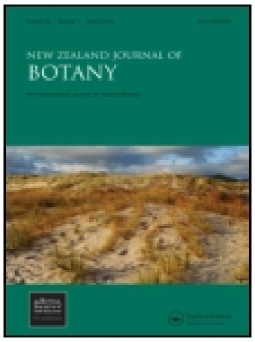

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Vegetation patterns in salt marshes of Otago, New Zealand

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Abstract Thirteen salt marshes of coastal Otago, New Zealand, were sampled and described using classification and ordination techniques, in an attempt to understand more about vegetation patterns both within marshes and amongst different marshes. Ordination indicates that the same set of primary factors is responsible for the salt marsh vegetation patterns of most marshes. These factors are all related to tides and are difficult to separate. Secondary factors common to most marshes are related to soil moisture, water ponding, and fresh water flow. This consistency results in characteristic and typical salt marsh communities zoned according to these factors. Each marsh, however, has anomalies which may be an important feature of that marsh. These create numerous peculiar and often unique plant communities which characterise the individual marshes. Often they can be correlated with edaphic differences or various cultural effects. With many marshes having been sampled, the simple community relationships seen within individual marshes become complex and difficult to interpret. As more marshes are examined the trends that can be seen by examining only a few marshes are seen to be misleading. Although superficially similar to salt marshes, lagoons are distinguished by a general absence of the typical plant communities. The flora is very similar to that of salt marshes, but the species associate in quite different ways.

Keywords salt marsh; vegetation zonation; plant communities; classification; ordination; community structure; lagoon margin; brackish marshes; New Zealand

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INTRODUCTION

Low species diversity, high species consistency, and geographical and ecological distinctiveness make a regional suite of salt marshes excellent for the study of aspects of plant community relationships. Few, but consistently occurring, species make description and comparison relatively simple. Geographical distinctiveness means that individual marshes can be treated as isolated units, while ecological distinctiveness results in identification of a salt marsh by its species and recognition of the importance in its environment of the tide, once described as the "master factor" (Chapman 1974).

There are a number of aspects of plant communities of interest in this study. The first is whether species do indeed occur together to form distinct communities, and if they do, how those communities are floristically and ecologically related to each other at different locations. Another important question is whether these particular communities are repeated in apparently similar environments at different marshes. In such studies it is easy to emphasise either similarities or differences as depending upon bias. It is therefore particularly important that random sampling and techniques of objective analysis be applied to such a study.

For a small country, New Zealand has a particularly diverse coastline. Included are regions in which estuaries are numerous such as in Northland, Western Bay of Plenty, Nelson, and Otago. There are however important regional differences in the salt marshes of these estuaries, caused by the southward disappearance of two physionomic dominants: the woody mangrove (*Avicennia resinifera**) which is restricted to the north of the North Island, and the tall rush *Juncus maritimus* var. *australiensis*, which has its main southern limit north of Otago. This leaves a relatively uniform regional grouping of the salt marshes in Otago of

*Nomenclature follows Allan (1960), Moore & Edgar (1971), and Cheeseman (1925) for native species, and Clapham et al. (1981) for adventives. Alternative names for various native taxa are found in Connor & Edgar (1987).

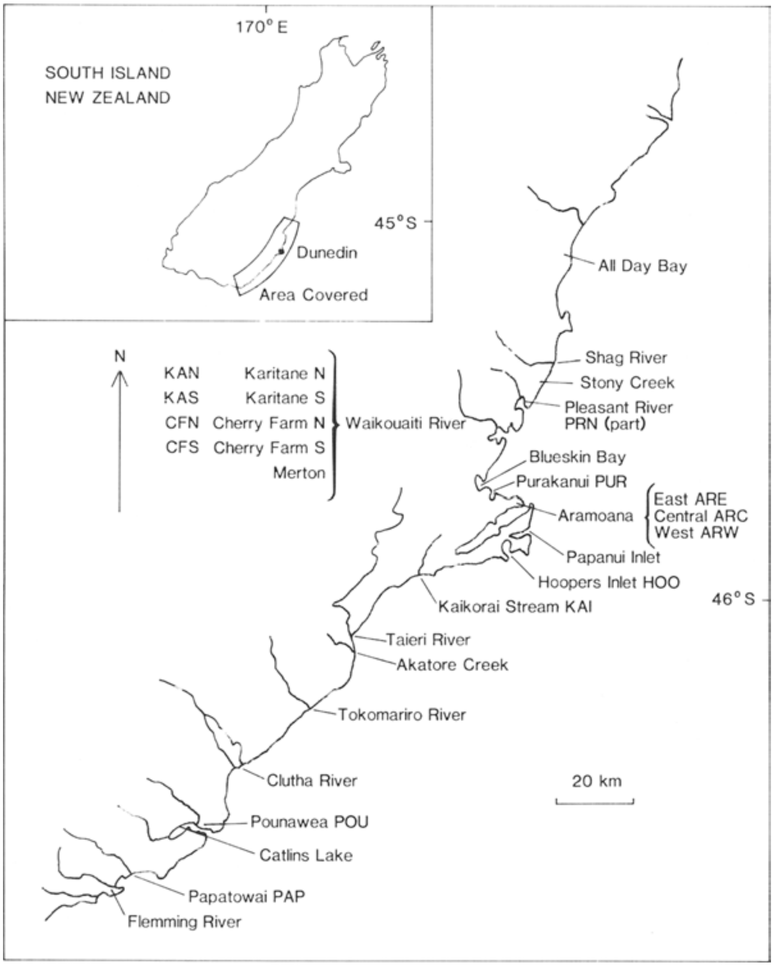

Fig. 1 Location map of main areas of salt marsh in coastal Otago. Those sampled are indicated by codes. Only part of the extensive Pleasant River marshes was sampled.

predominantly short turf vegetation, with tall (>10 cm) species being restricted to only the uppermost zones. This type of vegetation was not described by Chapman (1974). Of the few published accounts of New Zealand salt marsh vegetation, only one (Paviour-Smith 1956), refers to this region.

METHODS

Thirteen of the Otago salt marshes (Fig. 1) were selected for study. They were chosen to represent the full range of geographical variety and disturbance that can be found. Included are maritime (Fig. 2), riverbank, and lagoonal (Fig. 3) marshes and those that are both natural and modified by farming or reclamation practices.

Sampling was by restricted randomisation, using one 1.5 m × 1.5 m site (quadrat) per 900 m^2 for marshes larger than 0.1 km^2, and one per 225 m^2 for smaller marshes (Table 1). Species presence was recorded. Sites beyond the generally accepted concept of salt marsh were included if they contained species common to the salt marsh. This was done to obtain information regarding the relation between salt marsh and its adjacent vegetation.

Site and species classifications to produce dendrograms showing similarities were all performed using Cluster Analysis (Lance & Williams 1967), the sorting strategy was Flexible with Beta set at the somewhat space dilating value of −0.25. The measure of dissimilarity was the complement of Jaccard's coefficient (Williams et al. 1973). Ordinations to produce two dimensional diagrams showing vegetation trends were performed using Reciprocal Averaging (Hill 1973), though only the first three axes were extracted.

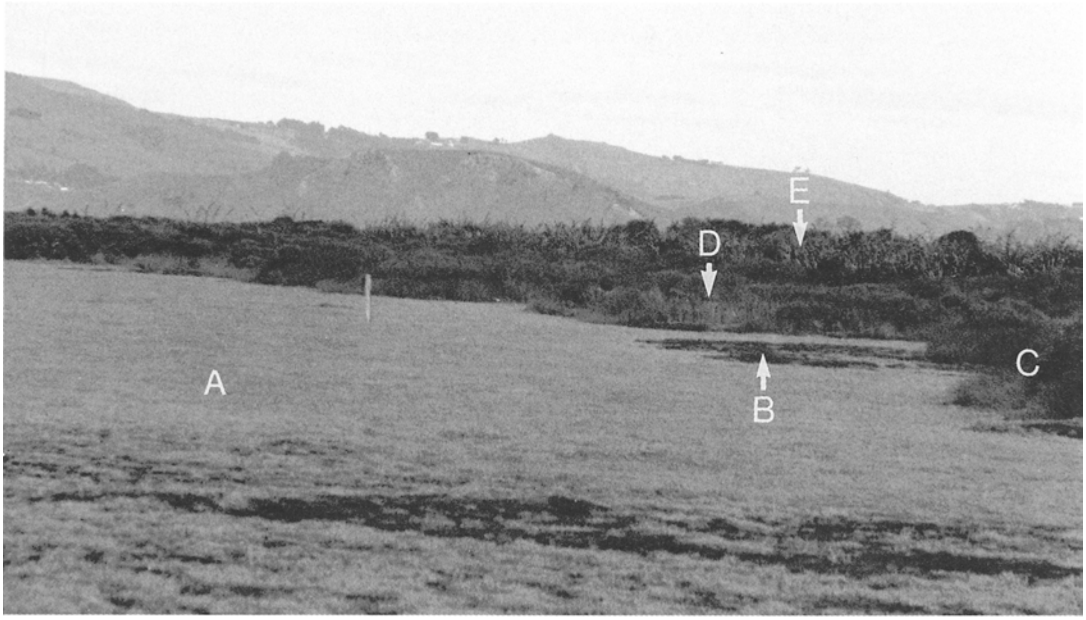

Fig. 2 Salt marsh communities at Aramoana East. This maritime marsh has very little fresh water mixing with the tide. Communities are: A lower marsh of *Sarcocornia quinqueflora* and *Samolus repens*, B middle marsh salt meadow of *Selliera radicans* and *Schoenus nitens*, C upper marsh of *Leptocarpus similis* and *Plagianthus divaricatus*, D dry upper marsh fringe of *Scirpoides nodosa*, E moist upper marsh fringe of *Phormium tenax*.

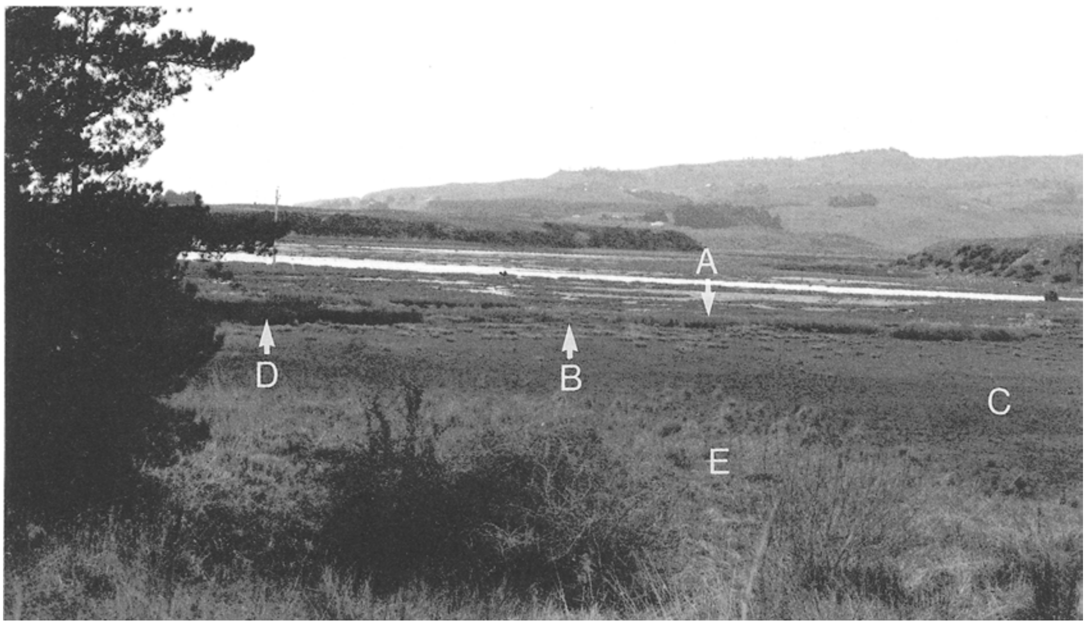

Fig. 3 Salt marsh communities at Cherry Farm South. This embayed marsh is partly lagoonal and does not completely empty with the tide. Communities are: A lower marsh of *Spartina anglica*, B lower marsh of *Sarcocornia quinqueflora* and *Puccinellia novae-zelandiae*, C middle marsh of *Selliera radicans* and *Samolus repens*, D ponding area of *Leptocarpus similis* and *Schoenoplectus pungens*, E highly modified upper marsh of *Festuca arundinacea* and *Agrostis stolonifera*.

Table 1 The 13 sampled marshes of Otago, with areas and the overlay grid sample size used at each. The codes are for use in Table 3.

Marsh	Code	Grid size (m)	Area (km^2)	Number of sites
Pleasant River	PRN	30 × 30	0.243	239
Karitane North	KAN	30 × 30	0.242	176
Karitane South	KAS	15 × 15	0.011	34
Cherry Farm North	CFN	15 × 15	0.021	75
Cherry Farm South	CFS	30 × 30	0.122	122
Purakanui	PUR	30 × 30	0.203	158
Aramoana East	ARE	30 × 30	0.467	285
Aramoana Central	ARC	30 × 30	0.118	124
Aramoana West	ARW	30 × 30	0.195	159
Hoopers Inlet	HOO	30 × 30	0.160	151
Kaikorai	KAI	15 × 15	0.074	278
Pounawea	POU	15 × 15	0.072	288
Papatowai	PAP	15 × 15	0.030	115

RESULTS

The sites from all marshes were combined for All Sites analyses, except that to reduce the computational load, of 2208 sites, only one entry was made for those which were identical in species composition, giving 841 unique 'types'. This procedure also removes the tendency of a space-dilating method to give common types undue prominence.

All sites classification

Interpretation of the site classification (Table 2) is hierarchical, the first level consisting of six groups numbered 1–6 and the second level totalling 26 sub-groups labelled a–z. A similar system is used for the species classification except the first level is indicated by letters and the first (A), the typical salt marsh species, is subdivided. Choosing a number of groups instead of a threshold similarity overcomes the criticisms of the Canberra/Jaccard measure by Bloom (1981).

Of the sites, 56% fall into site groups 1, 2, and 3. They are characterised by species group A (Table 2), are well distributed amongst the marshes (Table 3), and can be considered to be the typical salt marsh vegetation zones. A notable feature of the individual marsh classifications (not presented) was the abundant, species-poor, and repetitive lower marsh. However, in the All Sites analysis, it cannot be identified with any particular sub-group. Within each marsh the composition of the lower marsh is quite consistent, but the species mix varies from one marsh to another. Therefore, in the All Sites analysis, there is no consistent grouping to be found. Most of the lower marsh sites including the abundant pure *Sarcocornia quinqueflora* are classified in sub-group 1_a, an otherwise species-poor grouping with a high mean type frequency (Table 3). Others with more species may also be found in 4_m. The rest of group 1 sites are from various zones, each with distinctive characteristics, but little to connect them as a group. Modified marsh zones tend to occur here (e.g., with the adventive *Plantago coronopus*) as do many variants (e.g., with the sporadic *Suaeda novae-zelandiae*). Site group 2, however, is characterised by the dominance of all the species of A_1 and is middle marsh. Site group 3 has, in addition, the species of groups A_2, A_3, and A_4, and is upper marsh to marsh fringe.

Site groups 4–6 and species groups B–H contain vegetation and species from either above the marsh, but with some salt marsh species, or various peculiar types, often with restricted distribution. Site group 4 is diverse, including parts of the marsh in which water, usually brackish, ponds in depressions (4_o, 4_p, 4_q). It also contains variable sub-groups 4_m and 4_n, such groupings being a consequence of a space-dilating sorting strategy in classification (Lance & Williams 1966). The only abundant vegetation of these mixtures is the *Samolus repens* lower marsh found as an important constituent at one marsh only. The dry variants of all zones do not occur in site group 4, but in site group 1.

Vegetation including salt marsh species but which is above the salt marsh itself is in site group 5, and includes salt marsh with species of wetlands (5_t, 5_s), farmland (5_r), sand ridges of former beaches (5_u), and forest (5_v, 5_w). Adjacent vegetation is continued in two sub-groups of site group 6 as sand dune (6_x) and sandy embayment (6_y). The final sub-group 6_z is an important variant found at one marsh only, and is characterised by the tall rush *Juncus maritimus* var. *australiensis*, a species dominant there but absent from all other marshes.

In spite of differences in the proportion of the three major marsh zones (Groups 1–3, Table 3), for the reasons discussed above, Groups 1–3 are represented at almost all marshes, as is Group 4. It is at a finer level of vegetational differentiation that differences are seen. Some vegetation sub-groups are found at almost every marsh (e.g., 1_a, 1_e, 2_i, 3_j). Others are restricted to a few marshes, though they are often important on some of those marshes where they occur (e.g., 1_d at Karitane South, 1_f at Kaikorai, 3_k at Pounawea, 4_p at Karitane North, 4_q at Kaikorai, and 6_z at Purakanui).

Ordination

To further develop concepts regarding salt marsh vegetation patterns, Reciprocal Averaging ordinations were performed for each marsh except the very small Karitane South. These individual marsh ordinations are not presented.

The individual species ordinations were subdivided into eight columns on axis one, and the frequency of the species in each column is presented in Fig. 4. The species of group A_1 occupy the left side to the centre with *Sarcocornia quinqueflora* and *Puccinellia stricta* being consistently at the left. As indicated earlier, these species are those which extend down to the middle marsh and, in the case of the two specifically mentioned, the lower marsh. Groups A_2 and A_3 are the upper marsh, and A_4 the upper marsh fringe. Group B occurs in the lower marsh, but is more a feature of the lagoonal marshes, while group C is a mixture ranging from lower marsh (*Suaeda novae-zelandiae*) to upper marsh (*Hypochaeris radicata*), but tending to be less common.

The ordinations therefore support the suggestion from the classifications that there is a generalised lower to upper marsh sequence common to all marshes, and that this is relatively constant and predictable in composition. The interest in the other species groups is that they are the cause of most of the anomalies, and represent the major series of variations within, and between marshes. Many of these variations can be observed in the second axes of the ordinations. Of the two most extreme species found at either end of axis 2 of the individual marsh ordinations, a disproportionately large number are of species group C (54%, expected on species frequency = 23%), especially when compared to group A (42%, expected = 67%). Group B did not, however, feature often at the extremes (4%, expected = 10%). The eight column technique applied to axis 1 was uninformative with axis 2 as the bulk of the species is often clustered away from a few outliers.

In the marshes in which they are present, certain species are fairly consistent as to their relative positions on the second axes of the various ordinations. Consistently at one extreme are those of depressions within the marsh in which brackish water ponds (e.g., *Leptocarpus similis*, *Mimulus repens*, *Isolepis cernua*, *Schoenoplectus pungens*). At the other extreme are those of dry, sandy marsh areas such as lower marsh splash zones (*Suaeda novae-zelandiae*) and sand dune or ridge margins (*Scirpoides nodosa*, *Hypochaeris radicata*). Inconsistencies in this pattern, however, are numerous (e.g., *Plagianthus divaricatus*, *Agrostis stolonifera*, *Triglochin striatum*). The second axes therefore seem related to features of the moisture content of the sediments, but show greater variation between marshes than the first axes.

The All Sites ordination (with Kaikorai sites excluded) (Fig. 5) indicates the same trends in the first and second axes that were indicated in the individual marsh ordinations.

DISCUSSION

Ecological interpretation

Despite the overall structural similarities already outlined, the marshes have important and ecologically interesting differences in composition. These differences can be broadly grouped according to their causes as (i) edaphic, (ii) cultural, (iii) geomorphic, (iv) biogeographic. The first three can explain most differences, the fourth may be a possibility in one case only.

In the lower marsh, edaphic differences are the most important. The typical lower marsh is dominated by the succulent herb *Sarcocornia quinqueflora*, usually with scattered tufts of the grass *Puccinellia stricta*. At the Aramoana marshes, however, (and especially at Aramoana East) the lower marsh is mostly pure stands of the creeping herb *Samolus repens* (Table 3). Chapman (1974) considered that *Samolus repens* grew in more shingly sites than *Sarcocornia quinqueflora*. Of the Otago marshes, the maritime Aramoana East is the most exposed, so that the covering water is more agitated. At high tide, probably only the coarser grains are sedimented,

Table 2 Species frequency within each of the sub-groups of the total site classification.

		1_a	1_b	1_c	1_d	1_e	1_f	2_g	2_h	2_i	3_j	3_k	3_l	4_m	4_n	4_o	4_p	4_q	5_r	5_s	5_t	5_u	5_v	5_w	6_x	6_y	6_z
Number of unique sites		37	24	63	15	45	29	19	45	73	60	46	49	22	15	19	13	31	14	32	25	41	23	31	30	33	10
Number of sites		313	29	101	15	86	38	127	246	243	91	139	49	121	43	42	23	67	20	75	118	47	25	34	36	37	43
A[1]	*Sarcocornia quinqueflora*	95	83	87	93	67	59	84	96	85	82	24	4	9	47	21	60	3	7		4	20				9	
	Samolus repens	16	13	25	7	58	38	11	58	99	92	89	69	64	13	21	100	23	14	3		5	30	3	10	91	
	Selliera radicans	32	58	87	60	11	69	100	27	97	97	89	96						29			27	39				
	Puccinellia stricta	5	21	43		33		68	93	70	13	63	8	14	13	11	8		7								
	Triglochin striatum			13	20	93	69	37	18	67	3	17	31		13						4	5			7		
A[2]	*Cotula dioica*				7				2	5	15	20	55						14			5	9	3		33	
	Schoenus nitens	3	4	11	33	2		42	11	26	60	83	31	5			5		14			2			3	55	
A[3]	*Leptocarpus similis*			3		44	34	11		7	45	28	47		27	11				56	100	71		6	27	3	50
	Apium prostratum	5	17	29	80	7	7	21	7	10	52	20	69	14		5			21	31	20	47	91	10	7	3	20
	Lachnagrostis filiformis		25	86	40	4	100	11		11	63	22	43		7		8	6			8	15	22				
	Atriplex prostrata			40	7	2		11	18	3	10	13	12	9		5	8			19		7	35		17		20
A[4]	*Agrostis stolonifera*	3	46	13	20	16	21		2		3	2	45	14		5		42	100	31	8	66	13	61	100	97	
	Festuca arundinacea		17	41	93	7			9	4	2	59	20						100	97	4	15	91	97			
	Plagianthus divaricatus		4	8		2	7		2		12	15	33	5						72	28	80	52	19	3		
	Scirpoides nodosa	14		2	7		3		2		15	50	18	9								76	74	55	10	21	
	Poa cita		8	8	7		3					17	33							28		5	52				
B	*Isolepis cernua*	3	8		20	20	3	5	16	49	18	7	18	14		32	3	84		6		7			10	12	
	Spergularia media	19				2			24	19	2		2	9		11	5	87							7	6	
	Cotula coronopifolia	3		6		13	41		11	8		2	2			37	6	65				5				12	
	Puccinellia fasciculata	57	4	3	47	9	3				2				7		100	48			24				17		
	Juncus maritimus									1	8		20														100
	Schoenoplectus pungens					24	52			10	5		12	16		79	15	3			16				10		10
	Epilobium adenocaulon												2														
	Mimulus repens					11				4		2			40	5		26									
	Lilaeopsis novae-zelandiae					2								5				16								3	
	Suaeda novae-zelandiae	38		14	33	2			51		2	4		18													
	Zostera muelleri				7									14													
	Ruppia megacarpa													5													
	Disphyma australe		4								2			5													
	Coprosma crassifolia																				4						
	Acaena novae-zelandiae																					2					
	Centella uniflora																					2					
	Elymus laevis			2																3							
	Melicope simplex																							6			
	Asplenium lucidum																							3			
	Myrsine divaricata																							3			
	Festuca rubra		4																								
	Carex flagellifera			2	7					3		7	6						29			12					
	Holcus lanatus		8										6						7			7		3		12	

	Hypochoeris radicata		8	6			3						2	5								24				19	
	Juncus gerardii									1	3		1	9								2					
	Ammophila arenaria	16	17											5								7			3	6	
	Elymus pycnanthus													27							12	7			26		
	Phalaris canariensis													5											3		
	Senecio minimus			4																					3		
	Spartina anglica														47		8					5					
	Puccinellia novae-zelandiae	3				2	3				2				20												
	Cirsium vulgare														7				14								
	Dactylis glomerata								2										7						3		
	Plantago coronopus	19	100	52	87		3	16	4	1	3	2	8				8		29		5	5					
	Puccinellia distans	11	4	14		7			2																		
	Trifolium repens		4	4																					3		
	Trifolium dubium			6							2		6														
	Trifolium fragiferum		8	4									2														
D	*Sonchus oleraceus*	3																				2					
	Bromus mollis	3											2														10
	Lupinus arboreus																					2					
	Senecio biserratus																					5				3	
	Poa pratensis																		14			2					10
	Anthoxanthum odoratum		4																7								
	Rytidosperma unarede		4																			2					
E	*Carex coriacea*												2										4	29			
	Leptospermum scoparium																				4		9	32			
	Phormium tenax						3				2		18						7	9	40	24	30	42		3	
	Coprosma propinqua												2						7	28	8	2	57	90			
	Cortaderia richardii																				8						
	Coprosma rigida																				4	2	22	16			
F	*Juncus bufonius*			4																						12	
	Lolium perenne			2																							
	Cynosurus cristatus			2																							
G	*Lepidosperma australe*												2														
	Polypogon monspeliensis												4														
H	*Juncus articulatus*												6						7							12	
	Plantago raoulii																									15	
	Cerastium holosteoides		4										4													12	
	Sagina procumbens				13																					15	
	Rumex obtusifolius													18					7	3		2			50	52	
	Carex pumila	3																							7	58	
	Crassula moschata																								18	70	

Table 3 Number of sites of each site classification sub-group within each marsh. The duplication ratio indicates the degree of repetition of site composition.

Sub-group	PRN	KAN	KAS	CFN	CFS	PUR	ARE	ARC	ARW	HOO	KAI	POU	PAP	Number of unique sites	Number of sites	Duplication ratio
1_a	29	135	11	37	16	48	23	4	4	3	1	2		37	313	8.46
1_b	13	10	4	1				1						24	29	1.21
1_c	69		2	3	14			1	2	1	1	2	6	63	101	1.60
1_d			15											15	15	1.00
1_e	2			5	6	1	4	15	23	4	9	13	2	45	86	1.91
1_f	11					2					21		4	29	38	1.31
2_g	60			2	6	10	3	13	25	4		3	1	19	127	6.68
2_h	22	3			5	12	122	7	28	34	3	7	3	45	246	5.47
2_i	20	3	1	8	7	7	16	8	19	88	1	57	8	73	243	3.33
3_j	9	5			3	12	11	20	6	10	1	5	9	60	91	1.52
3_k	2						3	20	4	3		106	1	46	139	3.02
3_l				2	13	7	6	9	2	3	7			49	49	1.00
4_m	1				1		81	5	17	1	11	3	1	22	121	5.55
4_n		4	1	12	20							5		15	43	2.87
4_o	1				1	11			4		25			19	42	2.21
4_p		13									10			13	23	1.77
4_q											67			31	67	2.16
5_r				5	11	1						3		14	20	1.43
5_s		1			8			2			3	14	47	32	75	2.34
5_t					10	4	11	7	9		38	6	33	25	118	4.72
5_u		2			1		5	10	14		10	5		41	47	1.15
5_v												25		23	25	1.09
5_w									1			32	1	31	34	1.10
6_x								2	1		33			30	36	1.23
6_y											37			33	37	1.12
6_z						43								10	43	4.30

Fig. 4 Frequency of distribution of the most common species along axis 1 of the individual marsh ordinations.

giving the surface a firmness usually lacking in stands of *Sarcocornia quinqueflora*. We consider, however, that the effect of frequent agitiation might be to hinder seedling establishment of *Sarcocornia quinqueflora*, as it is a common species on equally coarse-grained, but raised, sandy areas. *Samolus repens*, in contrast, is able to spread effectively using stolons. Generally, in muddy marshes, such as at Cherry Farm, *Samolus repens* is rare, although it is also rare at Karitane North, a marsh with no muddy sediment.

At Karitane North, the species associated with *Sarcocornia quinqueflora* is a different grass, *Puccinellia fasciculata*, perhaps because the marsh is sandy and prone to drying when exposed. *Puccinellia fasciculata*, however, occurs also in the lagoonal Kaikorai marshes in quite a different habitat. The taxonomic status of this species in New Zealand is confused, and it may be made up of a number of different entities or ecotypes. Another species, the taller *Puccinellia novae-zelandiae*, seems restricted to sheltered muddy marshes at Cherry Farm and

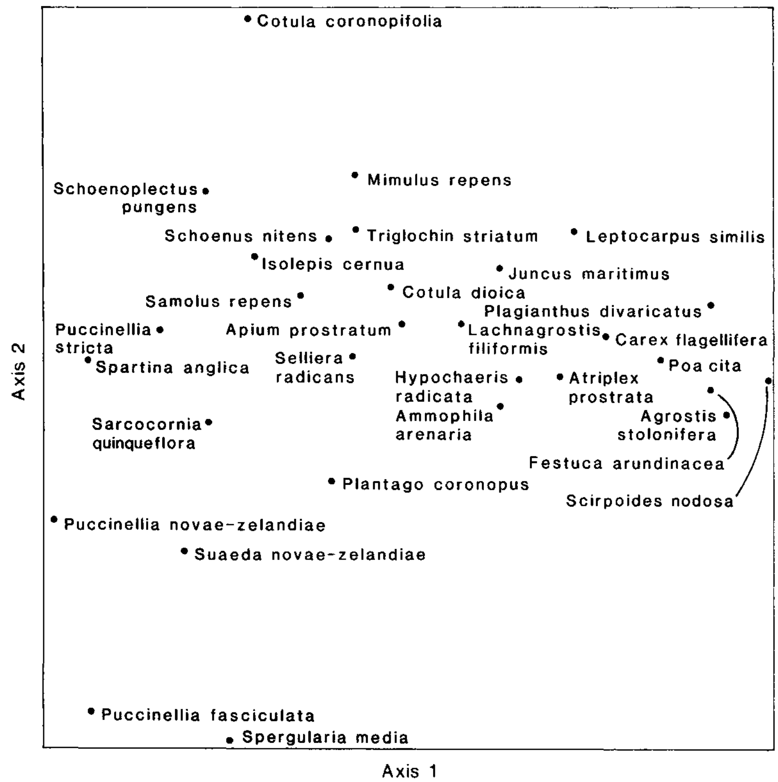

Fig. 5 Species Reciprocal Averaging ordination for the All Sites analysis (excluding Kaikorai), showing only the most common species.

Papatowai and occurs as a distinct but narrow band below the *Sarcocornia quinqueflora*.

Included in lower marsh are raised sandy margins that often occur around the seaward edge of exposed maritime marshes e.g., at Aramoana and Karitane. Wind-generated waves pile up sand and splash sea water on to these margins. *Sarcocornia quinqueflora* is common, but the species indicative of such wave-splash conditions is another succulent chenopod, *Suaeda novae-zelandiae*. Such areas become extremely saline when water evaporates, concentrating the salt. In similarly open areas of raised sandy vegetation, Kassas & Zahran (1967) observed extremely high salinites. At Karitane North, this vegetation may have a cultural origin via destabilisation of the adjacent sand dunes and deposition of sand on to the marsh during blow outs.

The most important cultural factor in the lower marsh has been the planting of *Spartina anglica* in the Waikouaiti River estuary (Karitane and Cherry Farm). This species can invade the *Zostera muelleri* sand flats and all salt marsh zones, although it is in the lower zones that it makes its greatest impact where it traps sediment and overtops the herbaceous vegetation. This niche is similar to that in European marshes (Chater & Jones 1957). The planting, spread, and problems with this species have been described by Bascand (1970) and Lee & Partridge (1983). At these two locations it has, however, hardly invaded the other salt marsh vegetation, and its impact is, so far, minor. It was formerly present at Pounawea but was removed during the 1970s, except for a few remaining clumps in the upper salt marsh.

The differences between estuarine and lagoonal marshes involve a wide variety of important edaphic factors affecting all zones. The major difference is that instead of regular tidal flooding, a lagoon has irregular, often sustained, flooding by brackish water as regulated by the frequency of opening of the sand bar at the river mouth. The most extreme example in Otago is at Kaikorai where, although many salt marsh species are present, they form communities bearing little resemblance to those at the true salt marshes. Here the lower salt marsh species have been replaced by a number of short-lived opportunists such as *Cotula coronopifolia* and *Spergularia media* which appear to invade the lower zones when they become exposed, and others which may survive the long periods of inundation such as *Isolepis cernua*. Short life cycles seem best suited to the irregularities of the flooding regime. The wetter, upper lagoon zones show similarity to the brackish depressions of salt marshes, with species such as *Leptocarpus similis* and *Schoenoplectus pungens* occupying these lower salinity areas. In dried upper lagoon areas however, the upper marsh vegetation is of species group H (Table 2). The presence of *Agrostis stolonifera* in all upper zones reflects the heavy grazing of the lagoon edge. The marsh at Hoopers Inlet bears some resemblance to Kaikorai, but is intermediate between it and the true salt marshes. The mouth of this lagoon/estuary remains open for longer periods than at Kaikorai, allowing regular influx of tidal water.

Cultural modification has had its greatest impact in the uppermost zones and usually involves encroachment of land development on to the marsh. Before this modification however, these zones would have differed between marshes as a result of the different edaphic factors that governed the adjacent vegetation. Four kinds of vegetation occurred above Otago salt marsh in pre-European times; forest, sand dune, low dune ridge, and swamp.

The sand dunes have lost their native vegetation of the dominant sand-binder *Desmoschoenus spiralis*, mostly as a consequence of induced instability. Planting of the introduced sand binder *Ammophila arenaria* and of *Lupinus arboreus* has resulted in re-stabilisation of many dunes. Instability has had significant results for the salt marsh. For instance at Karitane North, where the dunes are still somewhat active, sand is blown on to the marsh and the upper zones have been all but lost.

Stable low dune ridges, indicative of former beach fronts, have often been modified for farmland. Those which have been oversown contain a mixture of pasture grasses and remnant native species such as *Lepidosperma australe*, *Poa cita*, and *Scirpoides nodosa*. Where conversion by ploughing has taken place, the upper marsh may be partly or totally replaced by species such as *Agrostis stolonifera*, *Festuca arundinacea* (as at Cherry Farm), and *Plantago coronopus*. Where poorly maintained, *Festuca arundinacea* or *Lupinus arboreus* tend to take over the dune ridges; the former where the ground is wetter. At Pleasant River, intensive grazing has resulted in the weedy *Plantago coronopus* and *Atriplex prostrata* invading down to the middle marsh.

Swamp vegetation has usually survived better. Species of the upper marsh (*Leptocarpus similis*, *Plagianthus divaricatus*) extend into swamps which are brackish, while others are true fresh water swamps with species of *Carex* and *Juncus*, as at Purakanui where there is a constant water supply from runoff.

Most of the forested areas have been cleared, but at Pounawea and Papatowai, native forest still exists. Here the short tree *Leptospermum scoparium* and *Phormium tenax* are important, with lesser amounts of the shrubs *Coprosma propinqua* and *C. rigida*. The introduced tree *Pinus radiata* has been planted on to some sand dunes that back salt marshes.

In general, the greatest proportion of salt marsh sites is of lower marsh with successively lesser amounts of middle and upper marshes (Table 4). Cultural modification and geomorphology result in the different proportions of various zones amongst the marshes. Rarity of upper marsh usually indicates loss of this zone through, for instance, sand dune encroachment as at Karitane North, or through farming as at Hoopers Inlet. At Pleasant River, the middle marsh abruptly abuts a hill, giving no opportunity for upper marsh formation. Table 4 shows that in some marshes, the proportion of lower marsh sites is very small (e.g., Pounawea, Aramoana Central, Papatowai). Often in such places the marsh edge erodes to form a steep bank to the sand flats below, as at Pounawea and Aramoana Central. Papatowai is a fluvial marsh situated well upstream. As the tidal effects decrease upstream, there is a replacement of the lower marsh by species normally found at higher elevations, such as *Leptocarpus similis*. This species eventually becomes the lower marsh equivalent.

The most spectacular salt marsh variation is at Purakanui where the sheltered end of the marsh is dominated by the tall rush *Juncus maritimus* var. *australiensis* while the exposed end is like other marshes. It is difficult to conceive why this species should dominate at one marsh and be absent from all others. Indeed, the *Juncus maritimus* marsh zones are the same as those well north of Otago, where it is the typical dominant of salt marshes (e.g., Davies 1931). Lack of ability to disperse would seem a surprising explanation for restricted distribution of a cosmopolitan salt marsh species. An ecological explanation of its restricted distribution within the salt marshes of Otago, may be indicated by the observations that after high tide, all water did not recede from the area at Purakanui dominated by this species. Therefore it may represent a large lower marsh ponding area in which salt water rather than fresh water, as in the rather distinct upper marsh depression, is trapped. Such edaphic conditions are unlikely to be unique to Purakanui, but may be so extremely rare in the other marshes, that a combination of biogeographic and edaphic factors may be the cause of its absence.

Table 4 Frequency of the three major salt marsh zones at each marsh except Kaikorai.

	Percentage of sites described as			Number of sites not included
	Lower	Middle	Upper	
Pleasant River	22	68	10	–
Karitane North	89	8	3	16
Karitane South	38	62	–	3
Cherry Farm North	64	24	12	23
Cherry Farm South	31	38	31	42
Purakanui	61	18	21	15
Aramoana East	62	29	9	6
Aramoana Central	16	22	62	17
Aramoana West	41	38	21	19
Hoopers Inlet	25	61	14	–
Pounawea	6	32	62	32
Papatowai	13	48	39	72
Overall	39	37	24	

General discussion

Much has been published concerning plant communities in salt marsh, varying from descriptions of individual marshes to regional and geographic comparisons. Many of these have attempted to elucidate, by various means, the factors causing differences in communities both within and between marshes. Most have not involved objective techniques of sampling and comparison. An overall assessment suggests that the factors which appear responsible for determining salt marsh vegetation patterns in Otago are similar to those found in other studies (e.g., Haeck et al. 1985), these being a marsh zonation in relation to tides, and aspects of soil moisture in relation to ponding. However, in regard to the first, vegetation studies alone are insufficient in separating dominant from secondary aspects, salinity and inundation being the most usually considered. The second factor is often expressed in different ways, including soil moisture, fresh water input, and upstream changes. This study has indicated that all are related and produce similar effects, hence their overall importance. A third factor sometimes considered of importance is disturbance (e.g., Ferrari et al. 1985). In Otago, the kind and extent of disturbance differs to produce communities which vary greatly both within and between marshes. Environmental measurements were made but are to be presented and correlated with these vegetation patterns in a separate publication.

In the salt marshes of Otago, there is a generalised pattern of vegetation zonation governed primarily by tidal features, and secondarily by features related to water ponding depressions, at one extreme, and sandy areas, at the other. As indicated in the ordinations, the primary tidal vegetation patterns are particularly consistent from marsh to marsh. The secondary moisture patterns in contrast are not so easily defined, and tend to differ somewhat between marshes. Further patterns are confined to one or a small number of marshes. The species that make up these salt marsh patterns are ubiquitous and fairly predictable as to their "place" in the salt marsh in regard to the important features. There are, however, at every marsh, peculiarities controlled by separate edaphic features or which are the products of cultural modification or perhaps biogeography. These add a great deal of variation to the basic pattern, and reflect local features of individual or a small group of marshes, whereas the general pattern tells us about the important ecological factors common to all or most.

Within an individual marsh however, these less important differences can be of real significance, for example in the dominance of *Juncus maritimus* marsh at Purakanui. This emphasises the need to examine a number of marshes within a region if the generalised features affecting all are to be discovered. The total site classification did, however, show one consequence of this approach. As the number of marshes is increased, these individual marsh differences will accumulate to such an extent to prevent the recognition of more generalised patterns.

Some workers have attempted to identify salt marsh communities applicable to whole regions, or even to several regions (Westhoff & Schouten 1979;

Lausi & Feoli 1979; Adam 1981). Their methodology has been based on Braun-Blanquet's, and so has their philosophy of finding consistent communities within a region. Our analyses show that this cannot necessarily be done. In a habitat such as a salt marsh, with the correlated and overwhelming effects of the tide and of salinity, some repeatable vegetation groupings are very likely to emerge. However, at a finer level, species are associating in different ways on different marshes, making impossible any generalisation to ideal Braun-Blanquet type communities. It is quite possible to find simple vegetation patterns within a single estuary (e.g., Congdon 1981). By limited and subjective sampling it is possible to find broad regional patterns (e.g., Lausi & Feoli 1979). It is often assumed that the patterns will hold under more intensive sampling (Moore et al. 1970) but from our results, when detailed examination is made of a number of marshes, the generalisation can break down.

The Otago salt marshes are therefore made up of typical, well distributed communities, and those which are atypical and restricted. No salt marsh however, was so "typical" that it contained no atypical communities. As one moves from salt marsh into lagoon, there is an increasing number of atypical communities, and a gradual disappearance of the typical kinds. The connection between the two is that in the salt marsh there are some characteristic lagoon communities, and in the lagoon, communities also found in salt marsh. This then produces a gradient of areas from maritime salt marsh to permanently closed lagoon.

The communities described here can be compared with other studies in New Zealand. Of the eight communities (one with four subdivisions) described by Ward (1967) on shingle beaches at Auckland, North Island, four are comparable with communities in Otago. The presence at Auckland of the grass *Stipa stipoides* (= *S. teretifolia*), a dominant in many of the communities, makes comparisons difficult. Equivalent and comparable communities are (Auckland : Otago) *Sarcocornia* (= *Salicornia*) family : 1_a; *Suaeda* family : 1_a; *Sarcocornia-Suaeda* colony : 1_a; and of the *Stipa* consocies, *Stipa/Plagianthus* : similar to 5_v; *Stipa/Festuca* : similar to 5_r. In the South Island, the communities described by Evans (1953) for the lagoonal Lake Ellesmere are mostly also found at Otago. At Lake Ellesmere, as well as salt marsh communities (e.g., *Juncus maritimus* associes : 6_z; *Selliera* associes : 2_c; *Sarcocornia/Puccinellia* associes : 2_h), there are communities found in ponding areas at Otago (e.g., *Mimulus/Lilaeopsis* associes : included in 4_q; *Schoenoplectus pungens* (= *Scirpus americanus*) associes : included in 4_o). The typical upper marsh fringe at Lake Ellesmere is *Poa cita* (= *P. caespitosa*) grassland, equivalent to community 5_v. Davies (1931) described communities at Nelson. Although difficult to equate with those in Otago, mainly because of the dominance of *Juncus maritimus* and descriptions lacking in detail, the following are recognised; *Sarcocornia* community : 1_a to 1_f; *Sarcocornia* meadow : 2_g to 2_i; *Leptospermum scoparium* scrub : 5_w; *Juncus maritimus/Leptocarpus* : 6_z. Paviour-Smith (1956) described salt meadow at Hoopers Inlet, Otago. This clearly is community 3_j, once the misidentification of *Schoenus nitens* for *Isolepis cernua* (= *Scirpus cernuus*) is corrected (from illustrations).

In his classification of world salt marsh communities based on the Montpellier system, Chapman (1974) included communities found in New Zealand. Many of the communities at Otago can be included within this scheme, although some are minor at Otago. A number of Chapman's communities are included within one Otago community, while others of Chapman's communities cover a number found at Otago. For instance (Chapman : Otago), Zosteretum novaezelandiae : included in 4_m, Salicornetum australi : included in 1_a; Spartinetum townsendii-anglici : included in 4_n; Festuceto-Agrostidetum stoloniferae : 5_r; Leptocarpetu-Plagianthetum : 3_j to 3_l; Juncetum maritimi : 6_z. We find neither good correspondence between Chapman's and our communities, nor communities to accommodate some of those found in Otago (e.g., *Selliera-Schoenus* marsh). Others are difficult to assign in the absence of detailed descriptions.

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