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Executive Summary

Single-visit hydroacoustic surveys are likely to be an important tool in characterising the ecological status of Scottish freshwater bodies for the Water Framework Directive. In general however, the usefulness of such surveys is compromised by two areas of uncertainty: the temporal variation in survey results at individual locations, and the composition of species which detected targets represent. Here we examine the former by characterising seasonal and diurnal variation in the results of hydroacoustic surveys at a single water body, Loch Rannoch, and the latter by examining the consequences of different species compositions in two similar-sized oligotrophic water bodies, Loch Laidon and Loch na Sealga.

At Loch Rannoch, seasonal variation in target density was complex, varying between different components of the fish populations, but overall lower densities of fish-sized targets were recorded in the summer months, whilst higher densities were recorded from early autumn through till spring, with the exception of a period of uncertain duration (perhaps as from October to January) probably corresponding to the period of salmonid spawning. Since surveys aiming to characterise fish populations in a water body should be undertaken during the period that minimises the number of fish going undetected, for Loch Rannoch there appears to be a relatively narrow window representing the optimum season for daylight surveys: September, February, March and April. Night time surveys on Loch Rannoch yielded consistently higher apparent fish densities than day surveys. The magnitude of the increase however, ranged from 10 to 50% above the corresponding daylight survey, so that no simple 'correction' could be applied to a daylight survey. Once again the detailed picture was more complex, with substantial variation between surveys not clearly related to diurnal variation.

Surveys of Loch Laidon are contrasted with surveys Loch na Sealga. The former loch has no Arctic charr and a fish community dominated by Brown trout, while the latter has both charr and trout populations. Both daylight and night time surveys were conducted on each loch. Results differed markedly between the two lochs: daylight densities of targets >-54dB (equating to fish >4.5cm in length) varied more than fourfold (8.2 fish ha⁻¹ in Loch Laidon, only 1.9 ha⁻¹ in Loch na Sealga). During

darkness this situation was almost perfectly reversed, with detected densities of targets >-54dB of only 1.0 fish ha⁻¹ in Loch Laidon, and 10.4 ha⁻¹ in Loch na Sealga.

The results here indicate that considerable research effort is required before hydroacoustics can be used as a reliable form of assessment for the fish populations of Scottish lochs. They show that timing of surveys (both in terms of season, and day versus night) for different lochs may be crucial to the results obtained. From our sample it appeared that day surveys could lead to serious underestimates of fish densities in charr-dominated lochs, and that night surveys might lead to similar underestimates in trout dominated lochs. In each case the difference between daylight and night time estimates of density was in the region of an order of magnitude. If this result was repeated elsewhere it would have important consequences for the design and interpretation of hydroacoustic surveys. In Scotland, many lochs contain chiefly trout and charr, and the data here suggest that adequate surveys of either species, but not both, may be obtained by selecting either day (trout) or night (charr) time surveys. Furthermore, the scale of difference in detectability of the two species on Loch Laidon and Loch na Sealga indicate that the contribution of charr to the daytime survey estimates, and trout to the night-time survey estimates is minimal, and that the total fish density of lochs where both species are present could be estimated by treating day and night time estimates as additive. Similarly, the relative contributions of trout and charr to the total biomass might be inferred from the differences in recorded densities for day and night time surveys.

Introduction

There are estimated to be some 30,000 fresh water lochs in Scotland, most of which are entirely un-described scientifically. Freshwater is an abundant resource, of which flowing water constitutes only a tiny portion of the whole, yet with respect to fisheries it is only the rivers that have been systematically and extensively studied, reflecting the dominant tradition of river bank fly fishing for wild salmonids in Scotland. Accordingly the important recreational ecological resource that Scotland's lochs represent has been largely overlooked, and perhaps under-exploited.

The first step towards effective management is an assessment of the resource, but achieving this basic task has remained elusive in Scotland. In part this is due to the dominance of river-bank angling culture, in part due to the daunting nature of the task of assessing fish populations in large deep water bodies, and in part because of an increasing reluctance to use the destructive netting techniques that have formed, until recently, the only serious method for examining fish populations in lochs. Although hydroacoustic, or sonar, techniques have been widely used to detect fish in the marine environment since the first successful experiment in the late 1920's (Kimura 1929), the technique has only recently become a widespread tool in inland fisheries assessment, and offers great potential for informing science and

management. There is an emerging policy context for developing reliable freshwater hydroacoustic techniques in Scotland: hydroacoustic surveys formed part of the initial assessment of lochs designated as Special Areas for Conservation (SACs) (Winfield *et al* 2010) and hydroacoustic methods have been identified by SEPA as the principle means of Large Water Body assessment for the Water Framework Directive.

However, uncertainties regarding how to conduct such surveys in Scottish lochs exist at the most basic levels. It is uncertain when the most appropriate time of the year for surveys to be conducted: while for example summer months offer the most benign meteorological conditions for surveys, the density of zoo-plankton populations in lochs at that time may obscure juvenile fish. Similarly there are concerns regarding the diurnal timing of surveys. Results of hydroacoustic surveys are known to differ between day and night on some water bodies. For example, on Windermere consistent higher densities of Arctic charr (Salvelinus alpinus L.) are reported during night time surveys (Winfield et al 2007). As a consequence, the Environment Agency has all but abandoned the use of daytime surveys in England and Wales (J.Hateley, pers. comm.). Nevertheless, despite these acknowledged concerns, there may be difficulty in securing the resource for anything more than daylight surveys in Scotland, and so a research effort underpinning such surveys will have immediate benefits. For example, it may be possible to determine an effective calibration which can be applied to correct daytime survey results, as on Windermere (Winfield et al 2007). However, it is not known to what extent this day-night variability, is a function of an individual water-body or a function of the species assemblage, nor to what extent it may vary seasonally. It is unlikely that a single useful calibration can be found, and a series of calibrations for different conditions and water body types may be required.

Here we address the fundamental question of optimising the time of year and time of day for conducting fish assessment surveys, at a single Scottish water body, Loch Rannoch, which is known to contain significant populations of both trout (*Salmo trutta* L.) and charr. We explore the relationships in target-sizes and densities recorded during hydroacoustic surveys conducted over the course of a year and during both daylight and hours of darkness.

An allied concern is that hydroacoustic techniques cannot reliably determine the species to which a target belongs. Where there is previous knowledge about the fish community in a water body it may be possible to establish a target's species by inference; perhaps from the target strength or from the location and movements of the target within the water column. Interpretation of hydroacoustic data remains problematic in the absence of such knowledge. Even in Scotland, where species diversity is low, this may have important consequences for the usefulness of hydroacoustic surveys. In order to understand and compare hydroacoustic data from different lochs with unknown species assemblages it is important to know what effect different assemblages may have on estimates of biomass and fish abundance. For

example what differences might hydroacoustic surveys of lochs dominated by a) charr and b) trout encounter? Although charr and trout are both physoclists and are expected to have a similar target strength to body size relationship, their behaviour may make them more or less amenable to survey by hydroacoustic methods. Trout are thought to spend most of their lives near the surface, where the spatial coverage by conventional vertically-aligned sonar is very poor, and thus trout may be relatively hard to detect with hydroacoustic techniques. By contrast, charr are thought to be highly amenable to detection by vertically-aligned sonar, because they spend much of their time deep within the water column, where spatial coverage by vertically-aligned sonar is good.

In order to explore possible large-scale effects of fish community on fish density estimates derived from hydroacoustic surveys we selected two lochs of similar size but differing fish communities. Loch Laidon is one of relatively few large Highland water bodies known not to contain charr and has a species composition dominated by trout, plus a number of perch (*Perca fluviatilis* L.) (E.Verspoor pers comm.), whilst Loch na Sealga is known to contain both charr and trout. We explore differences between day and night surveys at each of these lochs in an attempt to draw insights into how differing detectabilities between species and behaviours may influence the results of simple hydroacoustic surveys

Methodology

Hydroacoustic equipment and methods

A vertically-aligned Simrad split beam 7C transducer and a Simrad ES120 transceiver were used in conjunction with Simrad ER60 software. The echo counting method was used, with post-processing conducted in the Sonar 4 software package. Full details of hydroacoustic methodology are described in Godfrey *et al* (2011).

Survey Design

A zig-zag pattern of transects was adopted in preference to a parallel transect pattern for reasons of expediency (see Godfrey *et al* 2011 for discussion). In order to minimise random errors in population estimation, the number of zig-zags transects for each loch was determined so that total track length/square root of loch area was >6 (Aglen 1983). For Loch Rannoch and Loch Laidon this resulted in a series of 20 transects, for Loch na Sealga 19 transects.

These transects were pre-programmed into a Garmin GPS unit, so that all the surveys of the loch sailed as near to identical survey tracks as the skill of the steersman, and the accuracy of GPS location could achieve. For Loch Rannoch (Map 1), Transects 1, 2 and 3 effectively sample a separate basin ("west basin"), and while these were surveyed during the day, the potential for running aground was high

on Transect 3 so these three transects were avoided at night for safety reasons. Wherever direct day and night comparisons are made in the analysis below therefore, these only use data from transects 4 to 20 ("main basin"). The west basin was analysed separately.

Mean densities from echo-counting were estimated as the mean of the individual mean densities for each of the transects. Densities are expressed as targets ha⁻¹ and are examined at different minimum echo-size limits to explore patterns in target-size distribution. There is no exact correspondence between target size and echo size, and there are systematic differences across species. For physoclists (like the charr and brown trout we expect to be the most common targets in the lochs surveyed here), a general relationship is widely used to give an indication of size: 20LogL-67.5 (where L is fork length in cm) (Foote 1987).

Ideally we would have carried out daytime and night time surveys in each month on Loch Rannoch, but were unable to do so, in part because of high wind speeds in the winter months. In all we obtained daylight surveys from 10 months, and night time surveys from three, with details shown in Table 1.

Map 1

The transects surveyed on Loch Rannoch. The three westernmost transects were not surveyed in darkness, and effectively represent the separate west basin, while the remaining transects sample the main basin.



Timing of hydroacoustic surveys at Loch Rannoch 2008-2009			
Date of survey	Time of day	Number of Vertical	
		Transects	
April 8 th -10 th 2008	Day	20	
April 8 th -9 th 2008	Night	17	
May 5 th 2008	Day	20	
May 27 th 2008	Day	20	
May 28 th 2008	Night	17	
July 7 th -8 th 2008	Day	20	
August 5 th 2008	Day	20	
August 5 th -6 th 2008	Night	17	
September 1 st 2008	Day	20	
October 27 th -29 th 2008	Day	20	
December 11 th -12 th 2008	Day	20	
February 24 th 2009	Day	20	

Surveys of Loch Laidon (Rannoch Moor) and Loch na Sealga (Wester Ross) in periods of both daylight and darkness were conducted in May and July respectively (Table 2). Day and night time surveys were conducted using the same transects. Unfortunately, due to the combination of dangerous shallows in some parts of Loch Laidon, coupled with inadequate GPS mapping available, it was thought prudent to reduce the scope of the survey. As a result the night-time survey of Loch Laidon consisted of only 11 transects at the east end of the loch (compared with the 19 transects of the full survey).

Table 2

Location and dates of hydroacoustic surveys

•	•	
Water body	Date of survey 2008	Number of Vertical
		Transects
Loch Laidon Day	7 th May	19
Loch Laidon Night	7 th -8 th May	11
Loch na Sealga Day	1 st July	21
Loch na Sealga Night	2 nd -3 rd July	21

Table 1

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Results

Loch Rannoch: seasonal and diurnal variation

In characterising temporal variation on the seasonal scale we report densities here for three different ranges of target- size, >-54dB (representing fish of lengths above 4.5cm), -54 to-60dB (approximating to a length of around 2.5cm to 4.5cm if fish, but also likely to incorporate echoes from very large zoo-plankton) and -60 to -70dB (likely representing echoes only from zoo-plankton). A summary of the recorded densities for the two larger groups are presented in Table 3.

For the -54dB target limit, daylight densities in the main basin of Loch Rannoch ranged within fairly narrow limits 13.0-20.5 fish ha⁻¹, with the exception of December, when the density of targets was much lower (8.0 fish ha⁻¹). Peak density of targets >- 54dB was in September (Fig. 1), but was similarly high in February and April, whilst the late spring and summer months had lower densities.

Of the three night-time surveys (16.3-28.8 fish ha⁻¹), two generated the highest density estimates yet reported from loch Rannoch, and all three were higher than those of daytime surveys conducted at the same period (around 50% higher density at night in April and August, but only 10% higher in June).

Table 3

Mean target densities (number targets ha⁻¹) and between transect standard error for a range of target size thresholds, in the main basin of Loch Rannoch

Survey	Minimum target strength threshold	
	-60dB	-54dB
	Mean density (s.e)	Mean density (s.e.)
April Day	34.2 (8.3)	19.9 (5.2)
April Night	41.3 (8.8)	28.8 (6.9)
May Day	19.8 (4.5)	13.0 (3.1)
June Day	32.9 (7.9)	14.7 (2.1)
June Night	24.0 (5.3)	16.3 (3.8)
July Day	22.5 (4.7)	13.0 (4.4)
August Day	22.8 (5.5)	13.4 (3.5)
August Night	41.2 (10.8)	21.9 (5.7)
September Day	34.0 (5.8)	20.5 (3.9)
October Day	26.5 (3.8)	15.8 (3.0)
December Day	13.0 (2.8)	8.0 (1.6)
February Day	27.0 (5.8)	19.4 (4.7)

For the analysis incorporating echoes from smaller targets (those potentially reflecting from very small fish and/or very large zoo-plankton) in general the number of additional echoes accepted was similar in proportion to the number of echoes accepted in the -54dB analysis (Table 3, Fig. 1). However, a distinct peak in both the absolute and relative density of echoes in the range -55 to -60dB occurred in June, this being the only month in which echoes of this size were more abundant than larger echoes (>-54dB). The simplest explanation for such a peak is that it represents the emergence of either young of the year fish, and/or the largest zoo-plankton. Echoes in the range -61 to -70 dB (likely to be reflections from zoo-plankton alone) show the expected summer peak (Fig. 1) from July to September.



Figure 1. Seasonal variation of target density in the main basin of Loch Rannoch, showing targets >54dB (assumed to be fish), -55 to -60dB (potentially very small fish or large plankton) and -61 to -70dB (assumed to be large zoo-plankton). Note log-scale of y-axis.

We explored the data further by separating targets from the 3m closest to the bottom of the loch (the benthic zone), from all other data (pelagic). We did this firstly because charr are known to exist in at least two different morphs in Loch Rannoch, one 'pelagic' and one 'benthic' (Adams *et al* 2007a), thus separating out data in this way might provide insight into differences between the two populations and aid our interpretation of the data; and secondly, because loch surface roughness conditions can affect the resolution of targets near the bottom, so that targets that are detectable in calm conditions may be indistinguishable from the bottom in rougher conditions.

a)







Figure 2. Seasonal variation in target density in the main basin of Loch Rannoch for echoes >-54dB (assumed to be fish), <-54 to -60dB (potentially very small fish or large plankton) and <-60 to -70dB (assumed to be large zoo-plankton) in a) pelagic zone and b) the zone within 3m of the loch bottom.

We examined how the different size targets were distributed between the benthic zone (within 3m of the bottom) and the pelagic zone (all other water) (Table 4 & 5, Fig. 2a and b). Higher densities of all sized targets were found in the pelagic zone (reflecting the greater volume of water involved). When separating the data this way it was apparent that the peak in June of targets in the -55 to -60 dB range (very large plankton/very small fish) occurred principally in the benthic layer, whereas the September peak in density in the > -54 dB target size range was apparent in both benthic and pelagic zones. The plankton peak in the pelagic zone was evident from

July to September, but appeared slightly earlier in the benthic zone (June to September).

Table 4

Target density (targets ha⁻¹) for targets with echoes greater than -54dB in the main basin of Loch Rannoch for two different sections of the water column

Loch Rannoch	Pelagic	Benthic
	Mean no targets ha⁻¹ (s.e.)	Mean no targets ha ⁻¹ (s.e.)
April Day	14.6 (3.5)	5.3 (1.7)
April Night	16.5 (2.5)	12.2 (4.4)
May Day	8.7 (2.1)	4.4 (1.0)
June Day	10.4 (1.0)	4.2 (1.2)
June Night	9.9 (1.3)	6.7 (2.5)
July Day	8.4 (1.6)	4.6 (1.8)
August Day	8.3 (1.7)	5.0 (1.9)
August Night	10.1 (1.3)	11.8 (4.4)
September Day	13.4 (1.4)	7.1 (2.5)
October Day	11.8 (1.8)	3.9 (1.2)
December Day	5.9 (0.9)	2.2 (0.7)
February Day	14.0 (2.6)	5.3 (2.2)

Table 5

basin of Loch Rannoch for two different sections of the water column.		
Loch Rannoch	Pelagic	Benthic
	Mean no targets ha ⁻¹ (s.e.)	Mean no targets ha ⁻¹ (s.e.)
April Day	24.4 (5.5)	9.9 (2.8)
April Night	23.1 (3.0)	18.2 (5.8)
May Day	13.8 (3.4)	6.0 (1.1)
June Day	19.9 (2.0)	13.0 (5.9)
June Night	14.3 (1.8)	9.7 (3.4)
July Day	15.6 (2.4)	6.9 (2.3)
August Day	15.1 (2.7)	7.7 (2.8)
August Night	18.5 (2.0)	22.8 (8.8)
September Day	21.0 (2.2)	13.0 (3.5)
October Day	20.1 (2.2)	6.4 (1.7)
December Day	9.5 (1.8)	3.5 (1.0)
February Day	20.0 (3.3)	7.0 (2.5)

Target density (targets ha⁻¹) for targets with echoes greater than -60dB in the main basin of Loch Rannoch for two different sections of the water column.

To explore local variability within Loch Rannoch, we analysed the shallow west basin of the loch separately. In this basin patterns of seasonal variability were similar (June peak in -55 to -60dB range) but with a slightly earlier plankton peak slightly early, June to August plankton peak). The density of plankton-sized targets (-60 to -70dB) however was more than an order of magnitude greater (Fig. 3). For the larger targets, there was a December minima, as in the main basin, but also a very low density of targets in May, which was not the case in the main basin and is not easily interpreted. On the whole though, and particularly during the summer months, the densities of fish-sized targets were also substantially higher than in the main basin.



Figure 3. Seasonal variation of target density in the shallow west basin of Loch Rannoch, showing targets >54dB (assumed to be fish), -55 to -60dB (potentially very small fish or large plankton) and -61 to -70dB (assumed to be large zoo-plankton).

To examine temporal variation on the diurnal scale we obtained data to compare day and night surveys from three months on Loch Rannoch: April, June and August, and the results are presented in Table 3, and Fig. 4. Densities of fish-sized targets were higher in each of the night-time surveys than their daytime counterparts, but the effect-size was not very large (around 50% higher density at night in April and August, but only 10% higher in June). No consistent day-night variation was observed in the size range corresponding to very small fish/very large plankton, but in the smallest, plankton-sized targets densities were slightly lower in night surveys than during the corresponding day surveys. It was noticeable that variation between transects for plankton-sized targets was a feature of the month of survey, rather than the time (day v night) of survey.



Figure 4. Distribution of different-sized echoes from daylight and night time hydroacoustic surveys of the main basin of Loch Rannoch. Echoes >-54dB are assumed to be fish, echoes from -55 to -60dB are likely to be very small fish and/or very large zoo-plankton, echoes from -61 to -70dB are assumed to be zoo-plankton. Bars show between transect standard error. Note log-scale of y-axis.

We explored the patterns of echo-detection between day and night in more detail, but separating the position of targets into upper pelagic (0-25m depths), lower pelagic (>25m depth) and benthic (within 3m of the loch bottom) zones (Fig. 5). In the upper pelagic zone, the only consistent pattern was for lower densities of plankton-sized echoes (-61 to -70dB) at night. There were substantial differences between the detection of echoes in the very small fish/large plankton range (-55 to -60dB) between day and night for each of the months: targets in this size-range were scarcer at night in April and June, but more common in August. Fish-sized target densities were very similar between day and night in April and June (in each case slightly higher at night), and in August the night time density of fish-sized targets was significantly greater in the upper pelagic zone (Fig. 5a).

In the deeper pelagic zone, there was little variation either between months, or between day and night in target densities (Fig. 5b), though there were slight trends toward lower densities of all targets at night.

In the benthic layer (Fig. 5c) the density of fish-sized targets was approximately twice as great during night-time surveys for all three months. While there were substantial differences in reported densities between day and night for the smaller target-size ranges, the directions of difference were not consistent.

a) upper pelagic







c) benthic layer



Figure 5. Distribution of different-sized targets in different zones of the main basin of Loch Rannoch, during daylight and night time hydroacoustic surveys. Echoes >-54dB are assumed to be fish, echoes from -55 to -60dB are likely to be very small fish and/or very large zoo-plankton, echoes from -61 to -70dB are assumed to be zooplankton. a) upper pelagic zone, from just below the loch surface to 25m depth, b) lower pelagic zone, in water below 25m depth, and c) benthic zone, in water within 3m of the loch bottom. Bars show between transect standard error. Note log-scale of y-axis

Loch Laidon and Loch na Sealga: effects of species composition

Mean fish densities from echo-counting were estimated as the mean of the individual mean densities for each of the transects for both Loch Laidon and Loch na Sealga. This procedure will tend to produce higher standard errors in narrower lochs (with shorter, and hence more variable transects). However it should not lead to systematic bias of the mean, and in any case the two lochs share a similar shape. Densities are expressed as targets ha⁻¹ (Table 6).

Results differed markedly between the two lochs: daylight densities of targets >-54dB (equating to fish >4.5cm in length) varied more than fourfold (8.2 fish ha⁻¹ in Loch Laidon, but only 1.9 ha⁻¹ in Loch na Sealga). During darkness this situation was almost perfectly reversed, with detected densities of targets >-54dB of only 1.0 fish ha⁻¹ in Loch Laidon, and 10.4 ha⁻¹ in Loch na Sealga.

Using a smaller target size threshold for accepting echoes for analysis (-60dB, a threshold that is expected to incorporate both the largest zoo-plankton and very small fish) revealed further marked differences between the two lochs. While estimates of target densities for Loch Laidon were broadly unchanged for either day or night surveys at the new threshold (indicating few additional targets in the size range - 60dB to -54dB), many more detections were made in the is range on Loch na Sealga, with the number of detections increasing 4-fold to 7.9 targets ha ⁻¹ during the

day, and almost doubling to 17.0 targets ha-1 at night. While this further difference between the two lochs might reflect some difference in plankton composition, or behaviour of small fish in the two lochs, another compelling interpretation could be that young of the year fish that might be expected to fall in the -60 to -54dB echo size range were not yet detectable or present in Loch Laidon in early May, but by the time of the July survey of Loch na Sealga had become so.

Table 6

Mean target densities (number targets ha⁻¹) and between transect standard error for a range of target size thresholds

Site	Minimum target strength threshold		
	-70dB	-60dB	-54dB
	Mean	Mean density	Mean density
	density(s.e)	(s.e)	(s.e.)
Loch Laidon Day	97.9(23.9)	8.4 (7.3)	8.2 (7.3)
Loch Laidon Night	41.6(9.3)	1.0 (0.7)	0.8(0.7)
Loch na Sealga Day	132.5(24.7)	7.9(1.8)	1.9 (0.4)
Loch na Sealga Night	84.2 (15.2)	17.0 (3.9)	10.4 (2.1)

There is no exact correspondence between target size and echo size, and there are systematic differences across species. For physoclists (like the charr and brown trout we expect to be the most common targets in the lochs surveyed here), a general relationship is widely used to give an indication of size: 20LogL-67.5 (where L is fork length in cm) (Foote 1987). When changing the minimum size of echoes for analysis from -54dB (expected to detect fish as small as 4.5 cm in length, but nothing smaller, according to Foote's (1987) equation) down to -60dB (expected to detect fish as small as 2cm in length (e.g. summer young of the year salmonids), but also to include echoes from larger zoo-plankton species, very few additional targets were detected in Loch Laidon, either by day or night (Fig. 6), suggesting that young of the year fish and large zoo-plankton species that reflect sound in this range were almost absent during the survey. By contrast, at Loch na Sealga both in the day (fourfold increase) and the night (twofold increase) the number of detected targets increased when lowering the threshold to -60db, indicating the presence of a large number of targets in the -60 to -54bD range.

When extending the minimum-size of echoes down to -70dB to incorporate a wide range of plankton species the number of detected targets rose similarly (by an about order of magnitude) at the two lochs. Slightly more echoes were detected at Loch na Sealga, and at each loch slightly more echoes were detected during the day than at night.



Figure 6. Differences in detected densities of targets using three different echo-size thresholds on Loch Laidon and Loch na Sealga on both day and night-time surveys. Note log scale of Y axis.

The percentage frequency distributions of fish-sized targets on the two lochs are presented in Fig. 7. These are based on all the single echo locations, and so data for individual fish may occur more than once, even in different size-classes. However, since the size of a target should not affect the number of single echo detections (SED) associated with it (Simmonds & MacLennan 2005), this distribution should closely resemble the true distribution.

Size frequency distributions differ between lochs and between day and night time surveys. On Loch Laidon a wide range of sizes were represented during the day, with the largest at -32dB (approximating to a fork length of around 60cm), whilst at night a more limited range of target-sizes were detected, with peak frequencies at -40dB (ca 23cm), -53dB (ca 5cm), and -59 (ca 3cm, or zoo-plankton).

On Loch na Sealga, the daytime frequency distribution showed a gradual decline in abundance with size, with possible peaks at -50db (ca 7cm) and -44dB (ca 15cm) and with the largest individuals at -35dB (ca 40cm). During the night-time survey there was a highly pronounced frequency peak at around -43dB (ca 16cm) and a smaller peak at around -36dB (ca 37cm), together with a larger number of targets of the size representing the interface between very small fish and large plankton.







Figure 7. Frequency distribution of targets detected in the size-range -60dB to -28dB as a percentage of all targets detected <-70dB, comparing daytime (open circles) and night time (closed circles) surveys for a) Loch Laidon and b) Loch na Sealga.

Discussion

Seasonal variation in densities of different target sizes during daylight surveys: implications for survey timing

A single water temperature was used to calculate as an input for the calculation of the speed of sound transmission, and we used water temperature measured at approximately 20cm below the surface from the midpoint of each transect. While the speed of sound in water is not very sensitive to temperature it is evident that surface temperature may differ substantially from average temperature throughout the water column. In the normal range of operating temperatures a discrepancy of 1°C between surface and mean temperature equates to an error of about 0.25% in distance estimation, in turn leading to a small error in volume (and hence fish density) calculation of less than 1%. Quantification of the influence of temperature on estimated density would require a full characterisation of the depth distribution of targets in relation to temperature in all transects, and is beyond the scope of the present work. However, temperature profiles we collected using a sond (not presented here) suggests that during spring to autumn using surface temperatures may have over-estimated mean column temperature by about 2°C, leading to an under-estimate of fish density of up to 2%. In calm winter conditions however there was potential for a similar-sized over-estimate of density. Bias in the results due to temperature variation is unlikely to be of sufficient magnitude to affect interpretation of seasonal variation in density.

On Loch Rannoch peak densities of fish-sized targets were found in September (Fig. 1), although there was relatively little seasonal variation, with the exception of the December survey, where densities were significantly lower than all the other months surveyed. A similar scale of variation in monthly stock estimates in a deep German lake have been shown to be strongly correlated with the abundance of fish in simultaneous of gillnet surveys (Mehner & Schulz 2002). December may correspond to the spawning (Walker 2007), or immediate post-spawning, period for charr in Loch Rannoch, during which time charr would be expected to aggregate in shallow water close to the loch shores, and so be unlikely to be detected by horizontal sonar techniques. Similarly trout may be spawning in streams feeding the loch at this time. There was a lower detected density of fish in October than in either April or February, and it is tempting to speculate that this slight decline might represent the beginning of the charr spawning migration. It is unfortunate that we were unable to conduct surveys in November or January to determine the duration of this apparent absence/undetectability of fish in the loch, but it might perhaps last as long as from October through to January. Lower densities were recorded in May to August. This could reflect loss of smaller fish to predation as the metabolic rates of larger fish rise with warmer temperatures, but might equally be caused by some behavioural difference associated with warmer waters leading to reduced detectability.

According to standard equations (Foote 1987) fish targets yielding echoes between -54 and -60dB size are expected to be between 2 and 5cm: the approximate size of recruiting 0+ salmonids. The appearance of echoes in this size range is therefore of particular interest. Unfortunately echoes of this size may also be caused by large or gas-bearing zoo-plankton such as Chaoborus spp. (Eckmann 1998, Godlewska & Jelonek 2006). It is possible in some circumstances to distinguish between plankton and small fish targets by simultaneously deploying transceivers operating at different frequencies (Jurvelius et al 2008) or by using more complicated post-processing methods and assumptions (Malinen et al 2005). Neither of these methods were available here, but previous published work has shown the potential of the hydroacoustic technique for studying young of the year fish even in the absence of these methods (Guillard et al 2006). In the main basin of Loch Rannoch as a whole there was a marked peak in echoes of this size (Fig. 1), and further analysis revealed that this peak was principally due changes in the benthic zone (i.e. within 3m of the loch bottom), though nevertheless also detectable in the in the pelagic zone (Fig. 2). Two equally plausible, mutually non-exclusive, and currently indistinguishable possibilities might explain this. Firstly it might reflect the emergence of Chaoborus larvae from the loch sediments. Secondly it might represent detections of young of the year fish as they emerge. In either case it is somewhat hard to explain why the peak of echoes should be so brief, unless mortality rates (whether of fry or Chaoborus) are very high. Certainly there was no pattern of declining density of echoes in the -54 to -60dB size-class after June alongside increasing densities of echoes in the >-54dB class, which would be expected if the echoes represented juvenile salmonids recruiting into the larger size class with growth.

In the small, shallow west basin of Loch Rannoch, where there was also a June peak in echoes of the size representing the very small fish/very large plankton interface (Fig. 3). Furthermore from July to September there is a pattern of decreasing density of these echoes concomitant with increasing densities of fish-sized echoes (thereafter a pattern consistent with fish 'disappearing' to spawn is seen, as in the main basin). Plankton densities in the west basin during the summer peak were of an order of magnitude greater than in the main basin. The likely explanation for the higher plankton density in the west basin is that there was reduced mixing due to shelter from westerly winds together with shallower water allowing warmer surface water temperatures to develop in the west basin. Perhaps also the influence of the inflowing River Gaur, draining two higher lochs, may have played a role. Fish-sized targets were also found at higher densities, particularly in the summer months, than in the main basin. The west basin may represent a more or less self-contained system, particularly for charr, separated as it is from the main basin by a ridge of very shallow water. There may be a temptation to regard lochs as homogenous for fishassessment purposes, but local spatial (horizontal) variation within lochs, can clearly be important.

These seasonal and spatial variations raise as many questions as answers, but several conclusions can be drawn. Despite representing the best conditions for carrying out hydroacoustic surveys from a logistical point of view, summer does not appear to be the ideal time biologically, at least in Loch Rannoch. Instead higher densities were found in early autumn and late winter. Late autumn and early winter, coinciding with salmonid spawning, is also unsuitable for hydroacoustic surveys. Accordingly there is a relatively short window representing the optimum season for daylight surveys: September, February, March and April, this window being all the narrower when the prevalence of suitable calm weather during these months is taken into consideration.

Target size distribution on Loch Laidon and Loch na Sealga

On Loch Laidon there were very few detectable targets in the echo size range -54dB to -60dB (likely representing fish of the length range 2-5cm and/or certain large zooplankton species), either by day or night. By contrast on Loch na Sealga, targets of this size were as common as targets >-54dB (likely representing fish > 4.5cm in length) during the night, and twice as abundant as targets of >-54bD at night. The simplest explanation for this discrepancy is that the survey on Loch Laidon (in early May) took place before young of the year fish (and/or large zooplankton species) had emerged. Loch na Sealga on the other hand was surveyed at the beginning of July, when young of the year might be expected to be giving reflections in the -60 to -54dB range, or equally, when large zoo-plankton had become more abundant in the loch. To determine whether young of the year fish might be contributing to the difference, or whether it could be explained by plankton populations alone, we collected samples of plankton in each of the lochs, at a variety of depths and with associated echograms, but these remain to be analysed and are not reported on here. Without direct methods of separating out the echoes from large plankton and small fish (e.g. Jurvelius et al 2008) it may be unwise to indulge in speculation regarding target size distributions, because, as Simmonds & MacLennan (2005) point out, there is a degree of stochasticity regarding the relationship between target size and echo strength. This is particularly the case here because we have as yet no direct measurements of fish size against echo size with our equipment.

When lowering the target threshold still further to include echoes from the -70 to -60db range (where no additional echoes attributable to fish would be expected) to explore zoo-plankton density, broadly similar densities were observed on the two lochs, with slightly higher densities on Loch na Sealga as would be anticipated due to seasonal growth and the timing of the surveys (Maitland 1981). For each loch however, slightly greater densities were observed in the daytime surveys. Zooplankton are known to undergo vertical diel migrations (Masson *et al* 2001), avoiding predation by sinking into darkness during the day, and rising to graze of phytoplankton during darkness. The slight reduction in night time densities reported here on Loch Laidon, Loch na Sealga and on Loch Rannoch, seems somewhat unexpected, but could reflect this movement if zooplankton were moving up to very close to the surface so as to become effectively undetectable by the vertically-aligned sonar equipment used here. In addition to the predictable diel migrations of plankton, it should be remembered that there can be important short term influences of weather, in particular recent wind-history prior to the survey, which could generate results in a less predictable way (Jones *et al* 1995).

Comparison with previous daytime surveys

Previously reported densities from five other Scottish lochs, including Loch Rannoch, using the same methodology are shown for comparison in Table 7 (see Godfrey *et al* 2011). Using the threshold of -54dB, the day time survey of Loch na Sealga, with 0.9 targets ha⁻¹ has markedly the lowest recorded daytime target density of the seven lochs now surveyed, differing by almost an order of magnitude from other surveyed water bodies. Loch Garry, a water body of similar size, shape and depth profile, and also known to contain both charr and trout, had a recorded density of 15 targets ha⁻¹. Whilst having densities four times greater than Loch na Sealga, Loch Laidon's recorded fish density was nevertheless amongst the lowest recorded thus far (only marginally higher (at 8.2 ha⁻¹) than at the Fionn Loch (8.0 ha⁻¹), the previously lowest density water body.

Table 7

Mean target densities (number targets ha⁻¹) for a range of previously surveyed Scottish lochs at two different dB thresholds (Godfrey *et al* 2011)

Minimum target strength threshold			
-60dB	-54dB		
Mean density	Mean density		
(s.e)	(s.e.)		
19.06 (3.39)	12.30 (2.19)		
31.48 (5.53)	18.51 (2.95)		
23.83 (7.29)	15.02 (4.38)		
32.30 (9.06)	11.73 (2.52)		
9.94 (2.51)	7.99 (2.13)		
131.34 (20.05)	17.89 (4.36)		
	Minimum target stru -60dB Mean density (s.e) 19.06 (3.39) 31.48 (5.53) 23.83 (7.29) 32.30 (9.06) 9.94 (2.51) 131.34 (20.05)		

When using -60dB as the target threshold, Loch na Sealga and Laidon had similar densities (7.9 and 8.4 targets ha⁻¹ respectively). These are both slightly lower density than the previously lowest reported density at this threshold of 9.9 targets ha⁻¹ on the Fionn Loch, and substantially lower than the densities previously reported from Lochs Rannoch, Quoich, Maree and Garry (Table7).

Target densities were anticipated to be lower in Loch Laidon than from those previously sampled, given the absence of charr, and given the expected under-

representation of surface-dwelling trout in the ensonified beam. Unfortunately we do not yet know to what extent trout are under-represented. Future MSS studies that involve gill-netting a range of Scottish lochs will shed some light on this matter. At present however, it is only known that trout densities in Loch Laidon are rather high compared with a sample of other lochs (E.Verspoor pers comm.).

The very low densities reported at Loch na Sealga during daylight were not anticipated, however. At the Fionn Loch, for example, which, though substantially larger, is nearby, in topographically similar terrain, and of similarly low nutrient status, yet had densities that were four times greater than Loch na Sealga. The reasons for this difference are not immediately clear. Perhaps genuine differences in the density of charr or trout in the loch are the reason, or perhaps particular conditions on the day led to targets being undetectable at different rates. Further surveys at Loch na Sealga, or alternatively further night time surveys of other lochs could help to distinguish between these two possibilities. One additional possibility is that the species assemblage is more heavily skewed towards charr than at other lochs, and that the higher reported densities from other lochs are composed chiefly of trout targets.

The fish densities on Rannoch in the present survey ranged from 8.0-21.5 targets ha⁻¹ in daylight, almost exactly mirroring the scale of variation between the single visits to lochs shown in Table 7 (from Godfrey *et al* 2011). Given this scale of variation, and without repeated visits to the other lochs their likely annual variation cannot be known, so there is too much uncertainty to claim that the different densities reported from single visits to these water bodies reflect any genuine difference in the density of fish populations they contain. While we have attempted to chart seasonal variation on Loch Rannoch here, and while our results conform to certain biological expectations, we cannot rule out that the possibility that variation is due to differences between individual days rather than between individual months.

Day-Night Differences: implications for survey timing

Large differences were found between the densities recorded in day and night surveys on Loch Laidon and Loch na Sealga, indicating the importance of daylight in considering survey design. However since the differences between day and night densities were in different directions on the two lochs, showing that there can be no simple "night is best" approach for a hydroacoustic assessment of Scottish freshwater fish populations such as that that adopted by the Environment Agency for England and Wales.

Given the different species composition of the two lochs, one plausible explanation for this unexpected result is that charr were relatively hard to detect during the day (Winfield *et al* 2007), whilst trout were relatively difficult to detect during the night. The densities recorded here suggest in fact that charr were barely detectable during the day, and trout barely detectable at night. The likely cause of low detectability of trout at night would be due to a migration to the surface in darkness (as previously reported for Lake Trout (Salvelinus namaycush) in Lake Superior (Hrabik et al 2006)), where they may be effectively undetectable by the vertically-aligned gear used in the present survey. Fish-sized targets were very scarce in the day survey of Sealga (1.9 ha⁻¹), and in the night survey of Laidon (1.0 ha⁻¹), but were similarly common during the night at Sealga (7.9 ha⁻¹) and during the day at Laidon (8.4 ha⁻¹). A previous comparison between day and night densities on the Fionn Loch, a loch adjacent to Loch na Sealga with likely a similar species assemblage, also found higher night-time fish densities, although the contrast was not so marked. However, investigation of the distribution of the fish in the water column on the Fionn Loch showed a striking difference between day and night, with fish sized targets being detected near the surface during the day, but near the bottom at night (Godfrey et al 2011). This suggests a likely explanation for the extreme day night difference on Loch na Sealga: that during the day fish approached so close to the surface as to become undetectable by vertical sonar equipment. It is evident that the timing of surveys (both in terms of season, but more importantly day versus night) for different lochs (and presumably species assemblages) may be crucial to the results obtained. Nor is it the case that all nights can be regarded as uniform representatives of nighttime in general: differences as large as 50% have been reported for fish density between different moon phases (Luecke & Wurtsbaugh 1993).

If this interpretation of different detectabilities of trout and charr by day and night at Loch Laidon and Loch na Sealga proves to be correct, and the result is repeated elsewhere, it has important consequences for the design and interpretation of hydroacoustic surveys. In Scotland many lochs are dominated by both trout and charr, and the data here suggest that adequate surveys of either species, but not both, may be obtained by selecting either day (trout) or night (charr) time surveys. Furthermore the scale of difference in detectability of the two species on the two lochs surveyed here indicate that the contribution of charr to the total daytime survey estimates, and trout to the total night-time survey estimates is minimal, and that the total fish density of lochs where both species are present could be estimated by treating day and night time estimates as additive. Similarly, the relative contributions of trout and charr to the total biomass could be inferred from the difference in recorded densities for day and night time surveys.

On lochs such as Rannoch, with substantial populations of both trout and charr therefore might appear to have higher densities of fish at night if charr were more abundant, or lower apparent night-time densities if trout were more abundant. Yet overall the results reported here from day and night surveys on Rannoch were somewhat equivocal and did not provide support for this view. In general, while substantial differences between day and corresponding night surveys were found in all the target-size ranges, these were not often consistent, suggesting a substantial amount of unexplained variation not necessarily related to time of day. However, diurnal variation in density of fish-sized targets in Loch Rannoch as a whole did show some consistency: we found higher densities (10-50% increases) on each of the night surveys when compared with its corresponding daylight survey. Given the apparent equivalence in low detection rate of charr during the day on Loch na Sealga and the low detection rate of trout during the day on Loch Laidon, this might suggest numerical charr dominance in Loch Rannoch. However, the abundance of deep-lying fish, presumably predominantly charr (based on previous gill-netting in the loch (E.Verspoor & R.Greer unpublished data)), showed little variation between day and night surveys. Only in the benthic zone was there a substantial and consistent difference in fish densities between day and night with numbers approximately twice as high at night. Most, though not all benthic fish were at substantial depths, and, again based on previous gill-netting, most likely to be charr. Fish resting on the bottom surface are probably undetectable by sonar, and the equipment we used is theoretically capable of distinguishing reflections from targets 10cm above the bottom surface. Perhaps the most likely explanation for increased detections in this bottom zone at night is that charr are more active at this time, and so more likely to be sufficiently above the bottom surface to be detected. However, given that the majority of these benthic zones must be permanently in complete darkness, it is not obvious why there should be diurnal variation in fish behaviour. An alternative solution, that some fish partition resources by feeding in daylight when possible and moving to areas of permanent darkness when no daylight is available cannot be entirely discounted.

The higher level of variability in the benthic zone and greater constancy in pelagic, especially lower pelagic zone found here in Loch Rannoch repeats the findings of previous work on the loch (Godfrey *et al* 2011) which divided Loch Rannoch in three zones: benthic zone (3m layer above the bottom), upper pelagic zone (top 25m) and lower pelagic zone (below 25m), and found that differences between surveys arose from a difference amongst the density of fish detected in the bottom 3m layer alone, with the densities amongst the two pelagic zones remaining approximately constant between surveys. This points the way towards a system of index-style surveys which may be able to detect relatively small changes in deep-water populations without an attempt to characterise population density of fish in the loch as a whole.

In the surface waters (down to 25m) where trout might be expected to dominate populations, particularly during the day, there was little evidence for much difference between day and night, except during August where fish-sized targets were more abundant at night. It is possible that similar densities reflected the movement of trout out of the detectable zone (perhaps closer to the surface or towards the loch shores, balanced by the movement of charr into this zone. However, in the absence of other supporting data for this view the principle of parsimony would support the view that relatively small differences between day and night time surveys reflect relatively small changes in the distribution of fish in Loch Rannoch between day and night. It would be very hard to detect large-scale, contemporaneous movements of different

fish population components using a mobile sampling technique, if the movements result in more or less similar over all densities. One way to address this is to use stationary echo-location, but, given the small angle of 'view', and given the low density of fish targets in the loch, adequate sampling by this means is likely to be highly intensive.

Most likely then there are no large-scale diurnal movements of fish in Loch Rannoch, of the sort suggested by the high variation in densities reported between day and night on Loch na Sealga. Nevertheless on average there was an increase in fish-sized targets detected at night in Loch Rannoch. Accordingly, we suggest that night time surveys offer an advantage since they appear to detect a higher proportion of fish. Moreover, since the magnitude of this increase was not consistent (varying from about 10% to about 50% in the three surveys we conducted) it is clear that daytime surveys cannot be 'calibrated' in a simple manner.

It has previously been regarded as likely that differences between the results of day and night surveys would vary both seasonally, and between individual lochs or loch types, on a systematic basis. If this were the case then the collection of both day and night data could lead to the establishment of relationships that could inform or facilitate future survey work (for example for the Water Framework Directive by the Scottish Environment Protection Agency), given that night surveys are inherently more difficult to conduct and so less attractive to survey planners. However, it is evident from the complicated results reported here that no single calibration or set of calibrations can be applied, and that in many cases both night and day surveys may be required as they may each assess entirely different components of the fish populations, rather than assess all components with variable efficiency. At the very least it is apparent that that single-surveys at any time of day are entirely inadequate to characterise fish populations, and that a great deal of supporting research will be required before hydroacoustics can form a reliable method of fish assessment in Scottish lochs.

References

Adams, C.E., Fraser, D., Wilson, A.J., Alexander, G., Ferguson, M.M. & Skulason, S. 2007a. Patterns of phenotypic and genetic variability show hidden diversity in Scottish Arctic charr. *Ecology of Freshwater Fish*, **16**, 78-86.

Adams, C.E., Bean, C.W., Fraser, D. & Maitland, P.S. 2007b. Conservation and management of the Arctic charr: a forward view. *Ecology of Freshwater Fish*, **16**, 2-5.

Aglen, A. 1983. Random errors of acoustic fish abundance estimates in relation to the survey grid density applied. *FAO Fish. Rep.* **300**: 293-298

Carpenter, S.R., Fisher, S.G., Grimm, N.B. & Kitchell, J.F. 1992. Global change and freshwater ecosystems. *Annual Review of Ecology and Systematics*, **23**, 119-140.

Eckmann, R. 1998. Allocation of echo integrator output to small larval insect (*Chaoborus* sp.) and medium-sized (juvenile fish) targets. *Fisheries Research*, **35**, 107-113.

Foote, K.J. 1987. Fish target strengths for use in echo integrator surveys. *Journal of the Acoustical Society of America*, **82**, 981-987.

Godfrey, J.D., Thorne, A.E. & Youngson, A.F. 2011. Hydroacoustic surveys of five Scottish lochs. *Scottish Marine and Freshwater Science Report*, Vol 2 No 7.

Godlewska, M. & Jelonek, M. 2006. Acoustical estimates of fish and zooplankton distribution in the Piaseczno reservoir, Southern Poland. *Aquatic Ecology*, **40**, 211-219.

Guillard, J., Perga, M.E., Colon, M. & Angeli, N. 2006. Hydroacoustic assessment of young-of-year perch, *Perca fluviatilis*, population dynamics in an oligotrophic lake (Lake Annecy, France). *Fisheries Management and Ecology*, **13**, 319-327.

Hrabik, T.R., Jensen, O.P., Martell, S.J.D., Walters, C.J. & Kitchell, J.F. 2006. Diel vertical migrations in the Lake Superior pelagic community. 1. Changes in vertical migration of coregonids in response to varying predation risk. *Canadian Journal of Fisheries and Aquatic Science*, **63**, 2286-2295.

Jones, R.I., Fulcher, A.S., Jayakody J.K.U., Layboutn-Parry, J., Shine, A.J., Walton, M.C. & Young, J.M. 1995. The horizontal distribution of plankton in a deep oligotrophic lake – Loch Ness, Scotland. *Freshwater Biology*, **33**, 161-170.

Jurvelius, J., Knudsen, F.R., Balk, H., Marjomäki, T.J., Peltonen, H., Taskinen, J. Tuomaala, A. & Viljanen, M. 2008 Echo-sounding can discriminate between fish and macroinvertebrates in fresh water. *Freshwater Biology*, **53**, *912-923*.

Kimura, K. 1929. On the detection of fish groups by an acoustic method. *Journal of the Imperial Fisheries Institute, Tokyo*, **24**, 41-45.

Kubecka, J. & Duncan, A. 1998. Diurnal changes of fish behaviour in a lowland river monitored by a dual-beam echosounder. *Fisheries Research*, **35**, 55-63.

Luecke, C. & Wurtsbaugh, W.A. 1993. Effects of moonlight and daylight on hydroacoustic estimates of pelagic fish abundance. *Transactions of the American Fisheries Society*, **122**, 112-120.

Maitland, P.S. (ed) 1981. *The Ecology of Scotland's Largest Lochs: Lomond, Awe, Ness, Morar and Shiel.* Junk, The Hague.

Malinen, T., Tuomaala, A. & Peltonen, H. 2005. Hydroacoustic fish stock assessment in the presence of the dense aggregations of *Chaoborus* larvae. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 245-249.

Masson. S, Angeli, N., Guillard. J., & Pinel-Alloul. B. 2001 Diel vertical and horizontal distribution of crustacean zooplankton and young of the year fish in a sub-alpine lake: an approach based on high frequency sampling. *Journal of Plankton Research*, **23**, 1041-1060.

Mehner, T. & Schulz, M. 2002. Monthly variability of hydroacoustic fish stock estimates in a deep lake and its correlation to gillnet catches. *Journal of Fish Biology*, **61**, 1109-1121.

Mehner, T., Hölker, F. & Kasprzak, P. 2005. Spatial and temporal heterogeneity of trophic variable in a deep lake as reflected by repeated samplings. *Oikos*, **108**, 401-409.

Romare, P. 2001. An evaluation of horizontal echo-sounding as a method for behavioural studies of 0+ fish in field experiments. *Journal of Fish Biology*, **57**, 1512-1523.

Simmonds, J & MacLennan, D. 2005. *Fisheries Acoustics: Theory and Practice, Second Edition*, pp437. Blackwell, Oxford.

Walker, A.F. 2007. Stream spawning of Arctic charr in Scotland. *Ecology of Freshwater Fish*, **16**, 47-53.

Winfield, I.J., Fletcher, J.M. & James, J.B. 2007. Seasonal variability in the abundance Arctic charr (*Salvelinus alpinus* (L.)) recorded using hydroacoustics in Windermere, UK and its implications for survey design. *Ecology of Freshwater Fish*, **16**, 64-69.

Winfield, I.J., Hateley, J., Fletcher, J.M., James, J.B., Bean, C.W. & Clabburn, P. 2010. Population trends of Arctic charr (*Salvelinus alpinus*) in the U.K.: assessing the evidence for a widespread decline in response to climate change. *Hydrobiologia*, **650**, 55-65.



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