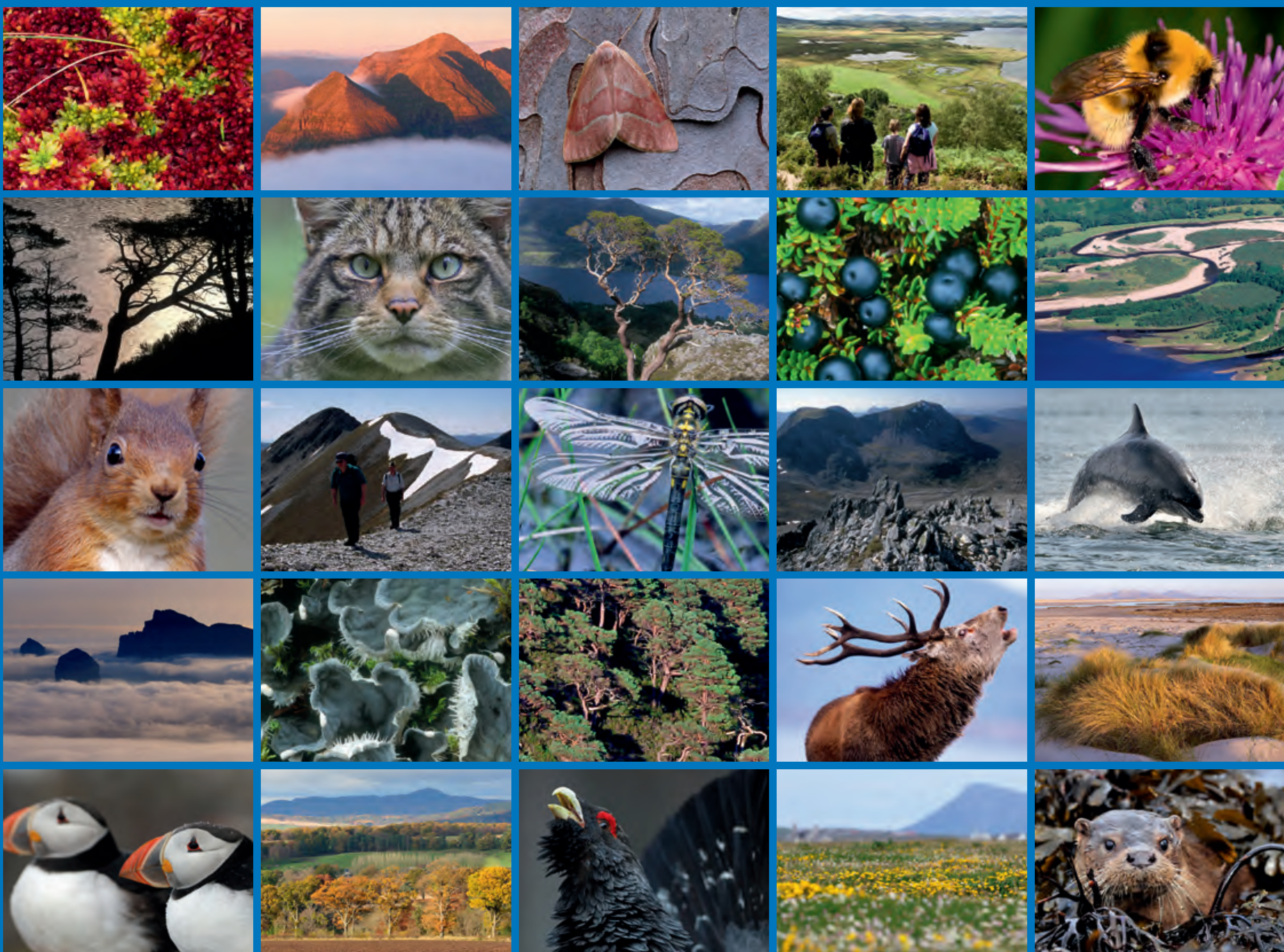
Scottish Natural Heritage
Commissioned Report No. 687

The Scottish Beaver Trial: Monitoring survey of aquatic and semi-aquatic macrophytes of the lochs 2011



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COMMISSIONED REPORT

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The Scottish Beaver Trial: Monitoring survey of aquatic and semi-aquatic macrophytes of the lochs 2011

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COMMISSIONED REPORT

Summary

The Scottish Beaver Trial: Monitoring survey of aquatic and semi-aquatic macrophytes of the lochs 2011

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Keywords

Aquatic; beaver; macroinvertebrate; Knapdale; loch; macrophyte; plant; trial.

Background

This report provides interim analysis of data collected as part of a SNH commissioned five-year monitoring programme of the Scottish Beaver Trial. Data collection began in autumn 2008, prior to the release of beavers in spring 2009. The University of Stirling is responsible for monitoring responses of aquatic vegetation in lochs to beaver activity. Data presented were collected in spring and autumn of 2011, from a subset of the original vegetation transects first sampled in 2008 and 2009. Across all of the primary lochs, an assessment has been made of species richness and cover, repeating the locations and protocol of the earlier surveys. Additional monitoring has also been put in place to quantify the vegetation and habitat changes at Dubh Loch that have occurred in response to dam building by beavers. As would be expected in a project of several years' duration, there may be differences in methods of analyses and presentation of results between this interim report and the final report covering the duration of the trial (CR688). Readers are referred to report CR688, as it supersedes the present report, which has been published for completeness.

Main findings

– Surveys in September 2011 revealed that beaver activity has had a clear and measurable impact on the macrophyte communities present in some of the Knapdale Lochs. At the gross level, this has been documented through fixed-point photography. Changes have also been recorded quantitatively along fixed transects.

– Data collected during the May 2011 survey show only subtle signs of impact. This is likely to reflect the low intensity of grazing over the preceding winter months and generally low productivity of Knapdale water bodies.

– The greatest impact of herbivory by beavers was found to be on *Schoenoplectus lacustris, Cladium mariscus, Nymphaea alba* and *Equisetum fluviatile*. This has resulted in a reduction in cover of these species, most notably in the Loch Linne-Fidhle system. As a proportion of the overall populations at Knapdale, impacts on *N. alba* and *E. fluviatile* were trivial, but selective grazing of *S. lacustris* and *C. mariscus* caused significant local reductions in these species. There are no apparent effects on the submerged plant

assemblages that form part of the basis for designation of the Taynish and Knapdale Woods Special Area of Conservation.

- Greatest effects of beavers on plant cover are evident on those lochs with lodges that have been occupied for three growing seasons. On lochs with shorter lodge occupancy, or where beavers only utilise the site as part of a larger territory, no negative effects on cover were recorded.

- The increased water level in Dubh Loch has resulted in major hydromorphological changes, including increased surface area and shoreline complexity, and a large expansion of aquatic habitat. Changes in bathymetry have been partly offset by the buoyancy of peat and associated vegetation. Major impacts on the vegetation communities have been recorded, including the reduced cover and extent of some emergent and floating-leaved macrophytes. The occurrence in newly created habitats of typical early colonising species suggests, however, that negative effects on other species may prove transient. Changes resulting from more recent but potentially similar alterations to the hydrology of Un-named Loch (North) have yet to be detected.

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1. INTRODUCTION

The five-year trial reintroduction of the European beaver to Knapdale commenced in spring 2009, following granting of a licence by the Scottish Government, in May 2008. By September 2011, beavers had occupied lodges on five of the eleven primary lochs included in the survey area, with a total of eight lochs confirmed to fall within the four beaver family territories (Harrington *et al*., 2012). This has allowed monitoring data to be collected from lochs that are subject to varying degrees of influence by beavers, as well as lochs that are unaffected, and for these data to be compared with the pre-introduction baseline. Project partners including the University of Stirling, independent from the licence-holders, were appointed by SNH to collect monitoring data. Independent monitoring of the trial is essential, ensuring a fair and balanced evaluation on completion of the five-year period. Thus, data on a range of ecosystem attributes are being collected by the project partners, to allow assessment of the ecological effects of beaver activity in a near-natural environment within the Scottish landscape.

In the present context, aquatic vegetation is of particular significance, because the release sites are located within or adjacent to the Taynish and Knapdale Woods Special Area of Conservation (SAC). Aquatic vegetation is a qualifying feature of this SAC, specifically oligotrophic to mesotrophic standing waters with vegetation of the *Littorelletea uniflorae* and/or of the *Isoeto-Nanojuncetea*, i.e. clear water lochs with aquatic vegetation and low to moderate nutrient levels. The aquatic vegetation of oligotrophic and mesotrophic standing waters is a qualifying feature of five lochs within the SAC (see Table 1). The underpinning SSSIs of the SAC, Taynish Woods SSSI and Knapdale Woods SSSI, are also designated for their standing water features. Consequently, assessment of the aquatic vegetation's response to the reintroduction of beavers is an important element of the trial.

This report presents data collected during the aquatic vegetation surveys undertaken in May and September 2011, as part of a wider programme of monitoring for the five-year trial reintroduction. Where appropriate, results have been compared to baseline data collected by the same surveyors during September 2008 or September 2009. Discussions of general trends at the loch level are provided based on these data.

Collection of macrophyte data serves two purposes. First, it will help to evaluate the success of the trial reintroduction. Second, it allows any impacts on the integrity of the Taynish and Knapdale Woods SAC to be identified at an early stage, as the trial progresses. The collection and analysis of data during 2011 allows an interim evaluation of the progress of the trial, and an indication of impacts. However, as this is an interim report, all conclusions should be viewed as preliminary. Such assessments may be used to inform adaptive management of the trial. Preliminary conclusions are presented in Section 1, along with a review of the monitoring schedule and recommended changes.

2. OBJECTIVES

The 2011 aquatic vegetation surveys aimed to achieve the following objectives:

1. to collect data from a subset of vegetation transects on each of the primary lochs within the Knapdale survey area (replicating three transects per loch resurveyed or first surveyed in 2009).
2. to provide comment on whether beaver activity has had any impact on the SAC-qualifying macrophyte species or assemblage.
3. to review the survey design and highlight any weaknesses or possible improvements.
4. to outline the next steps of the monitoring programme.

3. BACKGROUND

Beavers have the potential to affect aquatic vegetation through a variety of direct and indirect mechanisms that operate over a range of spatial and temporal scales (Rosell *et al*., 2005). Scales range from rapid but localised reductions in vegetation cover, resulting from preferential grazing of specific species (e.g. Fryxell and Doucet, 1993; Parker *et al.,* 2007), changes in light regime or physical habitat structure due to felling or caching activity (Naiman *et al.,* 1988; Jones *et al.,* 2009), through to larger scale changes in the type and distribution of vegetation due to changes in water level regime associated with damming (Pollock *et al.,* 2003). Aquatic plants have been demonstrated, through stable isoptope analyses, to form a major constituent of beaver diet, with the contribution varying seasonally and between habitats (Milligan and Humphries, 2010). Although it is evident that beavers can have an impact on the composition and biomass of herbaceous vegetation by direct herbivory, such effects are relatively poorly researched; impacts of beavers on herbaceous vegetation are typically attributed to the indirect effects of habitat modification (Parker *et al.,* 2007).

In developing a survey protocol for the assessment of aquatic vegetation in eleven lochs at Knapdale in 2008, Willby and Casas-Mulet (2010) considered the survey methods that had previously been applied to some of these lochs, for a variety of different purposes. These included the Scottish Loch Survey Project method (Lassiere, 1998), the Site Condition Monitoring method (Gunn *et al.,* 2004) and the method adopted for a previous baseline survey of the Knapdale Loch (Murphy *et al*., 2002). Criteria have been established to ensure that the output of monitoring provides for a fully informed outcome to the trial. It was argued that, in order to address specific criteria regarding the degree and nature of damage or enhancement to natural ecosystem features, the primary considerations given to survey design should relate to:

1. the ability to detect change at different spatial scales, and
2. the ability to discriminate between changes due to external factors and those attributable to beavers.

The recommended method was implemented in the surveys of eight primary lochs in 2008 (Willby and Casas-Mulet, 2010) and three additional primary lochs in 2009 (Willby *et al*., 2011). Primary lochs include the intended beaver release sites and adjacent lochs. Secondary lochs are a series of canal reservoirs situated on the edge of the release area and could potentially be utilised by wider-ranging beavers. Four secondary lochs were surveyed in 2008. Surveys followed the methods described by Lassiere (1998) and Murphy *et al*. (2002).

3.1 Location of lochs

The lochs included in the monitoring programme are located in and around the Taynish and Knapdale Woods SAC. Locations are shown in Figure 1, whilst grid references and the unique Water Body Identifier Code from the GB Lakes Inventory are presented in Table 1.

Table 1. Geographical and baseline survey information for the primary lochs routinely monitored as part of the aquatic and semi-aquatic vegetation surveys

Loch name	Grid reference	WBID[1]	Baseline Survey	Designation
Creagmhor Loch[2]	NR803910	25160	2008	SAC
Dubh Loch	NR784902	25202	2008	SAC[5]
Loch Barnluasgan	NR792912	25144	2008	SAC
Loch Coille-Bharr	NR782901	25179	2008	SAC
Loch Fidhle	NR799909	25145[3]	2008	SAC
Loch Linne	NR797910	25145	2008	SAC
Loch Losgunn	NR791898	25209	2008	
Loch McKay	NR798886	25264	2009	
Lochan Buic	NR789889	25242	2009	
Un-named (North)[4]	NR801910	25168	2008	SAC[5]
Un-named (South)	NR788885	25268	2009	

1 WBID - unique water body identifier code from the GB Lakes Inventory.
2 There are various derivations of this name used on different Ordnance Survey sheets.
3 As Loch Fidhle is contiguous with Loch Linne, it is not considered as a discrete water body by the GB lakes inventory.
4 In the GB Lakes Inventory, this loch is erroneously labelled as Loch Fidhle. Larger scale maps refer to this water body as Lochan Beag.
5 This water body lies within the SAC geographical boundary, but does not support the named feature of interest.

3.2 General views of the primary lochs

Figure 2 gives an indication of the character of each of the lochs encompassed by this survey and the overall setting. In general terms, these are well-vegetated water bodies, with extensive emergent and floating-leaved plant communities, characterised by species which are typical of Scottish lowland lochs of low to moderate alkalinity, on which there has been minimal impact. The surrounding topography is undulating and vegetation cover is dominated by commercial forestry and native broad-leaved woodland.

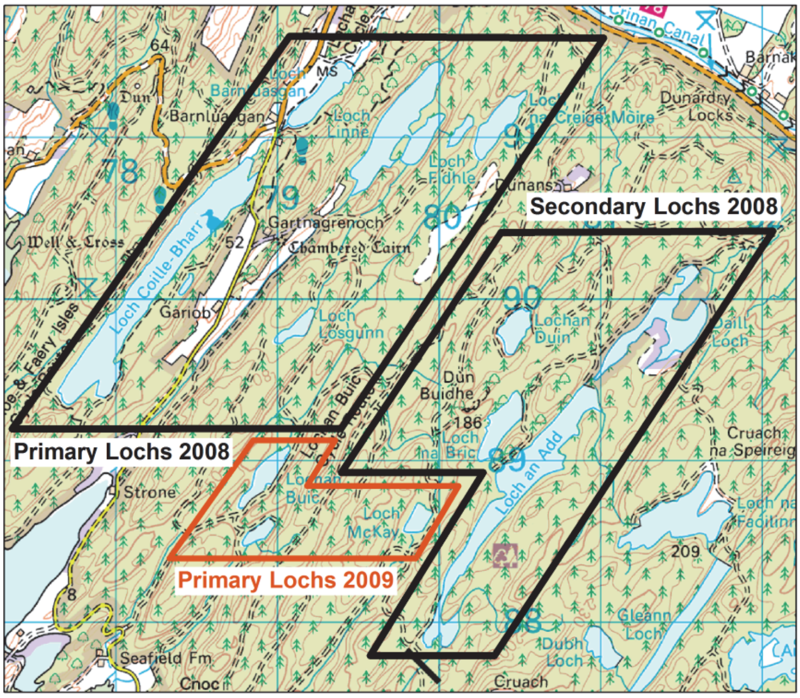

Figure 1. Location of the primary lochs surveyed in 2008 and 2009, and resurveyed at a subset of the baseline survey vegetation transects in 2011. Background OS tiles reproduced from Ordnance Survey map data by permission of Ordnance Survey, © Crown copyright and database right 2014. Ordnance Survey 100017908.

Loch Losgunn

Loch Fidhle

Loch Linne

Un-named south

Dubh Loch

Loch McKay

Creagmhor

Un-named North

Loch Barnluasgan

Loch Coille Bharr

Lochan Buic

Figure 2. Photographs illustrating the character of each of the primary lochs covered by the aquatic macrophyte surveys

3.3 Descriptive data

The lochs covered by the surveys differ with regard to both their physical character and water chemistry. In general, these are small to medium sized water bodies, with clear to humic, low to moderate alkalinity waters, of mostly shallow depth (<5 m). Basic physical and chemical data for the lochs are summarised in Table 2. Water chemistry is being monitored by SEPA, for the duration of the trial, and temporal trends will be reviewed in the final report in 2014. This information will aid in the interpretation of the biological changes presented in this report.

The Shoreline Development Index (SDI) (Hutchinson, 1957) was developed to allow the comparison of shoreline complexity by accounting for the influence of loch size on the perimeter to area ratio. A higher score indicates a more irregular shape or a greater number of inlets and bays. As such, it reflects the potential for development of littoral communities. The following equation (from Hutchinson, 1957) has been used to calculate the SDI for the primary lochs included in the monitoring programme:

$$\text{Shoreline Development Index} = \frac{\text{Shoreline Length}}{2 * \sqrt{\pi * \text{Loch Area}}}$$

The calculation has been applied to Ordnance Survey data for the Knapdale lochs, and to the new outline of Dubh Loch, following damming by beavers (section 5.5). The resulting SDI scores are presented in Figure 4.

Table 2. Key characteristics of the primary lochs: alkalinity, area, perimeter and Shoreline Development Index

Loch name	Alkalinity (meq L^{-1})	Area (ha)	Perimeter (km)	SDI
Primary Lochs				
Dubh Loch	0.32	0.4	0.3	1.34
Creagmhor Loch	0.20	5.2	1.1	1.36
Loch Barnluasgan	0.58	5.3	1.2	1.47
Loch Coille-Bharr	0.49	33.4	4.4	2.15
Loch Fidhle Loch Linne	0.21	16.5	3.1	2.15
Loch Losgunn	0.09	2.1	0.7	1.36
Un-named loch (N)	0.35	1.1	0.5	1.34
Additional primary lochs				
Lochan Buic	0.40	3.9	1.1	1.57
Loch McKay	0.28	1.9	0.6	1.23
Un-named loch (S)	0.12	1.6	0.5	1.12

Alkalinity data provided by SEPA based on approximately monthly sampling. Loch Fidhle and Loch Linne are contiguous, so values are given for the water body as a whole.

3.4 Rationale for methods

The 2011 spring and autumn surveys adopted the same approach as the 2008 baseline and 2009 monitoring surveys undertaken by the University of Stirling. This was developed from protocols described by Lassiere (1998), Murphy *et al.* (2002) and Gunn *et al.* (2004). The rationale of the survey design is to allow changes attributable to beaver activities and changes due to other influences to be discriminated, at a range of spatial scales, as described by Willby and Casas-Mulet (2010).

3.5 Monitoring schedule

Following the baseline surveys for the original eight primary lochs in 2008, which included up to five transects per loch, monitoring data for a subset of the vegetation transects (three per loch) were collected in September 2009, May 2011 and September 2011. In the same way, baseline data were collected in three additional primary lochs in September 2009 and these were resurveyed in May and September of 2011. The four secondary lochs (canal reservoirs) surveyed in September 2008 were revisited in September 2011, but since there was no evidence that any of these sites had been utilised by beavers, they are not considered further in this report. Figure 3 summarises the schedule for surveys throughout the project. At the same time as transect surveys were undertaken all lochs lying within beaver territories were circumnavigated and specific evidence of beaver feeding on aquatic vegetation was recorded.

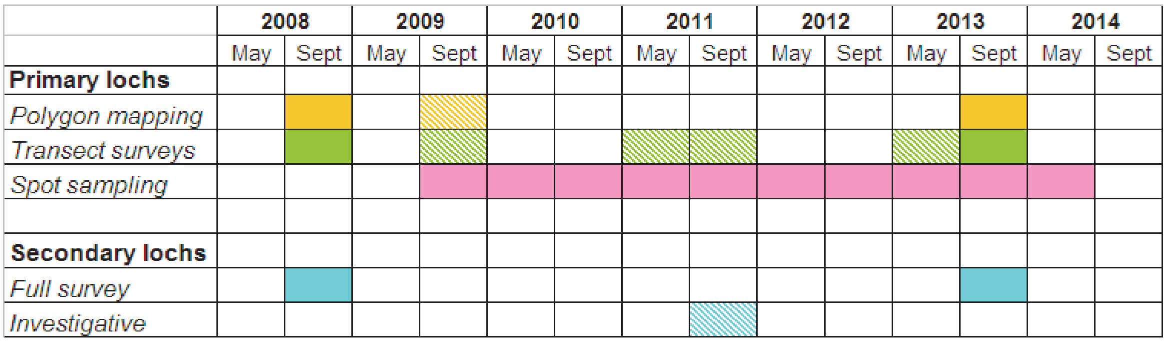

Figure 3. GANTT chart of the survey schedule for the project. Each survey type is shown in a different colour. Cells with hatched colour indicate periods when a subsample of sites will be or have been surveyed.

3.6 Additional monitoring activities

In the light of various changes associated with beaver activity at Dubh Loch, a number of new monitoring activities were initiated in 2011 and are likely to continue annually until the close of the trial. At that time, the data collected from these activities will be presented and analysed in the light of water level changes that have been measured as part of a separate hydrological monitoring programme. These new activities include:

- physical habitat assessment to map changes in the position of the shoreline associated with inundation of new areas caused by damming or canal construction;
- invertebrate sampling to assess colonisation of new habitat and in future to compare the assemblage at this site with that associated with beaver-generated wetlands elsewhere in Scotland or other parts of Europe; and
- extended vegetation sampling to incorporate former terrestrial areas, which were not included in the baseline survey of this site in 2008, but which are now inundated.

4. METHODS

4.1 Transect surveys

The full subset of transects established in the original eight primary lochs, and previously resurveyed in 2009, were surveyed again in the spring and autumn of 2011 (survey dates for each loch are given in Table 3). On each of the three additional primary lochs added to the survey in 2009, a subset of three transects was chosen for resurvey that best reflected the variation in plant cover and composition in that loch. This should favour scaling-up from transect level to estimate any effects of beavers on vegetation at the loch level. Experience from polygon surveys and transect surveys conducted in previous years was used to inform the choice of the subset of transects. Survey protocols were consistent with previous surveys, as described in Willby and Casas-Mulet (2010).

Percentage cover for each species present within the four 2 m x 2 m quadrats, distributed along each transect, was visually assessed (to the nearest 5%) and recorded on waterproof survey sheets. The position of the first three quadrats along each transect was, in most cases easily relocated, as the back edge of each quadrat had been staked previously. In some cases, markers had detached or were not visible due to high macrophyte cover or growth of epiphytic algae. Outermost quadrats, i.e. those furthest from the shore, could only be marked where water depth or substrate permitted. For unmarked quadrats and those with missing markers, a combination of GPS, alignment with other quadrats on the same transect, measured water depths and photographic records were used to find the correct position, although exact overlap of quadrats at the outer end of the transects proved impossible to achieve. Spatial overlap of these quadrats was estimated to be 50% - 70%, based on blind relocation of those outermost quadrats that could be physically marked. However, such quadrats were always located in large, relatively homogeneous beds of vegetation (for example as shown in Figure 4), so the consequences of quadrat drift are likely to be small. Across all quadrats on all transects, mean spatial overlap of sampling areas was estimated to be 90%.

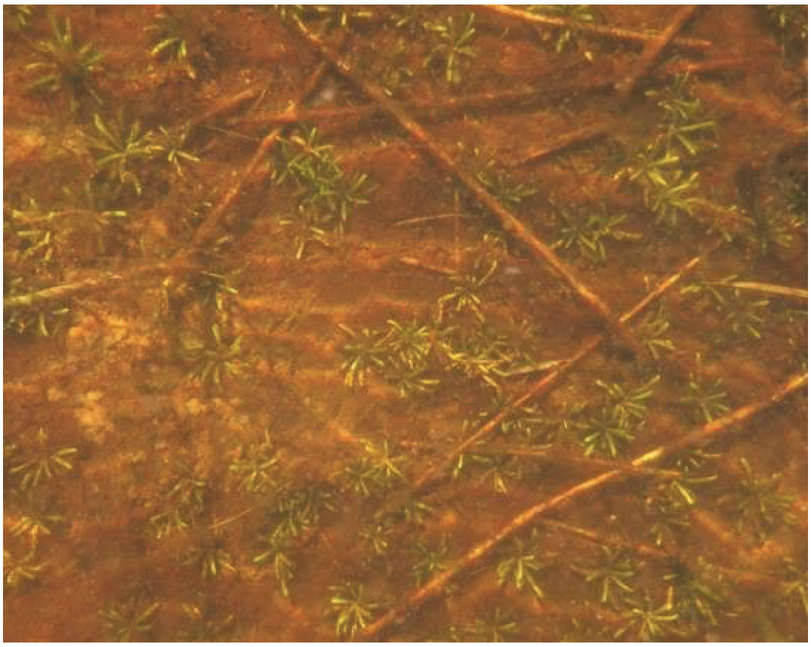

Figure 4. Underwater image demonstrating the relatively homogeneous nature of vegetation at the outer quadrat position on the loch macrophyte transects. Image approximately 1 m^2.

4.2 Survey details

Table 3. Details of survey methods and conditions during the 2011 spring and autumn surveys

Loch name	Spring survey	Methods[1]	Survey conditions[3]	Autumn survey	Survey conditions[2]
Creagmhor Loch	18/05/11	B,R,U	Poor	01/09/11	Moderate
Dubh Loch	19/05/11	R,U	Moderate	01/09/11	Moderate
Loch Barnluasgan	19/05/11	B,R,U,S	Moderate	01/09/11	Moderate
Loch Coille-Bharr	24/05/11	B,R,U,S	Poor	01/09/11	Moderate
Loch Fidhle	19/05/11	B,R,U,S	Moderate	31/08/11	Moderate
Loch Linne	19/05/11	B,R,U,S	Moderate	31/08/11	Moderate
Loch Losgunn	24/05/11	B,R,U	Good	31/08/11	Moderate
Loch McKay	24/05/11	B,R,U	Moderate	02/09/11	Moderate
Lochan Buic	24/05/11	B,R,U,S	Moderate	02/09/11	Good
Un-named (North)	18/05/11	B,R	Good	01/09/11	Good
Un-named (South)	24/05/11	B,R,U	Moderate	02/09/11	Moderate

1. Survey methods employed, where B - boat; R - rake; U - underwater viewing *in situ*; S - snorkelling
2. Good - still, strong incident overhead light; moderate - light wind; cloud and angled light, occasional light showers; poor - moderate wind, full cloud cover, intermittent heavy rain.

4.3 Polygon surveys

Polygon data were not scheduled for collection as part of the interim surveys. These data will be collected in September 2013.

4.4 Differential GPS survey of Dubh Loch

The perimeter of Dubh Loch was documented using differential GPS (Leica GPS1200). Positions were recorded every 10 m to 20 m to a precision of approximately 5 cm.

4.5 Collection of macroinvertebrate samples

Macroinvertebrate communities within the newly flooded zone of Dubh Loch were surveyed in May 2011 using a D-frame sweep net (0.5 mm mesh). Samples were collected by sweeping vegetation and disturbing benthic surfaces over an area of approximately 2 m^2 for 1 minute. These were preserved in 70% methylated spirits (industrial) and stored at 4°C prior to sorting. The locations of macroinvertebrate sampling points are shown in Figure 15. Data on macroinvertebrate sampling are not considered further in this report. They will be covered in the final monitoring report and discussed there in the context of similar sampling undertaken at other beaver sites in the UK and Sweden.

4.6 Statistical methods

Linear mixed effects modelling was applied to the quadrat data using the lme4 package (Bates *et al.*, 2013) for the [R] programming language (version 2.15.0). Two dependent variables were considered: species richness (i.e. number of species per quadrat) and summed cover (i.e. the sum of the individual species percentage cover values of species recorded in a quadrat). Species richness was modelled via a Generalised Linear mixed model procedure with a Poisson family distribution. For summed cover data, values commonly exceeded 100 due to multi-layering of vegetation. Data were normalised first (assessed by maximising the correlation coefficient in a Q-Q plot of the distribution of the model residuals) by raising them to the power of 0.66. Use of this transformation followed trials with a variety of widely used root and log transformations. A Gaussian distribution was used in the modelling. Loch, transect and quadrat position and their interaction terms with year of sampling were nested within the model as random effects, to account for the nested structure of data. These analyses were confined to data collected in September, as data collected in May was available only for one year.

To assess the potential effects of beaver activity on vegetation two measures of beaver 'activity' were used as fixed factor effects in each model. For the present purposes, beaver activity (Table 4) was defined in terms of (i) territory (thus distinguishing between the eight primary lochs that lie within the territories of the four beaver families, and the three primary lochs (McKay, Losgunn and Barnluasgan) that are outwith these territories (see Table 1 for listing of primary lochs)) and (ii) the duration (expressed in growing seasons) for which any lodge on a loch has been occupied (0, 1, 2 or 3). These terms are relatively unambiguous and allow the effects of the presence of beavers *per se* (territory term) to be compared with the existence of lodges and longer habitation (occupancy term) that would be expected to be associated with increased effects. Both terms can be clearly defined independently of the perceived levels of effect on non-woody vegetation, since to do otherwise would be tautological. Both terms were treated as factors in our models, as the duration of occupancy is unlikely to operate in a simple linear manner, at least not over periods as short as a few years, and this is confirmed by a simple graphical exploration of the data. In the final analysis, it may be possible to consider other indicators of beaver activity in these models, such as population size or presence of dams, but such models would be difficult to justify on the basis of the data set currently available.

Table 4. Assignment of lochs to different level of beaver activity based on presence in territory and number of years of lodge occupation in the years of data collection

Loch	2008	2009	2011
Creagmhor	N (0)	Y (1)	Y (2)
Dubh	N (0)	Y (1)	Y (3)
Barnluasgan	N (0)	N (0)	N (0)
Coille-Bharr	N (0)	Y (0)	Y (0)
Fidhle	N (0)	Y (1)	Y (3)
Linne	N (0)	Y (1)	Y (3)
Losgunn	N (0)	N (0)	N (0)
McKay	N (0)	N (0)	N (0)
Buic	N (0)	N (0)	Y (2)
Un-named (North)	N (0)	Y (0)	Y (1)
Un-named (South)	N (0)	N (0)	Y (0)

Territory: Yes - Y, No - N. Years of lodge occupation shown in brackets

Final models were therefore of the following form:

Model (1): Richness ~ territory + factor(occupancy) + factor(year) +
(1 | loch/transect/quadrat) + (1 | year*loch/year*transect)

Model (2): Cover ~ territory + factor(occupancy) + factor(year) +
(1 | loch/transect/quadrat) + (1 | year*loch/year*transect)

In these models, “1 |” is used to indicate a nested term (for example, transects are nested within loch, while quadrats are nested within transects). Since the determination of degrees of freedom associated with model terms derived by maximum likelihood approaches in linear mixed models remains the subject of debate, to determine the significance of the *t*-values associated with parameter estimates in model (2) an *a posteriori* simulation (Markov Chain Monte Carlo method) was used to make the necessary inference.

5. RESULTS

5.1 General patterns in transect data

Vegetation in all lochs typically changes from woodland understorey, fen or mire at the landward end of each transect (Quadrat 1) through a transition of open water and emergent species (Quadrat 2) to open water vegetation (Quadrats 3 and 4), in which *Nymphaea alba* and *Potamogeton natans* most commonly dominate. This gradient is reflected in higher richness (7-9 species on average) and total cover (~120%) in Quadrat 1, whilst richness (3-5 species) and cover (~50%) is lower and shows little change across Quadrats 2-4. This is the classical pattern to expect in a hydrosere. These changes are summarised in Figures 5 and 6.

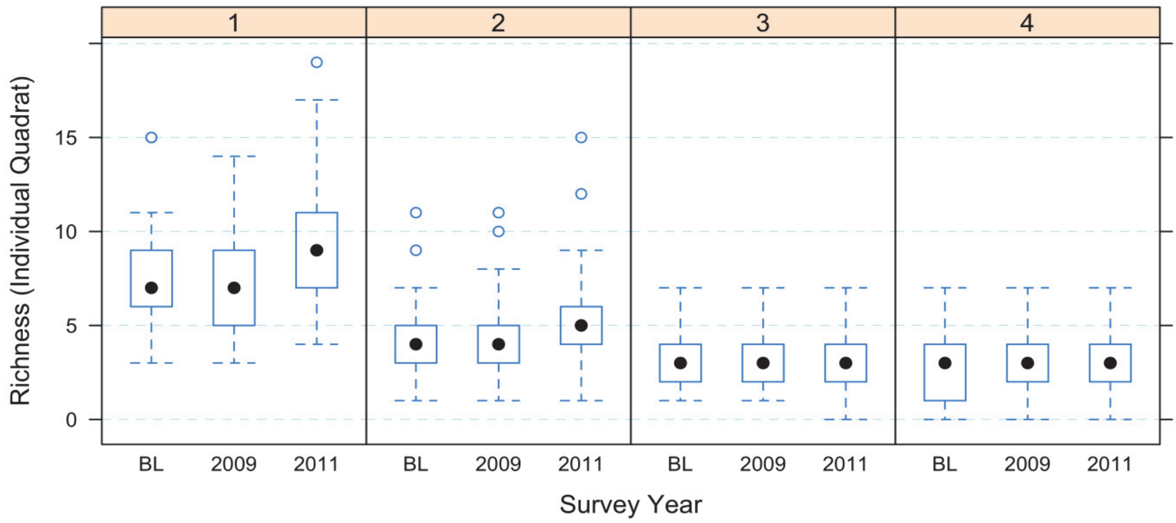

Figure 5. Comparison of mean quadrat level richness values across years for each quadrat position (upper label: 1-4) along a transect for eight primary lochs and three additional primary lochs

Note: transects extend from Quadrat 1 (shoreline) to Quadrat 4 (open water). Only September data are presented, to allow comparison with baseline data. BL- baseline data collected in 2008 (eight primary lochs) and 2009 (three additional primary lochs)

Figure 5 suggests that there may be a trend for increasing richness in the most landward quadrats (1 and 2) on a transect over time. The likely reason for this is increased detectability of species with increased frequency of sampling. This is an inevitable artefact of surveys being conducted by the same surveyors and being repeated at relatively high frequency, and might apply to almost any biological survey dataset. The same pattern does not apply to open water quadrats. Reasons for the selective increase in species richness at the landward end of quadrats may be related to the following factors. In open water quadrats, there are fewer species and lower cover, and the species concerned are larger and more easily detectable, even when their cover is low. A secondary reason for the increase in species recorded in landward quadrats is the reduction in tree cover at some lochs due to tree felling by beavers, or small reductions in dominant species caused by herbivory or water level change that favour recruitment or increased visibility of smaller species. This point is expanded in section 5.3.

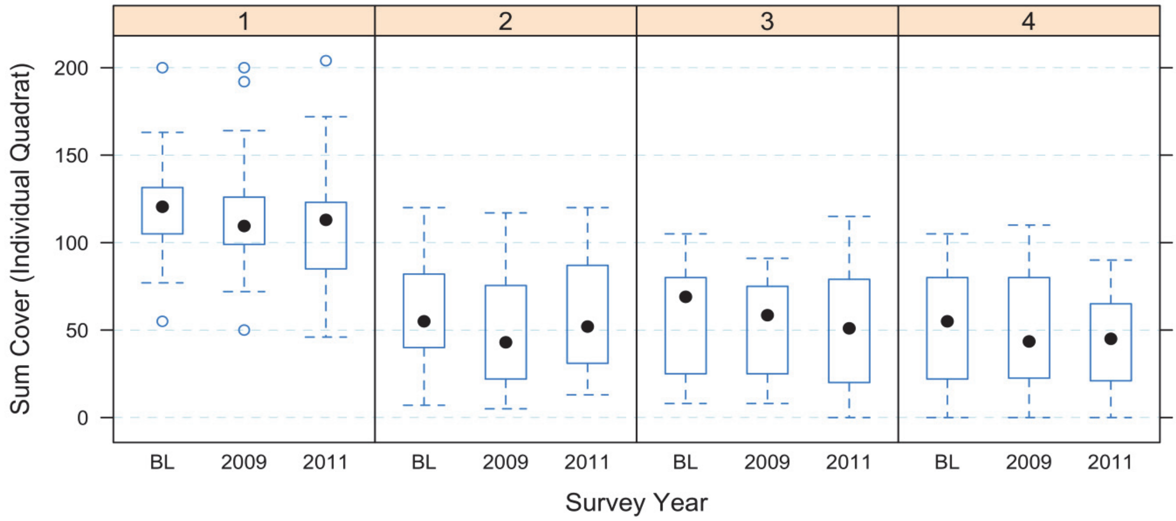

Figure 6. Comparison of mean quadrat level sum cover (total of the species cover values) for across years for each quadrat position (upper label: 1-4) along a transect for eight primary lochs and three additional primary lochs

Note: transects extend from Quadrat 1 (shoreline) to Quadrat 4 (open water). Only September data are presented, to allow comparison with baseline data. BL- baseline data collected in 2008 (eight primary lochs) and 2009 (three additional primary lochs)

Figure 6 suggests that there may be a weak trend for decreasing cover with time in the open water quadrats (Quadrats 3 and 4) that is not seen in the landward quadrats (Quadrats 1 and 2). In this dataset, this is most likely to reflect loss of vegetation due to herbivory by beavers and contraction of open water vegetation due to water level rise associated with dam building by beavers. A detailed analysis of these effects is given in section 5.3.

5.2 Seasonality in vegetation based on transect data

There were possibly some simple differences in vegetation between May and September transect data. Richness was generally lower in May (Figure 7), although the seasonal difference was comparatively small. In May, some later-season species were too small or undeveloped to be detectable, while fewer early-season species (smaller grasses and bryophytes, *Eriophorum vaginatum* and the herbs *Caltha palustris*, *Scutellaria galericulata* and *Lychnis flos-cuculi*), were most detectable. By September, these species have died back or if still present, occur at much lower cover, or are more difficult to detect amidst increased cover of larger species. Total cover (Figure 8) was possibly lower in May than in the same lochs in September, this being consistent with the timing of the growing season and the cover of most species peaking in late summer. For the commoner aquatic species, such as *Nymphaea alba* and *Potamogeton natans*, average cover in May was 30-40% lower than in September.

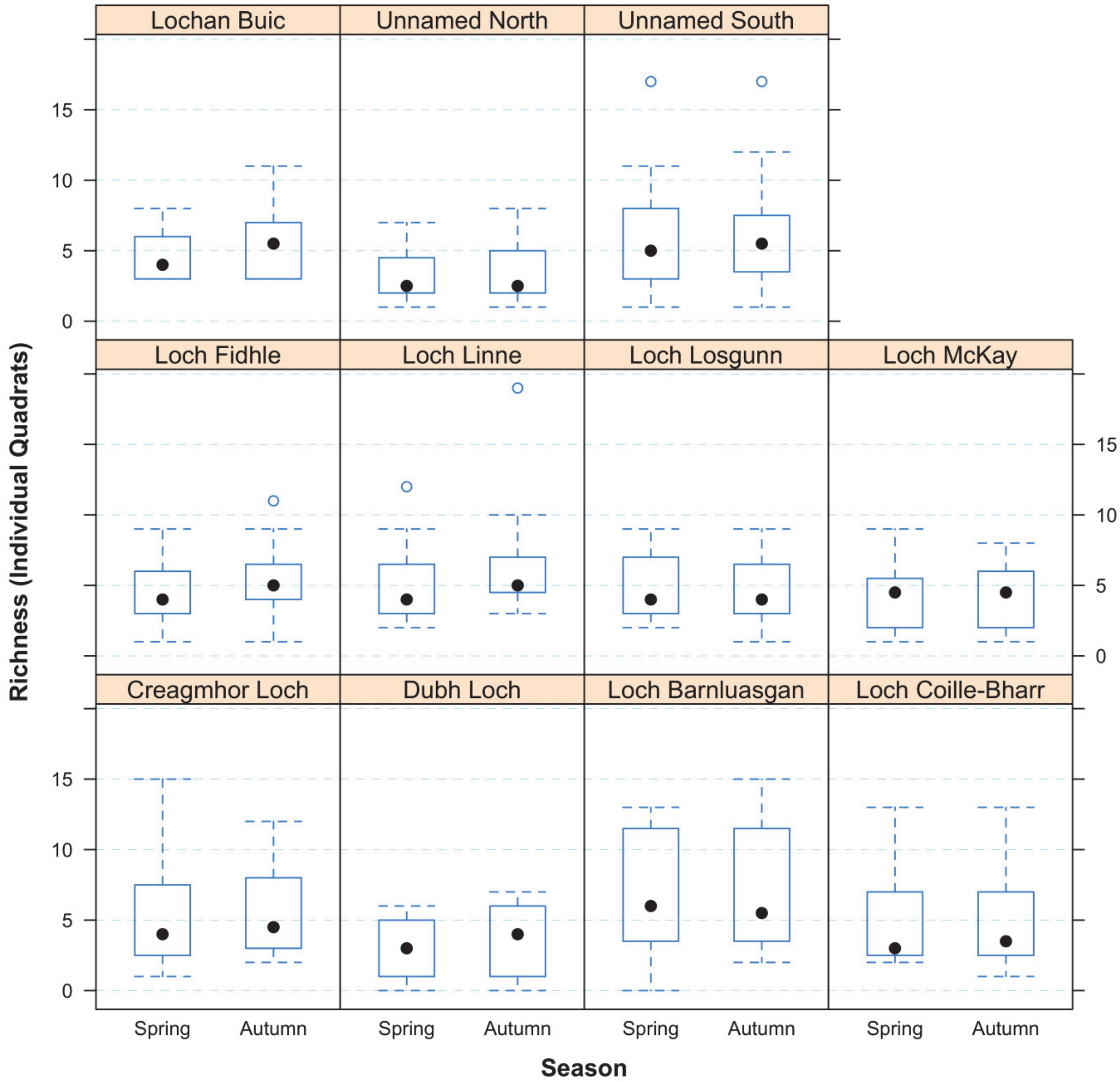

Figure 7. Quadrat data collected during the 2011 macrophyte surveys, summarised as mean richness per quadrat, for each of the lochs. Data are shown for the spring (May) and autumn (September) surveys.

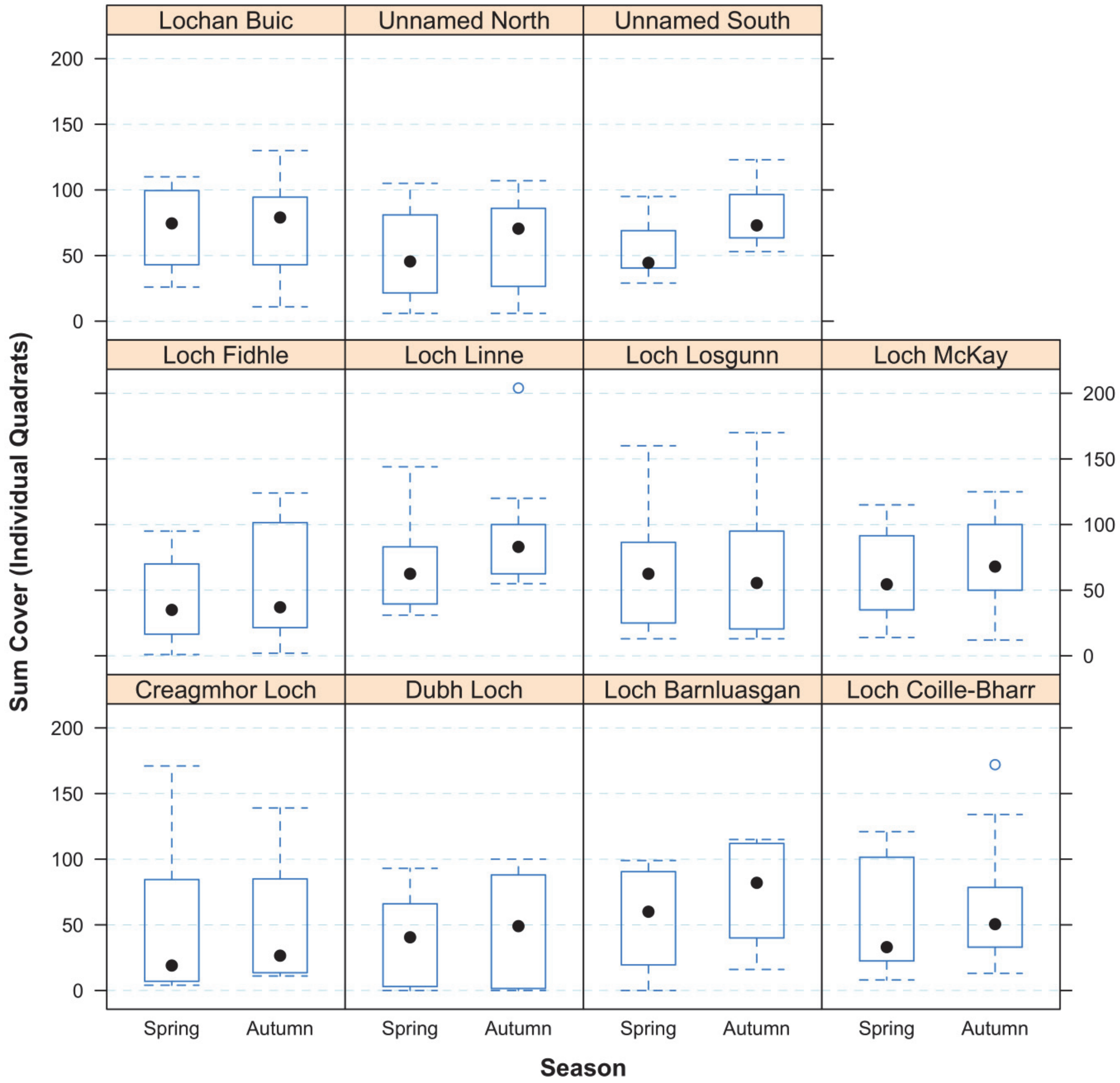

Figure 8. Quadrat data collected during the 2011 macrophyte surveys, summarised as mean summed cover per quadrat, for each of the lochs. Data are shown for the spring (May) and autumn (September) surveys.

5.3 Analysis of beaver effects

5.3.1 Species richness

The application of mixed effects modelling techniques allowed testing of the proportion of variability in richness that could be attributed to changes resulting from beaver activity (as defined by the presence of a site in a beaver territory, or the duration of occupancy of any lodge). Parameter estimates and their significance are summarised in Table 5 (page 20).

Changes in richness in individual lochs over time relative to the year of baseline data collection for that loch are shown in Figure 9.

The model for richness indicates that neither beaver 'territory' (p=0.59) nor beaver 'occupancy' (lowest p = 0.67) differ significantly from the reference level for these terms (loch outwith beaver territory, or zero years of occupancy). Over the duration of data collection to date, there is therefore no evidence that the presence of beavers *per se* or the duration of lodge occupancy has had a significant effect on the species richness per quadrat. The 'year' term in these models is weakly significant (p=0.052), with the data collected in autumn 2011 more species-rich than the baseline year (Figure 10). The most likely explanation for this is a sampling artefact caused by repeat sampling by the same surveyors. This may have been exacerbated in 2011 by carrying out surveys twice in the same year (as discussed in 5.1). It is likely that this effect is most acute in Quadrat 1 where richness is generally highest and chance of under-detection is increased due to the structural complexity of the vegetation. Re-running this model, excluding the data from Quadrat 1 on all transects, shows that there is still a positive trend in richness with time (Figure 11), but the year term is then no longer significant (p = 0.104). There is some evidence from Figures 10 and 11 that the trend for increased richness with time may be slightly accentuated at higher levels of beaver occupancy. This trend will repay further investigation with the increased volume of data that will be available by the close of the trial, but it may point to increased recruitment of new species where higher levels of beaver activity have led to changes in the dominant vegetation, or to a reduction of overhanging tree cover.

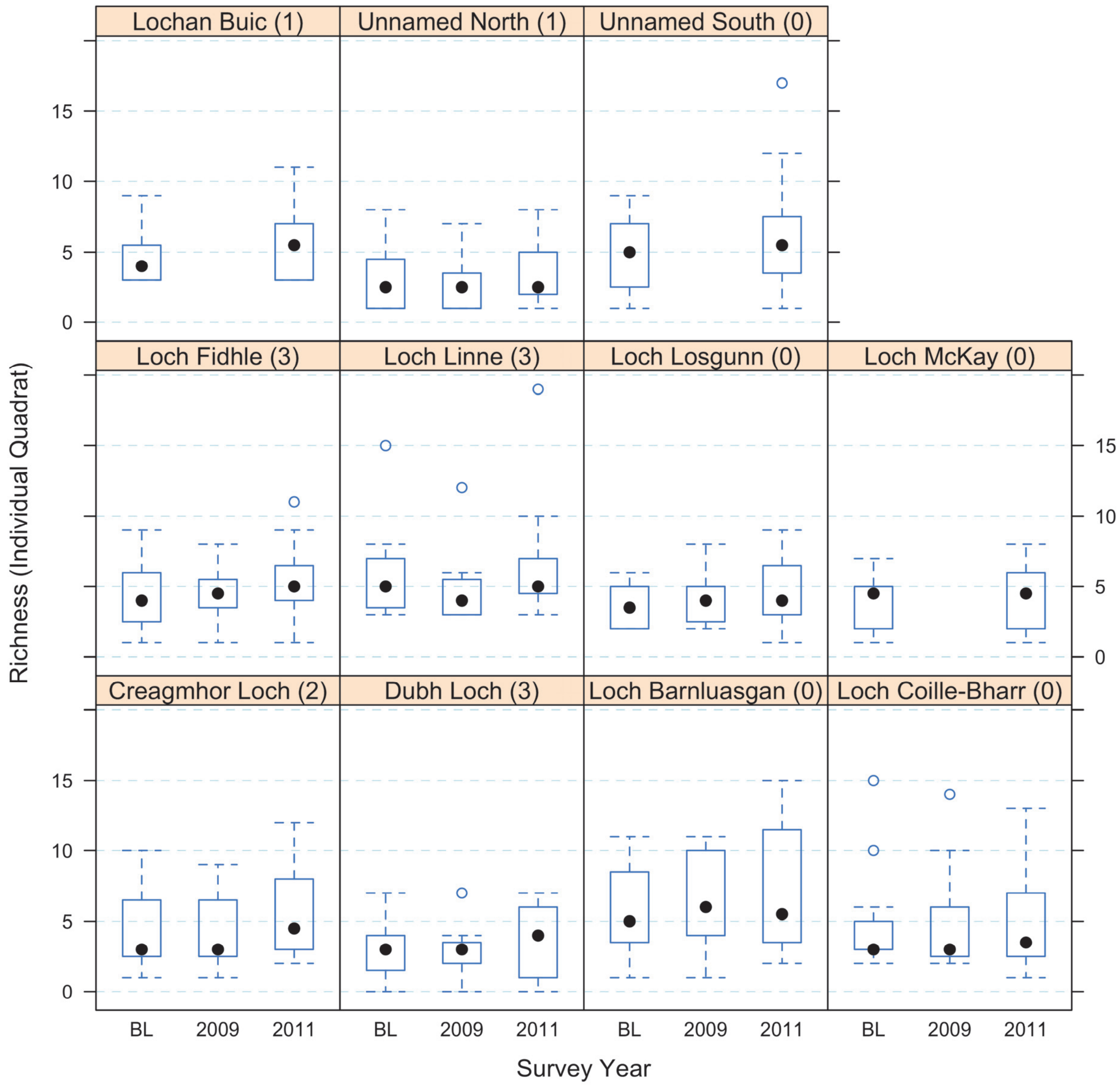

Figure 9. Comparison of mean quadrat species richness presented across years for individual survey lochs

Note: only autumn data are presented to allow comparison with baseline data. BL- baseline data collected in 2008 (eight primary lochs) and 2009 (three additional primary lochs). For each individual bar n =12. The six panels on the left of the figure refer to those lochs containing lodges in 2011.

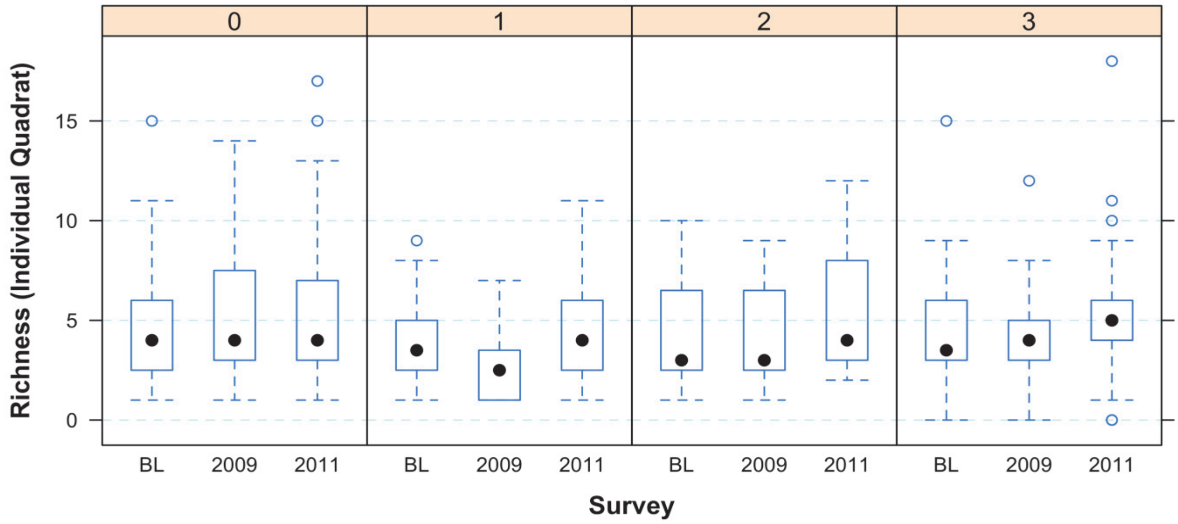

Figure 10. Comparison of mean quadrat species richness presented across years in lochs that differ by their number of growing seasons of beaver occupancy up to 2011 (indicated in upper label, 0-3)

Note: only autumn data are presented to allow comparison with baseline data. BL - baseline data only from those lochs with the indicated level of occupancy in 2011 (see Table 3).

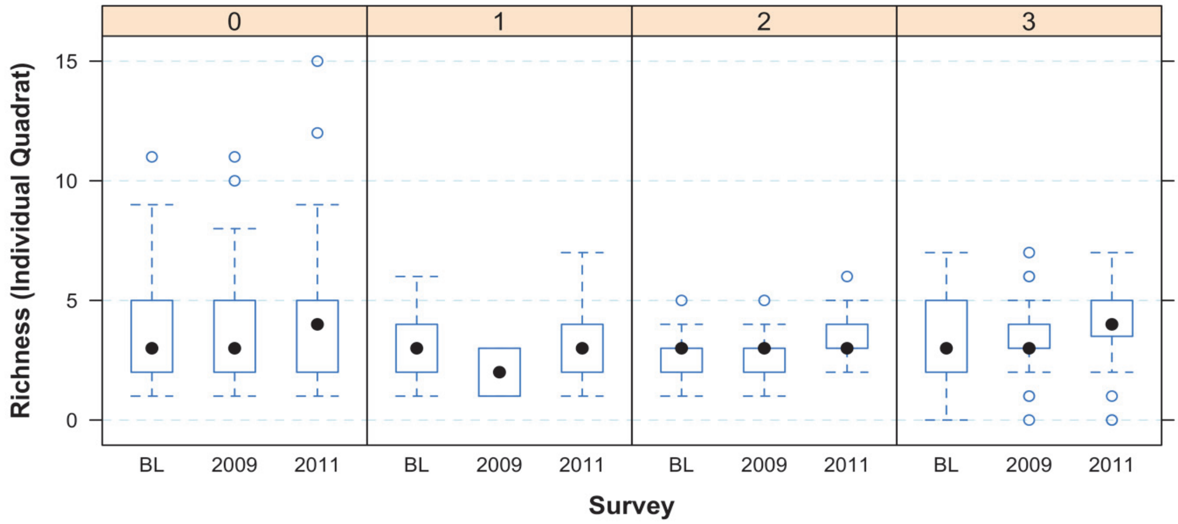

Figure 11. Comparison of mean quadrat species richness presented across years in lochs that differ by their number of growing seasons of beaver occupancy up to 2011 (indicated in upper label, 0-3), based only on data from quadrats 2-4 (i.e. excluding the most landward quadrat from each transect)

Note: only autumn data are presented to allow comparison with baseline data. BL- baseline data only from those lochs with the indicated level of occupancy in 2011 (see Table 4).

5.3.2 *Vegetation cover*

The application of mixed effects modelling techniques allowed testing of the proportion of variability in total cover that could be attributed to changes resulting from beaver activity (as defined by the presence of a site in a beaver territory or the duration of occupancy of any lodge). Parameter estimates and their significance are summarised in Table 5.

Changes in total cover in individual lochs over time relative to the year of baseline data collection for that loch are shown in Figure 12. Comparing September data, it is clear that a reduction in cover was recorded for Dubh Loch and Loch Fidhle, though trends were not clear for the other lochs – either with or without beavers. On Dubh Loch, the vegetation cover at individual quadrats has reduced by an average of 42% since the baseline year, with the outer quadrats dominated by floating-leaved species experiencing the greatest reduction. In Loch Fidhle, the average reduction in cover over the same period was 22% and this was mostly associated with high losses of *C. mariscus* from several transects.

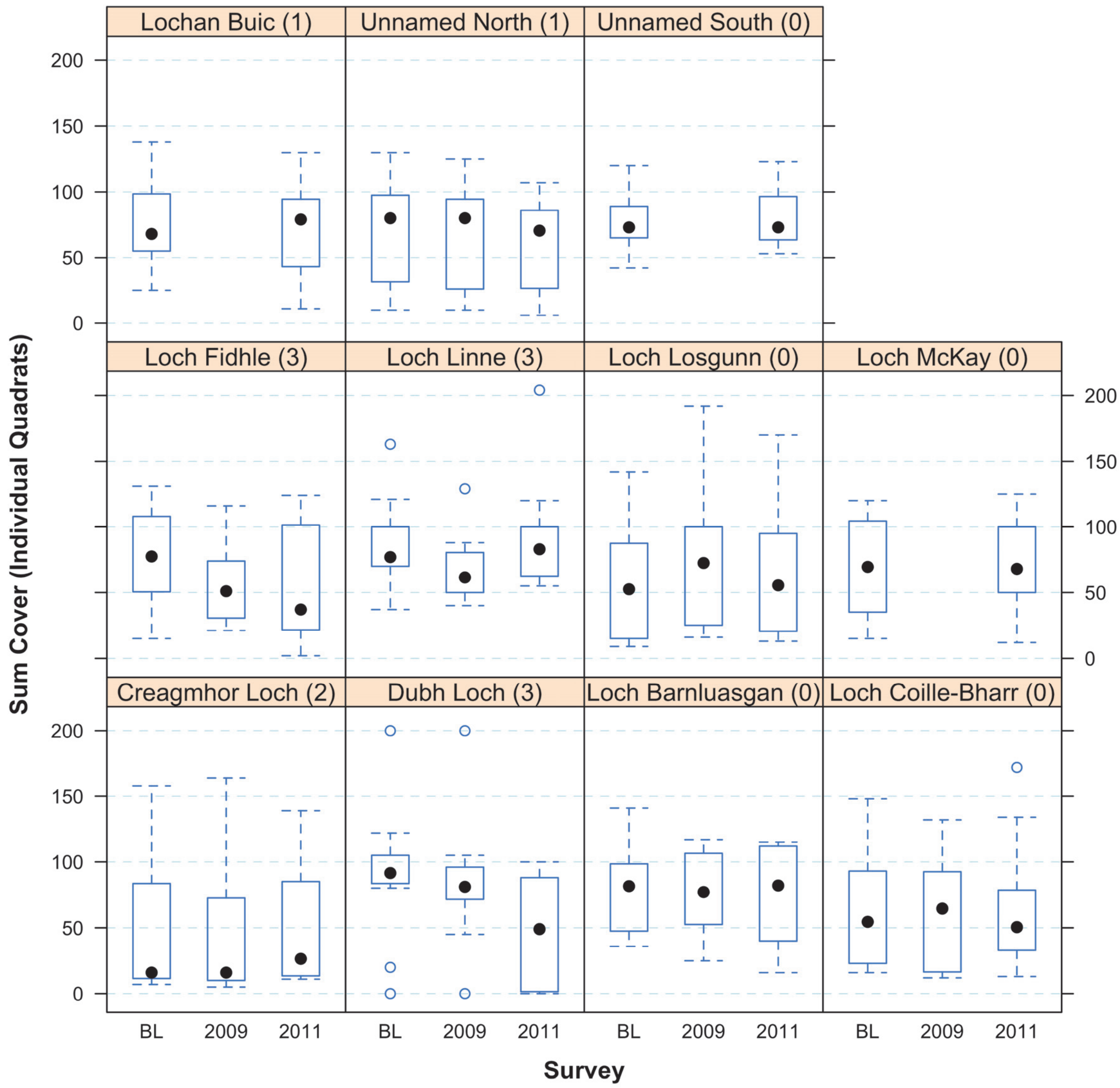

Figure 12. Comparison of mean sum cover (total of the species cover values) per quadrat across survey years for each loch

Note: only autumn data are presented to allow comparison with baseline data. BL- baseline data collected in 2008 (eight primary lochs) and 2009 (three additional primary lochs). For each individual bar n = 12. The six panels on the left of the figure refer to those lochs containing lodges in 2011, with the number of seasons of occupancy in September 2011 shown in brackets.

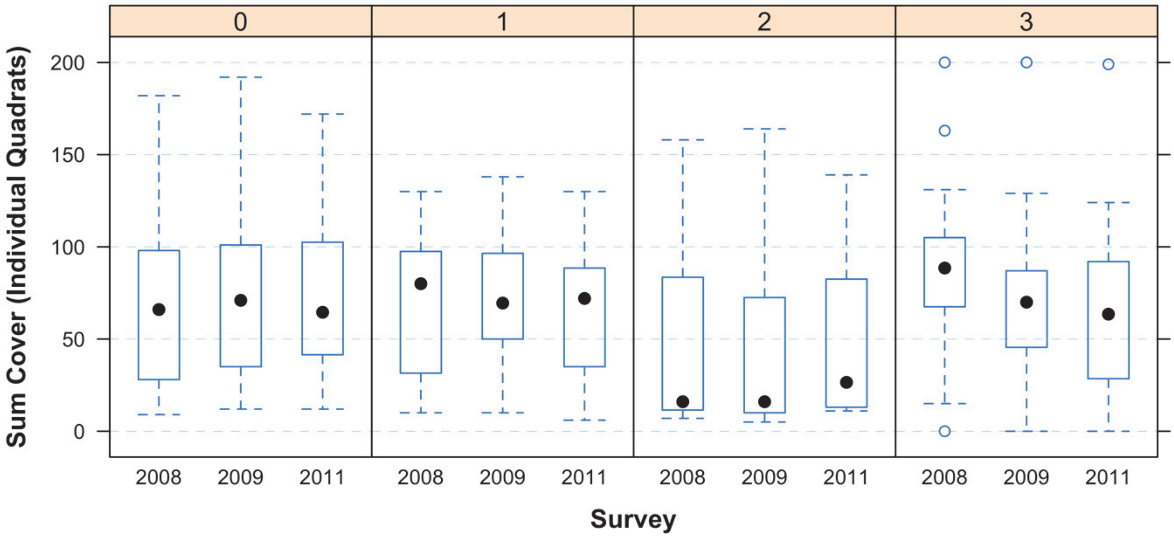

Figure 13. Comparison of mean quadrat summed cover across years (September only), in lochs that differ in their number of growing seasons of beaver occupancy in 2011 (indicated in upper label, 0-3)

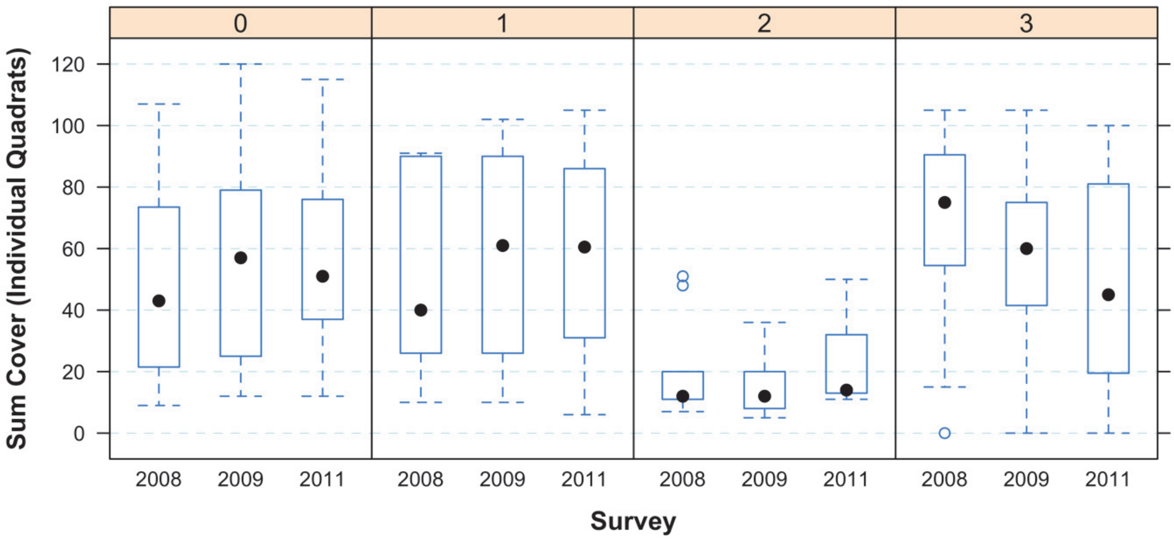

Figure 14. Comparison of mean quadrat summed cover presented across years (September only), in lochs that differ in their number of growing seasons of beaver occupancy in 2011 (indicated in upper label, 0-3), based only on data from Quadrats 2-4 (i.e. excluding the most landward quadrat from each transect)

Table 5. Parameter estimates and their associated significance in linear mixed effects models of plant species richness (upper panel) and summed cover (lower panel) in re-surveyed quadrats

Variable	Richness (all)					Richness (quadrats 2-4 only)				
	Estimate	*Std Error*	*z value*	*P*		*Estimate*	*Std Error*	*z value*	*P*	
(Intercept)	1.3469	0.0804	16.756	<0.00001	***	1.1235	0.0932	12.055	<0.00001	***
territory (YES)	-0.0583	0.1085	-0.537	0.5913		-0.1015	0.1370	-0.741	0.458	
factor(occupancy)1	-0.0432	0.1015	-0.426	0.6703		-0.0107	0.1317	-0.081	0.936	
factor(occupancy)2	0.0562	0.1837	0.306	0.7597		0.0768	0.2485	0.309	0.757	
factor(occupancy)3	-0.0005	0.1367	-0.004	0.9972		0.0238	0.1749	0.136	0.892	
factor(year)2009	0.0427	0.0915	0.467	0.6408		0.0977	0.1146	0.853	0.394	
factor(year)2011	0.1968	0.1012	1.944	0.0519	(*)	0.2061	0.1269	1.624	0.104	

Variable	Sum cover (all)					Sum cover (quadrats 2-4 only)				
	Estimate	*Std Error*	*t value*	*P*		*Estimate*	*Std Error*	*t value*	*P*	
(Intercept)	16.6931	0.8036	20.772	<0.00001	***	14.1025	1.0990	2.829	<0.00001	***
territory (YES)	-0.3414	1.1917	-0.287	0.7747		-0.3133	1.2130	0.258	0.797	
factor(occupancy)1	-1.4319	1.0854	-1.319	0.1880		-1.4518	1.0720	1.353	0.177	
factor(occupancy)2	-0.9606	2.0965	-0.458	0.6471		-0.0775	2.0710	0.037	0.970	
factor(occupancy)3	-3.3965	1.5231	-2.230	0.0264	*	-4.1508	1.5260	2.719	0.007	**
factor(year)2009	0.0918	1.0201	0.090	0.9284		0.2963	1.0320	0.287	0.774	
factor(year)2011	0.2249	1.1421	0.197	0.8440		0.5223	1.1780	0.443	0.658	

Significance: *** p <0.001; ** p <0.01; * p<0.05; (*) p<0.1

The model for sum cover (Table 5) indicates that the effect of beaver 'territory' (*p*=0.77) does not differ significantly from the reference level (loch outwith beaver territory), but at the longest duration of lodge occupancy (three growing seasons) there are significant (negative) effects (*p*=0.026) on cover, relative to the pattern of change in cover in lochs where there was no lodge (Figure 13). This is consistent with the effects observable at a site-specific level for the Dubh Loch and Loch Fidhle (but not Loch Linne), as depicted in Figure 12. No significant effects were observed at shorter durations of occupancy and there is no evidence of a 'year' effect that might be associated with a sampling artefact or major inter-annual differences in growing conditions. The lack of a significant territory effect in these models is unsurprising. It is not the presence of beavers *per se* that is significant – it is the increased activity associated with a lodge and the greater duration of occupancy of that lodge that matter. It should be noted that those lochs with two seasons of occupancy in 2011 have a lower absolute number of species than lochs with 0, 1 or 3 seasons of occupancy. The 2-season occupancy loch group in 2011 comprises only two lochs, Lochan Buic and Creagmhor Loch, of which the latter is comparatively unproductive. The beaver occupancy term reflects the cover within those lochs belonging to a particular occupancy category in a given year, relative to the cover in all lochs in all years, when occupancy was zero. In Figures 13 and 14, there is no clear trend in cover with time within the same group of lochs, except at the highest level of occupancy. The lochs in occupancy group 2 have low cover in 2011, but the same lochs also had similarly low cover prior to any beaver presence.

A selective analysis of the data, in which Quadrat 1 is excluded (Figure 14), confirms that the strongest negative effects on cover are associated with aquatic rather than riparian quadrats (see more strongly negative parameter estimate for occupancy 3 in Table 5 and lower *p*-value (*p*=0.007)). This effect is probably the result of decreases in floating-leaved and deeper water emergent species at sites in Dubh Loch and Loch Fidhle.

5.4 General patterns of herbivory

Table 6 provides a semi-quantitative indication of the extent of impact on different macrophyte species across the range of beaver-occupied lochs associated with direct grazing, foraging or water level rise. Essentially, five species are widely utilised, *Nymphaea alba*, *Schoenoplectus lacustris*, *Cladium mariscus*, *Equisetum fluviatile* and *Carex rostrata*. Of these, the latter is widely consumed, but only in small quantities. Although *N. alba* is well utilised in Lochan Buic and Un-named loch (North), the exploitation currently amounts to a very small proportion of the standing stock of floating leaves (<5%). It is only in the two longest-established territories of Dubh-Coillie-Bharr and Linne-Fidhle that water level rise and/or herbivory have contributed to an alteration in macrophyte communities that is readily detectable from fixed point photography and transect survey data. Whether the two more recently established territories (Creagmhor – Un-named (North) and Buic - Un-named (South)) in time exhibit similar changes will be confirmed by annual monitoring throughout the remaining period of the trial.

Table 6. Summary of vegetation data indicating the patterns of herbivory across the eight lochs lying within existing beaver territories based on observations from 2009-2011

		Dubh	Coille-Bharr	Linne	Fidhle	Creagmhor	un'd North	Buic	un'd South
Nymphaea alba	**White water lily**	● (large)	• (small)	• (small)	• (small)	• (small)	● (medium)	● (medium)	• (small)
Cladium mariscus	**Saw Sedge**	• (small)		• (small)	● (large)	• (small)		○	
Schoenoplectus lacustris	**Common Club-rush**		• (small)	● (large)	● (large)	• (small)			○
Equisetum fluviatile	**Water Horsetail**	● (large)	● (medium)	○	○	• (small)	• (small)	● (medium)	• (small)
Carex rostrata	Bottle Sedge	● (medium)	• (small)	• (small)	• (small)	• (small)	• (small)	• (small)	• (small)
Menyanthes trifoliata	Bogbean	• (small)	• (small)						
Phragmites australis	Common Reed		• (small)			○	○	○	
Sparganium erectum	Branched burr reed				• (small)				
Potamogeton natans	Broad-leaved Pondweed	● (large)	○	○	○	○	○	○	○
Carex paniculata	Tussock Sedge	• (small)							

Size of circle is approximately proportional to magnitude of change from large circles (moderate change), medium circles (minor change), small circles (evidence of feeding but effect negligible). Unfilled circles denote the presence of a species in a loch but no evidence of feeding.

5.5 Dubh Loch geospatial survey

At Dubh Loch, changes associated with the increased water levels include a large increase in water surface area. Geospatial data collected around Dubh Loch during May 2011 have been used to construct the outline of the new perimeter and calculate the new surface area. The surface area increased by approximately 337% from 0.38 ha (Ordnance Survey 1:10 000 scale data) to an area (measured in May 2011) of 1.66 ha, inundating 1.28 ha of willow and birch woodland and scrub to a depth of around 1 m (±0.5). At the same time, the Shoreline Development Index increased from its baseline value of 1.34 to a value of 1.7, a 27% increase, reflecting the increased extent of edge habitat relative to the overall increase in area. The present surface area of Dubh Loch is shown in Figure 15.

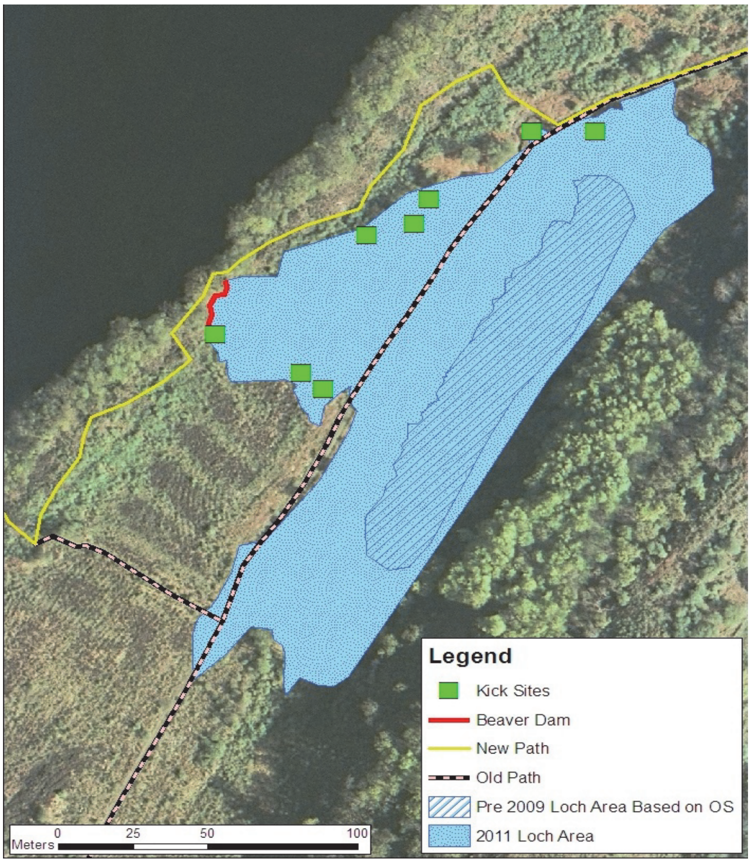

Figure 15. The outline of Dubh Loch in May 2011, relative to the outline according to Ordnance Survey data (reproduced from Ordnance Survey map data by permission of Ordnance Survey, © Crown copyright and database right 2014. Ordnance Survey 100017908) and 2005 aerial photography. Green squares indicate invertebrate sampling sites.

6. DISCUSSION

6.1 General effects on lake macrophytes

The observed patterns of grazing by beavers on individual species are largely consistent with those reported from elsewhere in Europe, although there are no published accounts referring to herbivory of *Cladium mariscus*. One paper refers to herbivory by beaver (*C. canadensis*) of the closely-related *Cladium jamaicense* in Louisiana (Chabreck, 1958). Of the species on which beavers have been observed feeding at Knapdale, all, with the exception of *C. mariscus,* are common and widely distributed in lochs both in Knapdale and Scotland in general. *Cladium mariscus* is an uncommon species in Great Britain, occurring in about 8% of hectads, although it is by no means rare and is frequently abundant where it occurs (Preston and Croft, 1997). In England, *C. mariscus* is commonest in calcareous fens in East Anglia, but in Scotland, it occupies a range of oligotrophic to mesotrophic peaty wetlands, mostly along the west coast. The area of the north Kintyre peninsula and Islay supports one of the larger concentrations of *C. mariscus* in Great Britain. Outside Britain, *C. mariscus* is common in Ireland (26% of hectads) and has a near-global distribution, tending to be most abundant in subtropical regions. There is no particular reason to suspect that beavers could adversely affect the status of *C. mariscus* in the UK, although this species is evidently highly palatable and beavers thus have the potential to reduce its abundance at sites where it occurs.

In terms of the specific elements of the *Littorelletea uniflorae* and/or of the *Isoeto-Nanojuncetea* plant associations (principally *Littorella uniflora*, *Lobelia dortmanna*, *Isoetes lacustris*, *Myriophyllum alterniflorum* and *Juncus bulbosus*) that form part of the basis of the SAC designation for the Knapdale lochs, there is no evidence of adverse effects associated with beavers. Records of beavers elsewhere utilising any of these species are very unusual, although Histøl (1989) reports Norwegian beaver feeding on both *L. dortmanna* and *I. lacustris*. Very limited collateral damage to some beds of *L. uniflora* and *L. dortmanna* was observed in Loch Linne-Fidhle where beaver had been uprooting and feeding on *Schoenoplectus lacustris* or *N. alba*. Such effects are probably inevitable and probably no greater than the disturbance associated with annual monitoring of macrophytes by human surveyors. Theoretically, since larger floating-leaved and emergent species, such as *N. alba* and *S. lacustris*, create quiescent habitat in lakes that supports isoetid plants, there might be a decline in such species if there were a large scale decline in their supporting habitat, but no indication of such an effect in any of the lochs inhabited by beavers has been observed during the present project.

6.2 Comparison of effects of beaver activity in different territories

In this discussion, the water bodies in which beaver activity was recorded are considered according to the four territories now established.

6.2.1 Dubh Loch and Loch Coille Bharr

Dubh Loch has experienced the most significant hydromorphological changes and is the location where water level changes have resulted in the most marked response in the macrophyte community (Figure 16). This will be tracked over the duration of the trial, after which it will be possible to determine whether macrophyte colonisation of newly inundated areas follows the pattern of colonisation observed elsewhere in beaver ponds (Ray *et al*., 2001). In 2011, these newly formed areas of aquatic habitat were still un-vegetated by aquatic plants, as they largely comprise flooded birch woodland understorey shaded by standing trees. It is therefore likely that Dubh Loch is in a transitional stage.

The responses of macrophyte communities are probably primarily attributable to the increased water level rather than direct herbivory by beavers present on the loch. The main phase of dam construction by beavers on Dubh Loch was during late autumn 2009. It led to a rapid water level rise that affected the whole loch over the growing season of 2010. Prior to this, beaver-related effects were confined to direct herbivory, or associated trampling of macrophytes. A comparison of survey data from September 2008 (prior to beaver introduction) and September 2009, about a month after beavers colonised Dubh Loch from Coillie Bharr, revealed only limited reductions in the cover of *Mentha aquatica*, *Equisetum fluviatile* and *Carex rostrata*. Since no sampling was carried out in 2010, the scale of direct herbivory in this period is unknown. There is, however, photographic evidence of beavers feeding on rhizomes of *N. alba* at Dubh Loch in 2010 and therefore, given the small size of the site relative to the number of beavers resident, herbivory might also be exerting an important control on vegetation.

The macrophyte species most significantly affected include *N. alba* (93% decline in cover) and *P. natans* (95% decline in cover). The decline of these species is readily evident from Figure 16. Since *P. natans* appears from our own observations (both at Knapdale and in Perthshire) and the literature to be unpalatable to beavers the decline in cover observed at Dubh Loch is almost certainly a response to water level change rather than herbivory. *Cladium mariscus* showed a 67% decline in cover, but there was little evidence of direct feeding on this species, compared to Loch Fidhle. Despite a decline in cover, the number of quadrats in which *C. mariscus* was recorded increased from three to five, perhaps suggesting an ability to colonise new areas quite rapidly as conditions change. *Lemna minor* increased from 1% cover in just two quadrats, to an average of 5% cover across all nine of the original quadrats. A summary for all species is provided in Table 7. At an overall site level, there is the impression that *Potentilla palustris* has increased markedly in cover, although this is not apparent from the transect surveys. Similarly, *E. fluviatile* has contracted significantly at the site level, but not in the transects, having been lost almost entirely from the 1-2 m wide fringe that this species originally occupied along the eastern shore. These trends should be confirmable by polygon mapping in September 2013.

Table 7. Average percentage cover for each of the species present in transects in Dubh Loch

Species	**Average cover (number of quadrats)**			
	Sept 2008	**Sept 2009**	**May 2011**	**Sept 2011**
Carex nigra	10(1)	10(1)	-	-
Carex paniculata	46(3)	46(3)	33(3)	43(3)
Carex rostrata	47(2)	40(2)	30(2)	22(4)
Cladium mariscus	46(3)	45(3)	18(4)	15(5)
Eleocharis palustris	5(1)	10(1)	-	5(1)
Equisetum fluviatile	13(7)	7(7)	11(8)	10(7)
Filamentous green algae	-	-	-	10(2)
Hydrocotyle vulgaris	3(2)	5(1)	-	-
Lemna minor	1(2)	1(2)	5(8)	5(9)
Lycopus europeaus	-	-	1(1)	2(1)
Mentha aquatica	7(2)	1(1)	-	2(1)
Menyanthes trifoliata	40(1)	30(1)	30(1)	50(1)
Nymphaea alba	41(5)	41(5)	3(2)	3(2)
Polytrichum commune	20(1)	-	-	-
Potamogeton natans	28(3)	27(4)	24(3)	1(2)
Potentilla palustris	-	-	2(1)	1(1)
Salix cinerea	100(1)	100(1)	20(1)	30(1)
Sphagnum auriculatum	65(2)	65(2)	10(1)	17(2)

Values are given as mean cover across all quadrats in which the species was recorded in each year. Number of records (n) involved in calculation of each value is given in brackets. (Additional quadrats surveyed in 2011 only are not included in the analysis).

Figure 16. Fixed point photography of the southern end of Dubh Loch showing the vegetation communities present in September 2008 (left) and September 2011 (right)

Figure 17. Benthic peat that had surfaced in Dubh Loch, at various stages of colonisation (mainly by Carex rostrata*), in September 2011*

One of the major changes in Dubh Loch, besides the increased water level and loss of vegetation, has been the appearance over the last 18 months of large floating platforms of benthic peat bound together by rhizomes of *N. alba* and *E. fluviatile* (Figure 17). In some cases, these have almost completely replaced the beds of *N. alba*, *E. fluviatile* and *P. natans* that originally occurred in these locations. These peat platforms appear to be caused by a build-up of gases in rhizomes and surrounding sediment caused by anaerobic respiration, as below-ground plant parts are no longer ventilated via contact with the atmosphere. Coupled with the greatly reduced weight of the overlying plants and reduced solubility of gases during the summer, the buoyancy of the peat causes it to rise to the surface. There is a significant sediment propagule bank associated with such material that results in rapid colonisation, mainly by *Carex* or *Juncus* seedlings, within a few months of emergence. The establishment of floating sedge beds on a large scale would dramatically alter the appearance of Dubh Loch in the future and could accelerate the large-scale transition to a floating mire. The phenomenon of floating peat platforms is not unique to Dubh Loch and was observable in several other Knapdale Lochs (Losgunn and Un-named (North)), prior to beaver introduction, albeit then on a much smaller scale. It is speculated that in these other lochs, the formation of floating peat mats is linked to management of water levels for fisheries purposes, or changes in runoff and sediment loading patterns associated with forestry that cause small-scale changes in water level or sedimentation in marginal areas.

Whilst buoyancy of benthic peat has readily observable effects, it should be noted that this same property also applies to much of the fringing vegetation and wetter woodland at Dubh Loch. In the middle of the armoured track which formerly ran alongside this Loch, but which is now mostly submerged, water levels have reached about 1.2 m at their deepest. Technically, this should mean that much of the *C. mariscus* and *Carex paniculata* mire that surrounds Dubh Loch should by now also be fully submerged, but evidently this is not the case. The loose anchorage of plants at the edge of the water body has enabled them to accommodate the increased water levels. This effect also extends to trees, which in places have risen by 0.5 m. This is readily observable in the exposure of large amounts of adventitious roots, which willows and other trees develop on submergence (Figure 18). Water levels have not fallen to reveal these roots (the normal scenario when such structures are visible) – the trees have risen. The buoyancy of benthic peat would largely invalidate attempts at bathymetric mapping at this site, although both the original and newly located stage boards appear to be sited in well-anchored substrate, where no change in bed position has occurred. Consequently stage board readings at Dubh Loch should remain reliable.

Figure 18. Emergence of willows at Dubh Loch revealed by exposure of adventitious roots formed during periods of submergence, in September 2011

Beaver activity has been focused on Dubh Loch, with very little recent activity and no observable changes to macrophyte communities being recorded on Loch Coille Bharr. The only activity detectable in Coille Bharr was in the well-vegetated sheltered bay in the south-western corner, where there was very sparing grazing of a range of species, and more conspicuous grazing of *E. fluviatile*. The latter was mainly in the vicinity of the submerged crannog, which presumably offers a safe and easy position from which beavers can forage. No damage to this structure was evident. It is likely that effects on macrophytes in Loch Coille Bharr will increase in future years as animals disperse there from Dubh Loch or are forced to use Coille Bharr as a source of aquatic vegetation following its decline in Dubh Loch.

6.2.2 Linne-Fidhle system

Regular removal of beaver dams constructed on the outflow ensured that beaver activity did not result in any hydromorphological change on the Loch Linne-Fidhle system (although note that, as a result of an amendment to the overall Scottish Beaver Trial licence, any dams will be left in place from November 2011, subject to conditions set by Scottish Government). No general reduction in mean vegetation cover was recorded for quadrats in Linne, however, changes were observed on specific transects and at other locations on the Loch. There was no evidence for a persistence of effects associated with the temporary dam-induced water level rise reported in Willby, Casas-Mulet and Perfect (2011). This suggests that such effects are readily reversible over the short term.

Figure 19 shows the change in *Schoenoplectus lacustris* densities at the southern end of Loch Linne by the boat jetty. Similar changes can be seen in the outflow bay and beavers are now increasingly exploiting stands of *S. lacustris* at the northern end of Loch Linne and within Loch Fidhle, which had not previously been utilised. There are no published accounts of beavers specifically grazing *S. lacustris* on the scale observed in Linne-Fidhle. However, Valta-Hulkkonen *et al*. (2004) described marked changes in the extent of this species in a Finnish lake associated with grazing and nest building by muskrats (*Ondatra zibethica*), whilst extensive feeding by beavers on *S. lacustris* has been observed in the Dalälven system in central Sweden (Willby and Law personal observation, 2012).

Figure 19. Fixed point photography from the southern end of Loch Linne showing the change in density and extent of Schoenoplectus lacustris *in September 2008 and September 2011*

Notable changes were observed in Loch Fidhle and recorded during the transect surveys. Most evident was a marked reduction in the extent of *C. mariscus*, as shown in Figure 20 and Figure 21. At a loch level, the overall reduction in this species was visually estimated to be 80%. The precise extent of any change will be determined by polygon re-mapping in September 2013. There was evidence for colonisation by *N. alba* of areas formerly occupied by *C. mariscus*. Isoetid species are likely to show much slower spread into these areas and it is even possible that re-establishment of *C. mariscus* will occur before isoetids could establish successfully.

Figure 20. Transect 3 on Loch Fidhle, in September 2009 (left) and September 2011 (centre). A comparison shows the loss of a band of Cladium mariscus *between surveys. In September 2011, washed up litter from* C. mariscus *partially obscured Quadrat 1 (right).*

Figure 21. Quadrat position 3 on transect 3 in Loch Fidhle. A comparison shows the marked reduction in Cladium mariscus *at this location, between the surveys of September 2009 (left) and September 2011 (right).*

6.2.3 Loch Creagmhor and Un-named Loch (North)

Beaver activity on Creagmhor has been primarily restricted to felling of riparian trees and animals have had an irregular presence on this loch since the outset of the trial. No reduction in cover was observed in any of the transects, despite the presence of both *S. lacustris* and *C. mariscus*, which are strongly favoured by the Linne-Fidhle family. Since mid-2010, there has been increased felling activity on the watershed between Creagmhor and Un-named Loch (North). In May 2011, there was no evidence that beavers were feeding directly on macrophytes in Un-named Loch (North), but during a visit to this site in July 2011, clear evidence of grazing in open water on *N. alba* beds was noted and a new lodge was observed to be under construction. The area of feeding had increased between

July and early September and was visually estimated to represent a loss of *N. alba* surface leaves of up to 5% (Figure 22). Such leaves are easily detected and quantified since the petiole becomes emergent upon removal of the weight of the floating blade during grazing. Through the measurement of petiole diameter of grazed and ungrazed leaves, it has proved possible to reconstruct the size of grazed leaves. This indicates that beavers have fed selectively on larger leaves, mostly situated in shallow water (Law *et al*., 2014a). Feeding by beavers on organs of lilies is commonplace (Northcott, 1972), but this degree of selectivity has not been previously demonstrated. Nevertheless within the fixed quadrats there was little observable change in macrophyte populations on Un-named Loch (North) and no reduction in cover was recorded. The construction of a dam on the outflow of Un-named Loch (North) and subsequent changes to the water depth (+0.3 m) observed in November 2011 had not occurred at the time of the macrophyte survey.

Figure 22. Effects of grazing of Nymphaea alba *leaves by beavers in Loch Un-named (North), late July 2011*

Figure 23. Beaver-cut woody material on the loch bed, observed around the margins of Creagmhor Loch

Although rarely found in the transects, beaver-cut woody debris was observed in a number of lochs. At some places, this was at locations with a carpet of aquatic macrophytes (Figure 23). It is expected that through the patchy occurrence of shading, nutrient input and physical shelter, this may generate a more heterogeneous environment for macrophyte growth. Its presence may also partially compensate for the loss of physical complexity associated with the submerged stems of species such as *S. lacustris*. Currently, macrophyte beds form relatively homogeneous bands around the loch, with water depth and associated light penetration as the forces driving habitat suitability. However, traction of woody debris during storm events could potentially also result in increased damage to beds of macrophytes in shallow water areas.

6.2.4 Lochan Buic and Un-named Loch (South)

No notable changes were recorded on Lochan Buic. There was widespread feeding on *N. alba*, with animals grazing leaves *in situ*, mainly in shallow water, or uprooting entire plants to feed on the rhizome, but in all cases this activity took place outwith sampled transects. Grazing of surface leaves typically occurred in patches of 5-20 m^2 in extent. The total loss of area of surface leaves of *N. alba* in Lochan Buic was visually estimated to be <5%. Contraction of the overall area of *N. alba* associated with complete uprooting of plants is probably trivial, but is difficult to estimate visually unless remains of such plants are found. Overall changes in polygon areas will be quantified during the September 2013 sampling. Curiously, despite the presence of plants within 20 m of the lodge entrance, *C. mariscus* beds in Lochan Buic were almost completely ignored by beavers.

In Un-named Loch (South), very limited fresh grazing of several species, mainly *N. alba*, was observed in July 2011, but this had not increased in extent in September and may have been associated with exchange of animals between the Buic-Un-named Loch (South) and Creagmhor-Un-named Loch (North) territories.

6.3 Timing of effects

Sampling in May detected only very subtle effects of beaver activity on macrophyte populations in Knapdale (beyond those already established through dam building in previous seasons). This is inconsistent with observations of a semi-captive beaver population in Perthshire, Scotland, where it was observed that herbivory of bogbean *Menyanthes trifoliata* was at its most intense in May and was established even in April (Law *et al*., 2014b). Other studies (e.g. Milligan and Humphries, 2010) have indicated that beaver herbivory of aquatic vegetation can be especially intense in standing water environments during periods of ice cover that should render such effects visible early in the subsequent growing season following thaw. Observations in Perthshire were also made during 2011, so any discrepancy with Knapdale cannot be readily attributed to inter-annual differences in climate. Certainly, the winter of 2010-11 was unusually harsh, which may have delayed the onset of feeding and reproductive activity in Knapdale, but it may also be that beaver-related effects are dependent on the race, origin or previous experience of populations, or the productivity of the environment in which they are present. The generally oligotrophic nature of the Knapdale lochs is likely to delay the onset of macrophyte growth compared to naturally more productive sites in Perthshire, which may have attendant effects on the timing of beaver activity. Population density, constraint and the limited availability of woody material may also render the Perthshire population of limited comparability.

7. CONCLUSIONS AND RECOMMENDATIONS

7.1 Main findings

Through a combination of direct grazing and associated activity (trampling or tree felling and removal), alongside water level change in some cases, beavers are having clear and measurable effects on aquatic vegetation in some of the Knapdale lochs in which they are now resident. These effects are evident at a water body scale through fixed-point photography, and at a local scale, through resampling of fixed quadrats. Four main species, *Nymphaea alba*, *Schoenoplectus lacustris*, *Equisetum fluviatile* and *Cladium mariscus* have been exploited to a greater or lesser extent, with populations in some lochs (Dubh and Linne-Fidhle) being substantially reduced. However, effects were hardly perceptible in May and effects on individual species vary markedly between different lochs, making any transferable predictions difficult. There is no evidence of direct or indirect effects specifically on the *Littorelletea uniflorae* and/or of the *Isoeto-Nanojuncetea* plant associations that form part of the basis of the SAC designation. The following are the key findings at a site-specific level (see Figures 11 and 14, Table 5):

- Dubh Loch – no change in richness, but significant reduction in cover associated with herbivory and water level rise due to damming. Colonisation of inundated formerly terrestrial habitat in early stages.
- Coille-Bharr – no significant effects on richness or cover. Minor evidence of herbivory in south-western bay.
- Loch Linne – no significant effects on richness or cover in transects. Photographic evidence of decline in cover of *S. lacustris* (Figure 19).
- Loch Fidhle – no significant effects on richness but significant reduction in cover, mainly of *C. mariscus* (Figures 20 and 21). Extensive feeding on *S. lacustris* outwith transects which was not evident in 2009.
- Creagmhor Loch - no significant effects on richness or cover and very little evidence of recent activity except freshly cut saplings.
- Un-named Loch (North) - no significant effects on richness or cover but increased activity in months prior to sampling including modest losses of cover of floating leaves of *N. alba* due to herbivory (Figure 22). Recently constructed lodge now in place.
- Lochan Buic - no significant effects on richness or cover, but modest losses of cover of *N. alba* leaves in patches of active feeding. No utilisation of *C. mariscus* in contrast to Fidhle.
- Un-named Loch (South) – no significant effects on richness or cover. Minor evidence of herbivory.

In general, the effects of beavers have been to alter the macrophyte community and overall habitat structure through reductions in targeted species. In Dubh Loch, dam building by beavers has initiated large-scale change in plant community structure and created new aquatic habitat, which is now in the process of colonisation. Beaver effects at this site could be considered positive in the sense that they have increased the extent of aquatic habitat and re-established a naturally more dynamic state. In the other lochs, beaver-related effects are best described as neutral, since they only alter vegetation composition at a local scale. Currently, beavers could not be considered to have a detrimental impact on the specific aquatic vegetation feature for which the SAC has been designated.

7.2 Future work

7.2.1 Further data collection

7.2.1.1 May 2012

A field campaign is planned for May 2012, to include:

- resurvey of the shoreline of Dubh Loch.
- survey of the shoreline of Un-named Loch (North) to identify possible effects of increased water level on loch area and shoreline complexity.
- collection of repeat invertebrate samples from marginal habitat around Dubh Loch.
- an investigative survey of the secondary lochs.

7.2.1.2 September 2012

The subset of vegetation transects will be resurveyed on all lochs in September 2012 (instead of a May 2013 survey as originally planned). This will provide a near-continuous annual data set (with the exception of 2010), providing improved scope for the interpretation of the data series.

7.2.1.3 May 2013

The survey of vegetation transects planned for May 2013 will be dropped in favour of a September survey in 2012. Sampling in 2011 indicated that May is too early in the growing season in the Knapdale lochs for macrophytes to be sufficiently well-established that they are utilised by beavers.

7.2.1.4 September 2013

The final macrophyte survey is planned for autumn 2013, when all quadrats on all transects will be resurveyed. Additionally, macrophyte polygons will be remapped. These surveys follow the survey strategy, as set out at the start of the trial (Willby and Casas-Mulet, 2010). It is recommended that attention is focused on remapping stands of preferred food species, which are readily visible and can therefore be remapped with the highest precision.

7.2.2 Data analysis

As outlined in the survey plan, detailed analysis of the vegetation data, alongside hydrology and water chemistry data collected for the lochs, will be undertaken in 2013/2014, after surveys for the final field season planned for September 2013. These results will be reported, together with those of the September 2012 surveys. The analysis will consider the effects of beavers *per se* on aquatic vegetation, relative to effects that may be mediated indirectly through changes in hydrology and water chemistry. The analysis will include quadrat level data of the type reported here and will assess changes over the five years of the trial, in relation to plant species richness and cover, but also turnover in species composition. Through the use of species indicator scores (e.g. Ellenberg soil moisture values), possible environmental drivers for observed changes in species composition will be identified. The focus of these analyses will be to determine whether there is a directional effect of beavers on aquatic vegetation that follows a simple trajectory (e.g. declining cover), or if, over a five year period, there is evidence of vegetation adjustment, which is reflected in a change in this trajectory. It is likely that mixed effects models of a similar design to those employed here will be used to test the significance of beaver effects on the different indicators of vegetation response. Remapping of polygons will also allow coarser scale changes in plant abundance and composition to be quantified in each lake and will provide a check on the validity of scaling up from quadrat level analyses to the whole lake scale.

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