Long-term dynamics in Scottish saltmarsh plant communities

Rebecca B. Taubert and Kevin J. Murphy

IBAHCM, Graham Kerr Building, University of Glasgow, G12 8QQ, Scotland

E-mail: taubertr@gmail.com

ABSTRACT

In 2011, we conducted a resurvey of saltmarsh plant communities present at six sites along the mainland coasts of Scotland, previously surveyed in 2006. Three sites located on the Isle of Mull (Inner Hebrides) that were previously studied in 1957 were also resurveyed. The data, analyzed using TWINSPAN classification and CCA ordination procedures, suggested that geographical factors were more important than time in driving the observed differences in plant community composition. For example, only at Ardmore Point (Firth of Clyde), and Aberlady and Skinflats (Firth of Forth), were there distinct pioneer zones containing *Salicornia europaea* found in 2011**.** All sites supported recognizable mid-marsh and upper marsh communities. Overall, this study provides evidence for some degree of stability in Scottish saltmarsh plant communities, whether over a short timescale of 5 years or a longer period of 54 years.

INTRODUCTION

Saltmarshes develop on wave-protected shorelines in temperate regions worldwide as a result of interactions between vegetation and tidal action, relative sea level rise, climatic extremes, and sediment deposition rate (Harvey and Allan 1998; Beeftink 1977). The accumulation of sediment, vegetation fragments and various other suspended materials deposited by the tide creates a mudflat, which facilitates the settlement of specialist halophytic vegetation such as *Salicornia* and *Puccinellia* spp. (Fariña et al 2009; Steers 1977). This leads to an increase in the elevation and stabilization of substrate and ultimately, to the formation of creeks, channels and other conditions favourable for plant species less tolerant of frequent tidal submergence (Steers 1977). The change in elevation gives rise to distinct patterns of vegetation, known as zones, which typically occur in belts that run parallel to the shoreline (Adam 1990).

Most established saltmarshes can be divided into three distinct vegetation zones (species given as examples here relate to UK saltmarshes, though many of the saltmarsh plants have rather broad, cosmopolitan distributions in Europe): (1) a pioneer/low marsh zone defined by soft sediments, seaweeds and a few specialist halophytes such as *Salicornia europaea* and *Puccinellia maritima*, (2) an accretion/mid marsh zone that usually displays a large variety of environmental conditions and supports common saltmarsh species such as *Festuca rubra*, *Juncus gerardi* and *Agrostis stolonifera*, and (3) a mature/upper marsh zone, which occurs towards the upper limit of tidal influence and contains species less tolerant to salt and regular submergence, such as *Elymus pycnanthus.*

Saltmarshes offer a plethora of ecosystem services, including biodiversity preservation, water quality improvement, flood abatement, shoreline stabilization and carbon and nutrient sequestration. They also provide valuable habitat for migratory waterfowl and young commercially important species of fish (Zedler and Kercher 2005). Since vegetation plays a crucial role in the establishment and growth of saltmarshes, monitoring the changes in the composition of plant communities over time is one way to determine whether these systems are functioning properly. Such studies can then provide an indication of any significant variation occurring and whether these changes are due to anthropogenic pressures, such as abnormal rise in sea level, invasive species or development (Gedan et al 2009).

Previous long-term studies of saltmarsh plant communities have focused on the effects of sudden and extreme changes of weather, planned technical interference, dynamics of vegetational change (Beeftink 1979) and grazing intensity (Andresen et al 1990) to identify the responses of different species to environmental disturbances. Studies of the long-term composition of saltmarsh vegetation through the use of permanent plots (accurately marked plots where vegetation releves have been sampled repeatedly over a period of time), have been undertaken at Boschplaat on the island of Terschelling in The Netherlands, where a saltmarsh began to form on a sand flat after the construction of a sand dam in the 1930s (Leendertse et al 1997; Roozen and Westhoff 1985; Smits et al 2002).

Scottish coasts contain about 15% of the UK's 44,000ha saltmarsh resource, of which the marshes in the Solway Firth account for 8% (Hansom and McGlashan 2004). Saltmarshes in Scotland occur mainly in estuaries and at the heads of sea lochs (Harvey and Allan 1998). Two previous studies of vegetation communities of various saltmarshes in Scotland include Gillham's 1957 survey of three sea loch marshes located on the Isle of Mull in the Inner Hebrides, and Zimmerman and Murphy's 2006 survey of three sea loch and four estuarine marshes on the east, west and southern mainland coasts.

We were able to obtain the raw plant species abundance data from both studies, which made it possible to visit and resurvey these sites in 2011 in order to examine the dynamics of Scottish salt marsh plant communities over a short time scale of five years at the mainland sites, and a longer period of 54 years at the sites on the Isle of Mull. In addition to this comparison of historical and recent vegetation data, environmental variables such as soil pH, vegetation height, and soil conductivity were measured in the current study to assist in determining what factors are responsible for plant community patterns within a marsh (zonation) and between different marshes (geographical location).

METHODS

Study Sites

Nine sites from earlier studies were resurveyed (Fig. 1). Three of these were previously surveyed in 1957 by Gillham and are situated along sea lochs located on the Isle of Mull in the Inner Hebrides: Loch Guin, Loch naKeal and Loch Scridain. The other six sites were last surveyed by Zimmermann and Murphy in 2006 and included four along the west coast of mainland Scotland: Port Appin, Loch Etive and Loch Creran near Oban; and Ardmore Point in the Inner Clyde, plus two on the east coast: Aberlady Bay in the outer Firth of Forth and Skinflats, which is also located in the Forth, near Falkirk. The tenth site, Powfoulis New Lagoon, is a newly restored saltmarsh, on previously reclaimed farmland, which is located directly inland from the Skinflats site: no historic data (prior to restoration) were available for this site.

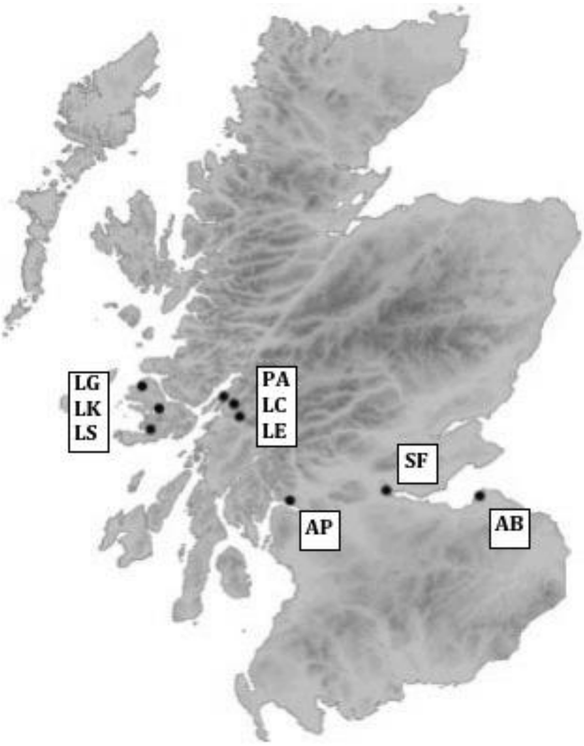

Fig. 1. 2011 Survey site locations. AB = Aberlady Bay, AP = Ardmore Point, LC = Loch Creran, LE = Loch Etive, LG = Loch Guin, LK = Loch naKeal, LS = Loch Scridian, PA = Port Appin; SF = Skinflats (Powfoulis New Lagoon, PNL, also exists at Skinflats, as a newly-created saltmarsh site behind the seawall).

These locations were primarily chosen because data existed from previous years from which to compare possible shifts in vegetation communities over different time scales. They are also representative of the different habitats in (estuaries and sea lochs) and environmental conditions (West and East coasts; island and mainland; and lower and higher latitudes) under which saltmarshes may develop in Scotland. Zimmerman and Murphy (2007) also sampled a site in the Solway Firth (River Cree), but we were unable gain access to the site late in the season, at the time of the fieldwork for this study.

Survey Methods

Surveys of the ten sites were done late September through mid-November 2011. At each site, samples from three randomly located replicate stations were collected from each of three sub-sites corresponding with the three distinct vegetation zones: pioneer/low marsh, accretion/mid marsh and mature/high marsh. One GPS reading was taken (using a Garmin Etrex instrument) to accurately geolocate every sub-site. Plant species abundance was quantified by using a 0.5m x 0.5m quadrat subdivided into twenty-five 0.1m x 0.1m squares and scoring how many of the twenty-five squares within the quadrat were occupied by each species. Vegetation height was recorded at three randomly chosen points in each quadrat. Plant community diversity was recorded simply as total number of species present per sample. A soil sample was taken from each quadrat to measure pH and conductivity levels. The pH level was recorded in the field using a Hanna pH EP4 meter while conductivity was determined back at the University with a Jenway 4071 conductivity meter. Grazing pressure and environmental disturbance were scored on a scale of one to three with one corresponding to areas with a minimal amount of disturbance and three to more heavily impacted sites. In total, 99 samples were collected from the ten sites.

Data Analysis

Species abundance scores from the 2011 survey were converted by simple multiplication into percentages (%A). The multivariate classification procedure Two-Way Indicator Species Analysis (TWINSPAN: Hill and Šmilauer, 2005) was then utilized in order to group together the samples in the 2011 dataset that had similar assemblages of species. A second TWINSPAN analysis was done on the complete dataset (1957, 2006 and 2011 data) to compare and contrast past and present species assemblages. In order to make the year datasets comparable, modifications of the raw data were required. Raw data scores from the 2006 survey were averaged and multiplied by four in order to convert the values to %A values. Data were extracted from the 1957 paper by determining percentage abundance of each species present from individual sections along the detailed transect diagrams given in the article.

Prior to performing statistical tests in Minitab (version 15), the raw 2011 environmental data set was tested for normality by performing Ryan-Joiner tests and certain variables were then $\log_e$ transformed, where necessary, in order to normalize the data. One-way analysis of variance and Tukey's mean comparison tests were used to determine whether there were any significant differences in mean values for soil pH, conductivity, vegetation height and plant species diversity, between the groups designated by TWINSPAN.

Ordination of the 2011 vegetation and environmental data was done using Canonical Correspondence Analysis (CCA, utilizing CANOCO: ter Braak and Šmilauer, 1998). CCA is a multivariate procedure, which can be used to identify patterns of plant species distribution in the context of the environmental variables measured. A Monte Carlo test was used to determine whether the variation explained by the CCA results was significant, across the first (major) axis, or all axes combined for the ordination. Plant assemblages for each zone at each site were allocated to National Vegetation Classification (NVC) saltmarsh/maritime communities using the program TABLEFIT (Hill, 1996).

RESULTS

In total, 37 species were observed in the 2011 resurvey. The five most common species were *Puccinellia maritima*, *Glaux maritima*, *Triglochin maritima*, *Festuca rubra* and *Juncus gerardi*.

TWINSPAN initially divided the 99 sample stations from 2011 into a large group (n=81) and a smaller group (n=18) with an eigenvalue of 0.514. At the next level, both groups were further divided into two groups each to create four groups in total (Group A: n=13 and Group B: n=68; eigenvalue = 0.474 and Group C: n=11 and Group D: n=7; eigenvalue = 0.770). Analysis stopped by the third division because eigenvalues became weaker (0.388 or less), suggesting substantial overlap between species composition of sample-groups at this point. ANOVA analyses confirmed that there were significant differences between the four TWINSPAN groups for mean soil pH ($P < 0.027$), mean soil conductivity ($P = 0.000$) and mean vegetation height ($P = 0.000$). There was no significant difference in mean species diversity among the groups (Table 1).

Group A was made up entirely of sample stations located in the pioneer zones of Aberlady, Skinflats and Ardmore Point. The indicator species listed were *S. europaea* and *Cladophora* spp. This group had the highest mean conductivity and the shortest mean vegetation height.

Group B was the largest one classified by TWINSPAN containing more than half of the total sample stations. This group contains data from all survey locations and is composed primarily of mid-marsh sites with pioneer and high marsh sites that did not display distinct high marsh (Groups C and D) or pioneer marsh (Group A) species. The indicators were *G. maritima*, *F. rubra*, and *J. gerardi* and mean conductivity, pH levels and vegetation height values were intermediate compared to values for the other three groups.

Groups C and D consist exclusively of high marsh zone sample stations. Group C included data from Ardmore Point and Powfoulis New Lagoon (by Skinflats). *E. pycnanthus* was the indicator species and this group had the highest mean vegetation height but the lowest mean soil pH. Samples from Port Appin, Loch Creran, Loch Scridain and Loch Na Keal comprised Group D. Group D's indicator species were *Cochlearia officinalis* and *Agrostis Stolonifera.* The average conductivity for this group was the lowest, but the average sediment pH was the highest.

Variable	**TWINSPAN sample groups**								P_{ANOVA}
	A		**B**		**C**		**D**		
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	
Soil pH	7.16	0.18	6.91	0.07	6.86	0.15	7.54	0.26	$P < 0.027$*
$\log_e$ mean soil conductivity (µS/cm)	8.76	0.12	7.66	0.10	7.90	0.17	6.69	0.29	$P = 0.000$***
$\log_e$ mean vegetation height (cm)	1.91	0.17	2.04	0.08	3.35	0.18	2.43	0.28	$P = 0.000$***

Table 1. Mean values (±1 standard error) of statistically significant environmental variables compared between the 2011 TWINSPAN groups. For group A, n = 13; B, n = 68; C, n = 11; and D, n = 7. Stars next to P-values reflect different levels of significance (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

The CCA ordination of the 2011 survey data, constrained by environmental variables (Fig. 2), suggests that several of the environmental factors measured are good predictors of saltmarsh plant community composition for the sites surveyed (Monte Carlo test for axis 1: $P < 0.002$, all axes: $P < 0.002$). Mean vegetation height, mean soil conductivity, longitude and latitude proved to be the significant environmental variables in predicting saltmarsh plant community distribution while factors such as soil pH, environmental disturbance and grazing pressure were less important. The overlay of the TWINSPAN groups from the 2011 data shows a strong association between high mean soil conductivity and Group A and between mean vegetation height and Group C. Groups B and D were not associated with any environmental variable in particular. The location of Group B was not displayed on the ordination graph because it consisted of sampling stations that were ubiquitously distributed across the plot.

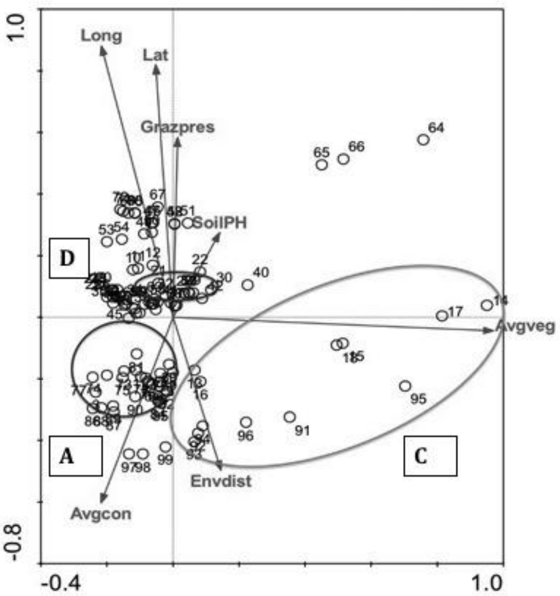

Fig. 2. Canonical Correspondence Analysis sample ordination for the 2011 survey data. Approximate location on the plot of samples making up three individual TWINSPAN sample groups is indicated for groups A, C and D. The fourth group (B) had a more scattered distribution of component samples across the ordination plot. Lat = latitude; Long = longitude; Grazpres = grazing pressure score; SoilPH = mean soil pH; Avgcon = mean soil conductivity; Avgveg = mean vegetation height; Envdist = environmental disturbance score.

Table 2 displays the 12 NVC community and sub-community types assigned to the 30 sub-sites sampled in 2011. The goodness of fit for the NVC communities allocated to the sub-sites ranged widely, from 96% and 94% for pioneer/low marsh sub-sites at Powfoulis New Lagoon and Skinflats, to 49% and 50% for mature/high marsh sub-sites at Powfoulis New Lagoon and Ardmore Point.

Another four TWINSPAN groups emerged from the comparison of the historical and current vegetation data:

Group A was composed of samples collected in 2011 only and contains data from Ardmore Point, Port Appin, Loch Creran, Loch na Keal, Loch Scridain, Aberlady Bay, Skinflats and Powfoulis New Lagoon. Species indicators included *Phalaris arundinacea*, *F. rubra, C. offinalis* and *E. pycnanthus.*

Group B consisted of samples collected from all three years and was the largest group defined. At least one sample from every site from the 2011 survey was represented except for Powfoulis New Lagoon. The majority of the samples taken during the 2006 survey were allocated to this group with sub-sites from Ardmore Point, Port Appin, Loch Creran, Loch Etive, Aberlady Bay and Skinflats. All the data points extracted from the 1957 survey were also included (samples from Loch Guin and Loch Scridain). The species indicators were *J. gerardi, Plantago maritima, G. maritima* and *Armeria maritima.*

Group C was the smallest and the majority of the samples were from the 2011 survey at Powfoulis New Lagoon, with one sample each from Aberlady Bay, Loch Creran and Skinflats. The rest of the samples were from the 2006 survey and were located at Ardmore Point. The indicator species were *Aster tripolium, A. maritima, Plantago maritima* and *Spergularia maritima.*

Group D very closely resembled Group A from the 2011 TWINSPAN analysis containing sub-sites from Ardmore Point, Aberlady Bay, Skinflats and Powfoulis New Lagoon with additional samples from the 2011 survey of Loch na Keal and a sample from Aberlady Bay that was from 2006. The indicator was *Cladophora* spp.

DISCUSSION

In 2011, a classic zoned plant community was present at every site, but there were differences in the precise composition of the vegetation communities between different sites.

Ardmore Point, Aberlady Bay and Skinflats were grouped together by TWINSPAN as being the only sites with pioneer zones colonized by *S. europaea*. This group has the highest average mean conductivity and the shortest average mean vegetation height, which is reflected in the CCA analysis because its sample stations are placed among those most positively associated with high mean conductivity and those most negatively associated with mean vegetation height. Salt water contains a high concentration of ions and halophytes such as *S. europaea* and *Puccinellia maritima* achieve tolerance of high salinity at the expense of growth (Adam 1990).

Sub-site	NVC Community	NVC Community	NVC Code	Goodness of Fit (%)
AP 1	*Puccinellia maritima* saltmarsh	None	SM 13	80
AP 2	*Festuca rubra* saltmarsh - *Juncus gerardi*	*Juncus gerardi*	SM 16b	86
AP 3	*Juncus maritimus* saltmarsh	None	SM 18	49
PA 1	*Festuca rubra* saltmarsh - *Juncus gerardi*	*Festuca rubra*	SM 16d	71
PA 2	*Festuca rubra* saltmarsh - *Juncus gerardi*	*Juncus gerardi*	SM 16b	85
PA 3	*Pucinellia maritima* saltmarsh	*Glaux maritima*	SM 13b	84
LC 1	*Festuca rubra - Armeria maritima* maritime grassland	Typical	MC 8a	67
LC 2	*Festuca rubra* saltmarsh - *Juncus gerardi*	None	SM 16	67
LC 3	*Puccinellia maritima* saltmarsh	None	SM 13	84
LE 1	*Festuca rubra* saltmarsh - *Juncus gerardii*	None	SM 16	97
LE 2	*Puccinellia maritima* saltmarsh	None	SM 13	77
LE 3	*Pucinellia maritima* saltmarsh	*Glaux maritima*	SM 13b	51
LG 1	*Festuca rubra* saltmarsh - *Juncus gerardi*	*Puccinellia maritima*	SM 16a	87
LG 2	*Festuca rubra* saltmarsh - *Juncus gerardi*	None	SM 16	79
LG 3	*Festuca rubra* saltmarsh - *Juncus gerardi*	None	SM 16	69
LK 1	*Festuca rubra* saltmarsh - *Juncus gerardi*	*Leontodon autumnalis*	SM 16e	70
LK 2	*Festuca rubra* saltmarsh - *Juncus gerardi*	None	SM 16	83
LK 3	*Festuca rubra* saltmarsh - *Juncus gerardi*	*Puccinellia maritima*	SM 16a	83
LS 1	*Juncus maritimus - Triglochin maritima* saltmarsh	None	SM 15	68
LS 2	*Puccinellia maritima* saltmarsh	None	SM 13	79
LS 3	*Pucinellia maritima* saltmarsh	*Glaux maritima*	SM 13b	78
AB 1	Annual *Salicornia* saltmarsh	None	SM 8	94
AB 2	*Festuca rubra* saltmarsh - *Juncus gerardi*	*Puccinellia maritima*	SM 16a	79
AB 3	*Festuca rubra* saltmarsh - *Juncus gerardii*	*Juncus gerardii*	SM 16b	82
SF 1	*Festuca rubra* saltmarsh - *Juncus gerardii*	*Festuca rubra*	SM 16d	63
SF 2	*Puccinellia maritima* saltmarsh	*Limonium vulgare - Armeria maritima*	SM 13c	71
SF 3	*Puccinellia maritima* saltmarsh	None	SM 13	94
PNL 1	*Elymus pycnanthus* saltmarsh	None	SM 24	50
PNL 2	*Spergularia marina - Puccinellia distans* saltmarsh	None	SM 23	84
PNL 3	*Puccinellia maritima* saltmarsh	None	SM 13	96

Table 2. National Vegetation Classification (NVC) community designations for sub-sites surveyed in 2011. For site codes see caption to Fig. 1

The largest TWINSPAN group contained representatives from all sites and zone types. The indicators were *G. maritima*, *F. rubra*, and *J. gerardi*, which are species characteristic of the mid-marsh zone (Rodwell 2000). The sample stations were widely distributed about the CCA ordination plot, suggesting that this group tolerates a large range of environmental conditions. None of the NVC low-marsh designations were typical of Loch Guin or Loch naKeal, but a *Puccinellia maritima* sub-community was still assigned indicating a presence of low marsh species. Since Loch Guin and Loch naKeal are island sea lochs that are very rocky and receive a large amount of rain compared to the other areas surveyed, this may have caused a more uniform plant community distribution.

High marsh sample sites from Ardmore Point and Powfoulis New Lagoon were associated with *E. pycnanthus* and *Juncus maritimus* dominant communities—both typical of upper marshes with soils of high organic content. A fenced grazing area for livestock (horses) backs the Ardmore Point marsh, so runoff from this area may result in nutrient enriched soils. Since Powfoulis New Lagoon used to be an agricultural field separated from the site at Skinflats by a seawall, it is also appropriate that it would be characterized by a *S. maritima* dominated community, which commonly occurs on or behind seawalls and generally in areas of disturbed soil and variable salinity (Rodwell 2000). This TWINSPAN group had an intermediate mean conductivity and the highest average vegetation height, which is probably due to the estuarine nature of the sites and the relatively high nutrient runoff from farmland and urban centres.

The Port Appin, Loch Creran, Loch na Keal and Loch Scridain upper marsh sites that comprise group D differ from those in group C (Ardmore Point and Powfoulis New Lagoon) almost certainly since they are all located within sea lochs. These sites collectively had the lowest average conductivity - mainly because of fresh water influence from inland rivers (the conductivity of fresh water being much less than sea water).

Puccinellia maritima, F. rubra, J. gerardi, G. maritima and *T. maritimum* were the five commonest species observed in 2011. Four out of five of these species were the same as those from the 2006 survey. The one exception was that *Plantago maritima* was much more abundant than *Puccinellia maritima* in 2006. *Plantago maritima* was also one of the commonest species found during the 1957 survey of the Isle of Mull sites. However, this species was only present in the upper marsh of Loch naKeal in the 2011 survey.

The general absence of *Plantago maritima* from the 2011 survey is most likely because it is a herbaceous perennial plant, which blooms in the spring and summer months and dies back to the rootstock in autumn. The sampling for the 2011 survey was done in autumn, while sampling in 1957 and 2006 occurred during the spring and summer months.

The shift in dominance from *Plantago maritima* to *Puccinellia maritima* might also signify retrogressive succession to an earlier successional stage, which usually occurs as a result of a decrease in marsh elevation and increase in sea level rise (Warren and Niering 1993). Leendertse et al (1997) observed a change in species dominance from *Puccinellia maritima* in 1957 to *Plantago maritima* between 1967-1990 in three mid marsh plots during their study. Increases in elevation and silt thickness coupled with a decrease in the number of floodings per year were cited as the causes. This suggests that if elevation and silt thickness were to decrease while the number of floodings per year increased, the plant community dominance might regress from *Plantago maritima* to *Puccinellia maritima.* This could perhaps contribute to the relative the lack of *Plantago maritima* observed in 2011—especially considering the absence of *Puccinellia maritima* from Loch Scridain in 1957 and its abundance of it in 2011. However, historical measurements of elevation and flooding frequency at these sites are unavailable to allow further examination of this point.

Another change we noticed was the appearance of a *S. europaea* dominated pioneer zone at Skinflats in 2011 that was absent in 2006. The site at Skinflats was backed by a sea wall separating it from an agricultural field (historically reclaimed salt marsh) up until recently. By the time the present survey was conducted, the Royal Society for the Protection of Birds (RSPB) had introduced a regulated tidal exchange scheme between the field and the survey site. This action is part of a salt marsh restoration programme with the purpose of creating more migratory waterfowl habitat and preventing further erosion of the area. Since the hydrology of the site was altered as a result of this endeavour, this could account for a change in the intensity of the wave action, possibly generating conditions along the shoreline more conducive to the establishment of *S. europaea* seedlings.

In addition to these differences, *Elymus. pycnanthus,* a species not commonly observed north of the Solway Firth, was present at four of the sites surveyed in 2011: Powfoulis New Lagoon, Ardmore Point, Loch Scridain and Port Appin. The species had been observed at the Ardmore Point and Loch Scridain sites in previous years, however, its presence at the Port Appin site had not been recorded before, to our knowledge. Reasons for the difference in distribution of this species could include climate change, seed dispersal through vectors such as birds, wave or wind action or both, as seed distributing animals such as birds may alter their distributions to cope with climate change (Walther et al. 2002; Howe and Smallwood 1984). At the new Powfoulis New Lagoon site, the presence of *E.pycnanthus* could also be due to the introduction of a seed mix (normally used to re-vegetate sand dunes) by RSPB there in order to help vegetate the newly constructed lagoon banks, which would be likely to include seed of *E. pycnanthus* (N. Chambers, RSPB, pers. comm.).

TWINSPAN classification of the past and present vegetation data generated four groups, three of which contain data from more than one year. One group in particular (Group B) contained 55% of the sample sites from 2011, 100% of the samples from 1957 and 91% from 2006 (Fig. 3). When comparing the plant species present at each site in 2011 to those species existing there in the previous survey, 25 - 64% of the species were the same. Since conditions in the saltmarsh ecosystem can fluctuate dramatically, the fact that the sites retained about 45% of the plant species, on average, that were observed during previous surveys provides evidence for some degree of vegetation community stability over time, whether over a short timescale of 5 years (mainland sites), or a longer period of 54 years (Isle of Mull sites).

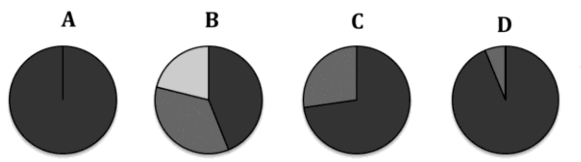

Fig. 3. Composition of the TWINSPAN sample groups (A-D) produced by classification of vegetation data from all three surveys by year (Black = 2011, Grey = 2006 and White = 1957)

Resistance and resilience to perturbations are strong influences on ecosystem stability (Tilman and Downing 1994). Long-term stability of saltmarshes is regulated by interactions between factors such as tidal inundation, land elevation, primary production and sediment accretion (Morris et al 2002). Sea level rise, invasive species and development are major threats to saltmarsh stability (Gedan et al 2009). If the level of the sea rises at a faster rate than the salt marsh can accumulate sediment and increase its elevation, then the marsh will be completely submerged, leaving behind mudflats or open water (Leendertse et al 1997). Invasions of non-native species and development of the coast can exacerbate this condition by leading to severe disruptions in salt marsh plant communities, causing the marsh to erode (Gedan et al 2009).

For future studies of long-term change in Scottish salt marsh plant communities, it would be useful to monitor additional variables such as sediment type, land elevation, sediment accretion, biomass and tidal height and frequency, in addition to those looked at in this survey. This way, if there is a very prominent change in the abundance of a certain species, such as the development of a *S. europaea* dominated pioneer zone, we can make inferences based on these measurements and observations as to whether anthropogenically-induced threats to salt marsh existence and functioning (such as sea level rise, development and invasive species) are the cause or whether natural change in the species dynamics of salt marsh ecosystems are of greater importance in explaining and predicting such vegetation changes.

ACKNOWLEDGMENTS
A special thanks to Nick Chambers of RSPB and John Harrison of East Lothian District Council for helping us gain access to the sites at Skinflats and Aberlady Bay.

REFERENCES

Adam, P. (1990) *Saltmarsh Ecology*. Cambridge Studies in Ecology, Cambridge University Press.

Andresen, H., Bakker, J.P., Brongers, M., Heydemann, B., & Irmler, U. (1990) Long-term changes of salt marsh communities by cattle grazing. *Plant Ecology* 89: 137-148

Beeftink, W.G. (1977) The coastal saltmarshes of Western and Northern Europe: An ecological and phytosociological approach. *Wet Coastal Ecosystems* (Ed. By V.J. Chapman), pp. 109-55. Elsevier, Amsterdam.

Beeftink, W.G. (1979). The structure of salt marsh communities in relation to environmental disturbances. *Ecological processes in coastal environments: The 1st European Ecological Symposium and 19th Symposium of the British Ecological Society, Norwich, 12-16 September 1977*. (Ed. By Jefferies, R.L. *et al.*) pp. 77-93. Blackwell Scientific Publications, Oxford.

Fariña, J.M., Silliman, B.R. & Bertness, M.D. (2009) Can conservation biologists rely on established community structure rules to manage novel systems? Not in salt marshes. *Ecological Applications* 19: 413-422

Gedan, K.B., Silliman, B.R. & Bertness, M.D. (2009) Centuries of human-driven change in salt marsh ecosystems. *Annual Review of Marine Science* 1: 117-41.

Gillham, M.E. (1957) Coastal Vegetation of Mull and Iona in Relation to Salinity and Soil Reaction. *Journal of Ecology* 45: 757-778

Hansom, J.D. & McGlashan, D.J. (2004) Scotland's coast: understanding past and present processes for sustainable management. *Scottish Geographical Journal* 120: 99-116

Harvey, M.M. & Allan, R.L. (1998) The Solway Firth saltmarshes. *Scottish Geographical Magazine* 114: 42-45

Hill, M.O. (1996) *TABLEFIT Version 1.0 for Identification of Vegetation Types.* Institute of Terrestrial Ecology.

Hill, M.O. & Šmilauer, P. (2005) *TWINSPAN for Windows version 2.3*. Centre for Ecology and Hydrology & University of South Bohemia, Huntingdon & Ceske Budejovice.

Howe, H.F. & Smallwood, J. (1984) Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201-228

Leendertse, P.C., Roozen, A.J.M. & Rozema, J. (1997) Long term changes (1953 - 1990) in the salt marsh vegetation at the Boschplaat on Terschelling in relation to sedimentation and flooding. *Plant Ecology* 132: 49-58.

Morris, J.T., Sundareshwar, P.V., Nietch, C.T., Kjerfve, B. & Cahoon, D.R. (2002) Responses of coastal wetlands to rising sea level. *Ecology* 83: 2869-2877

Rodwell, J.S. (ed) (2000) *British Plant Communities, Vol.5; Maritime Communities and Vegetation of Open Habitats*. Cambridge University Press, Cambridge.

Roozen, A.J.M. & Westhoff, V. (1985) A study on long-term salt-marsh succession using permanent plots. *Plant Ecology* 61: 23-32

Smits, N.A.C., Schaminée, J.H.J. & van Duuren, L. (2002) 70 years of permanent plot research in The Netherlands. *Applied Vegetation Science* 5: 121-126

Steers, J.A. (1977) Physiography. *Wet Coastal Ecosystems* (Ed. By V.J. Chapman), pp. 109-55. Elsevier, Amsterdam.

ter Braak, C. J. F. & Šmilauer, P. (1998) *CANOCO reference manual and users guide to Canoco for windows: software for canonical community ordination (version 4).* Micro-computer Power, Ithaca, USA

Tilman, D. & Downing, J.A. (1994) Biodiversity and stability in grasslands. *Nature* 367: 363-365

Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature* 416: 389-395

Warren, R.S. & Niering, W.A. (1993) Vegetation change on a northeast tidal marsh: Interaction of sea-level rise and marsh accretion. *Ecology* 74: 96-103

Zedler, J.B. & Kercher, S. (2005) Wetland resources: Status, trends, ecosystem services and restorability. *Annual Review of Environmental Resources* 30: 39-74.

Zimmermann, S. & Murphy, K.J. (2007) Plant communities and vegetation diversity in Scottish saltmarshes in relation to land use. *Botanical Society of Scotland News* 89: 26-31.