walker (eds), 1994. The Loch Leven trout fishery—its future. Institute of Fisheries Management, Pitlochry.

Kirby, R. P., 1971. The bathymetrical resurvey of Loch Leven, Kinross. Geographical Journal 137: 372–378.

Kubečka, J., U. S. Amarasingh, S. A. Bonar, J. Hateley, P. Hickley, E. Hohausová, J. Matěna, J. Peterka, P. Suuronen, V. Tereschenko, R. Welcomme & I. J. Winfield, 2009. The true picture of a lake or reservoir fish stock: a review of needs and progress. Fisheries Research 96: 1–5.

Maitland, P. S., I. J. Winfield, I. D. McCarthy & F. Igoe, 2007. The status of Arctic charr *Salvelinus alpinus* in Britain and Ireland. Ecology of Freshwater Fish 16: 6–19.

May, L. & L. Carvalho, 2010. Maximum growing depth of macrophytes in Loch Leven, Scotland, United Kingdom, in relation to historical changes in estimated phosphorus loading. Hydrobiologia 646: 123–131.

May, L. & B. M. Spears, 2011. A history of scientific research at Loch Leven, Kinross, Scotland. Hydrobiologia. doi: 10.1007/s10750-011-0929-4

May, L. L. H. Defew, H. Bennion & A. Kirika, 2011. Historical changes (1905–2005) in external phosphorus loads to Loch Leven, Scotland, UK. Hydrobiologia. doi:10.1007/s10750-011-0922-y

Montgomery, D., 1994. Management of the Loch Leven trout fishery. In Hutchinson, P. & A. Walker (eds), The Loch Leven trout fishery—its future. Institute of Fisheries Management, Pitlochry: 26–28.

Munro, D., 1994. Loch Leven and the River Leven: a landscape transformed. The River Leven Trust, Markinch.

O'Grady, M. F., P. Gargan & W. Roche, 1993. A fish stock survey of Loch Leven and management proposals for this resource as a trout fishery. Central Fisheries Board Report to Scottish Natural Heritage. Scottish Natural Heritage, Edinburgh.

Paxton, C. G. M., I. J. Winfield, J. M. Fletcher, D. G. George & D. P. Hewitt, 2004. Biotic and abiotic influences on the recruitment of perch (*Perca fluviatilis*) in Windermere, U. K. Journal of Fish Biology 65: 1622–1642.

Spears B. M., L. Carvalho, R. Perkins, A. Kirika & D. M. Paterson, 2011. Long-term variation and regulation of internal phosphorus loading in Loch Leven. Hydrobiologia. doi: 10.1007/s10750-011-0921-z.

Stewart, D. C., S. J. Middlemas, W. R. Gardiner, S. Mackay & J. D. Armstrong, 2005. Diet and prey selection of cormorants

(*Phalacrocorax carbo*) at Loch Leven, a major stocked trout fishery. Journal of the Zoological Society of London 267: 191–201.

Thorpe, J. E., 1974a. Trout and perch populations at Loch Leven, Kinross. Proceedings of the Royal Society of Edinburgh, B 74: 296–313.

Thorpe, J. E., 1974b. Estimation of the number of brown trout *Salmo trutta* (L.) in Loch Leven, Kinross, Scotland. Journal of Fish Biology 6: 135–152.

Thorpe, J. E., 1977. Daily ration of adult perch, *Perca fluviatilis* L. during summer in Loch Leven, Scotland. Journal of Fish Biology 11: 55–68.

Thorpe, J. E. & R. J. Roberts, 1972. An aeromonad epidemic in the brown trout (*Salmo trutta* L.). Journal of Fish Biology 4: 441–451.

Winfield, I. J. & N. C. Durie, 2004. Fish introductions and their management in the English Lake District. Fisheries Management and Ecology 11: 1–7.

Winfield, I. J., J. M. Fletcher & P. R. Cubby, 1998. The impact on the whitefish (*Coregonus lavaretus* (L.)) of reservoir operations at Haweswater, U.K. Archiv für Hydrobiologie, Official Journal of the International Association for Theoretical and Applied Limnology. Special Issues: Ergebnisse der Limnologie 50: 185–195.

Winfield, I. J., J. M. Fletcher & A. A. Lyle, 2008a. Assessment of the vendace refuge population of Loch Skeen. Final Report. Centre for Ecology & Hydrology Report to Scottish Natural Heritage. Scottish Natural Heritage, Edinburgh.

Winfield, I. J., J. M. Fletcher & J. B. James, 2008b. SCM of fish in standing waters 2007/2008 (Phase I). Final Report. Centre for Ecology & Hydrology Report to Scottish Natural Heritage. Scottish Natural Heritage, Edinburgh.

Winfield, I. J., J. M. Fletcher & J. B. James, 2008c. The Arctic charr (*Salvelinus alpinus*) populations of Windermere, U. K.: population trends associated with eutrophication, climate change and increased abundance of roach (*Rutilus rutilus*). Environmental Biology of Fishes 83: 25–35.

Winfield, I. J., J. M. Fletcher, J. B. James & C. W. Bean, 2009a. Assessment of fish populations in still waters using hydroacoustics and survey gill netting: experiences with Arctic charr (*Salvelinus alpinus*) in the UK. Fisheries Research 96: 30–38.

Winfield, I. J., J. M. Fletcher & J. B. James, 2009b. SCM of fish in standing waters 2007/2008 (Phase II). Final Report. Report to Scottish Natural Heritage. LA/C03380/6.

Winfield, I. J., J. M. Fletcher, J. B. James, C. W Bean & C. Duigan, in press. Setting reference values for lake fish abundance: observations from unexploited or lightly exploited vendace (*Coregonus albula*), whitefish (*C. lavaretus*) and Arctic charr (*Salvelinus alpinus*) populations in the U.K. In Cowx, I.G. (ed), Assessing the Ecological Status of Rivers, Lakes and Transitional Waters. Fishing News Books, Blackwell Scientific Publications, Oxford.

Wright, G. A., 2003. Impact of cormorants on the Loch Leven trout fishery and the effectiveness of shooting as mitigation. In Cowx, I. G. (ed.), Interactions between fish and birds: implications for management. Fishing News Books. Blackwell Scientific Publications, Oxford: 288–297.