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The salt-marsh vegetation of New Zealand

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with 5 figures and 10 tables

Abstract. Observations of salt-marshes were undertaken throughout the three main islands of New Zealand. The proportion of introduced vascular plant species – either deliberately or accidentally introduced – within the salt-marshes is, at 49 %, slightly higher than it is for New Zealand's vegetation in general. The bulk of species come from the Holarctic which can be explained by the history of European settlement and trade links. Observations of species richness along 13 degrees of latitude reveal an increase of species from the subtropical north of New Zealand to the cool temperate south. Altogether some 74 species could be found within the salt-marshes of New Zealand seven of them being endemic.

As in other parts of the world, the most severe human impacts to salt-marshes in New Zealand are drainage, reclamation for industrial plants and agriculture. Furthermore, introduced species have not only altered the natural composition of salt-marsh communities, in some cases they have become established as solitary stands which cover sometimes large areas. Besides, the introduction of species have changed the topography of estuaries as well.

By applying the phytosociological method of Braun-Blanquet, 27 associations and rankless communities of salt-marsh vegetation were differentiated and are presented in constancy tables. Three associations (Leptinelletum dioicae, Plagianthetum divaricati, and Puccinellietum walkeri) are endemic to New Zealand.

The sigmasociological approach was also applied on the salt-marsh vegetation of New Zealand. As a result, the Juncetum kraussii Geosigmetum consisting of four vegetation complexes (sigmeta) was described.

Resemblance of the New Zealand salt-marshes to those of Australia was discussed.

Keywords: anthropochores, phytosociology, saline vegetation, species richness, vegetation complex.

1. Introduction

Less than two hundred years of mainly European settlement has altered the natural coastal vegetation of New Zealand considerably.

Due to the history of European settlement, as well as trade links to many parts of the world, the bulk of introduced plant species come from the Holarctic (comprising North-America, Eurasia as well as North-Africa) but species from South-Africa as well as the tropics can also be found in the salt-marsh vegetation. These observations match those found for Tasmania (ROZEFELDS et al. 1999).

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The aim of this paper is to describe the salt-marsh vegetation in New Zealand and to point out the kind of changes that have taken place so far in floristic, phytosociological, and sigmasociological respects.

The countrywide investigation of the salt-marsh vegetation of New Zealand has been fragmentary. Most of the studies have their focus on a certain area and are therefore locally restricted (Chapman & Ronaldson 1958, Partridge & Wilson 1988, 1989, Wardle 1977). The first large-scale phytosociological investigation of the New Zealand salt-marshes was presented by Thannheiser & Holland (1994).

2. Study area

2.1 Topography

The three main islands of New Zealand (North Island, South Island and Stewart Island), have a total coast length of about 10,000 km (McLean 1985). The three islands make up the biggest part of the archipelago, and extend across 1,500 km from 34°09' to 47°17' S and span approximately 13 degrees of latitude (Wardle 1991).

Salt-marshes are widespread in New Zealand (Fig.1). Soil profiles show characteristic lamination: clay and sand layers alternating with humus. The abundance of sandy material in New Zealand salt-marshes is a notable feature. Extensive areas with halophytic vegetation are predominantly found in bays, lagoons, and estuaries where ocean currents are low and accumulation of fine marine sediments can take place (McLean 1985). Salt-marshes are also found in the shelter of small islands and at river mouths, where the coastline offers the necessary conditions for extensive areas of siltation. Small-sized salt-marshes are found in dune slacks as well (Wardle 1991).

In the north, west and south of the South Island there are mud deposits with salt meadows along stretches of flat shore interrupted by rock outcrops or bare sandy and shingle beaches. In the southwest of the North Island a diverse halophytic vegetation has developed close to river mouths. North of 38° S there are extensive salt-marshes, the spread of which is limited by a mangrove girdle.

The tides are in all parts of the three main islands semi-diurnal (12-hour cycle), the mean tidal range is about 1–2 m at the predominant coastal areas. In sheltered parts, as at the Firth of Thames, west of Coromandel Peninsula on the North Island, as well as at Tasman Bay and Golden Bay in the north of the South Island, the tidal range rises to up to 2–3 m. In the south of the North Island the tidal range is less than 1 m (McLean 1985).

2.2 Climate

The climatic conditions of New Zealand differ very much across latitudes and climate zones. The North Island belongs to the Warm Temperate Sub

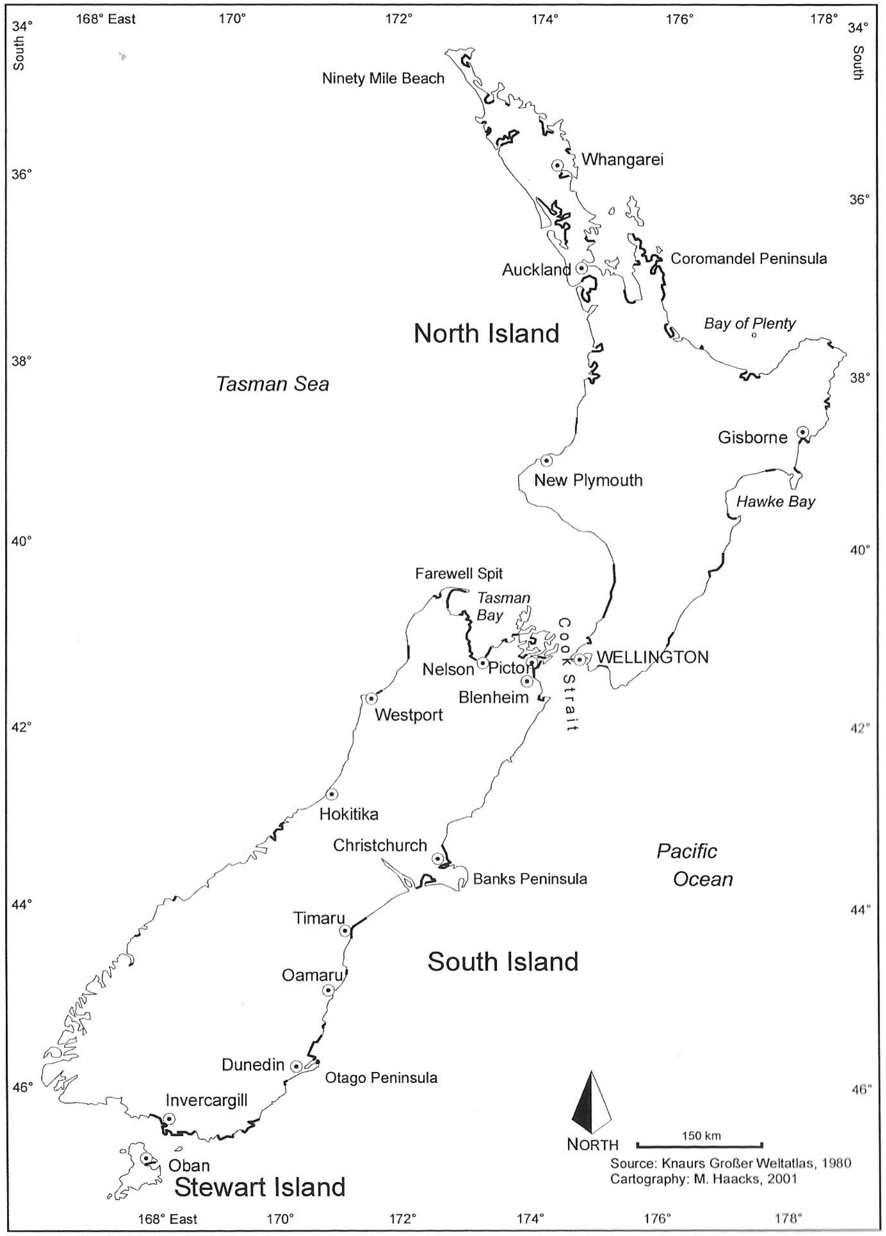

Fig. 1. Generalised map showing the main salt-marsh areas in New Zealand (bold line: salt-marshes, thin line: remaining coastline).

tropical Zone, whereas the South Island belongs to the Cool Temperate Zone (following TROLL & PAFFEN 1966). The climatic variations are reflected by the different occurrence of certain plant species and plant communities (COCKAYNE 1958).

The influence of latitudes via differences in solar energy is remarkable. During summer the solar energy in Auckland in the north corresponds to that in Invercargill in the south. Differences are only related to heterogeneous distribution of clouds. But in the winter months the solar energy in Invercargill is only 50 % of the energy in Auckland (COULTER 1975). The shielding of subtropical radiation by clouds leads to lower mean monthly temperatures compared to radiationally similar areas. As an example, the central part of New Zealand (41°–42° S) corresponds in terms of radiation to South Europe in the Northern Hemisphere, but in terms of temperature it corresponds to the cooler Central Europe.

In connection with this, the distributional limit of the frost-intolerant mangrove (*Avicennia marina*) is of special interest. The limit coincides with the 13°C isotherm and more or less with the 38° latitude. In a worldwide view, this is the southernmost limit for a mangrove species, obviously controlled by the influence of warm ocean currents (SAENGER et al. 1977).

The climate of New Zealand is characterised by heavy rainfalls (WEISCHET 1996), which causes a large amount of surface-flow in the salt-marshes. The boundary between saline and non-saline vegetation is therefore much more diffuse than it is in salt-marshes of the Northern Hemisphere (THANNHEISER & HOLLAND 1994).

3. Methods

3.1 Phytosociology and sigmasociology

Following the floristic-sociological approach of BRAUN-BLANQUET (1964), 724 relevés in 180 salt-marshes along the coastline of the three main islands were sampled and grouped into vegetation units. The relevés were sampled in homogenous stands and had an average size of 9 m². Each community is represented by a constancy table. The taxa are listed with their constancy class in each community. Constancy class + means present in less than 5 % of the records, I means present in less than 20 %, II present in 20–40 %, III present in 40–60 %, IV present in 60–80 % and V in more than 80 %. A Spearman rank-correlation test was performed to show correlations between native and introduced plant species over the different degrees of latitude.

The salt-marsh vegetation was additionally assessed by means of the sigmasociological method according to GÉHU (1991) und SCHWABE (1997). The size of the single relevés varied from 5,000 to 20,000 m², depending on the size of the investigated salt-marsh area, and were of square or rectangular shape. The cover of the phytocoenoses in the relevés were estimated using the Braun-Blanquet scale. The compilation was done by summarizing the relevés and developing a constancy table with identical constancy classes as used for the communities. Denomination of the vegetation complexes is based on the characterizing communities.

In a further step the vegetaion complexes identified in the salt-marshes, as a coastal physiotope, were unified in one geosigmetum, following GÉHU & RIVAS-MARTÍNEZ (1981). The chosen geosigma relevés were evenly distributed in the salt-marsh area and the including vegetation units (associations, communities and stands) were taken.

In the present study 131 sigma relevés and 111 geosigma relevés were sampled. This paper is based upon investigations during the years 1992, 1994, 1999, and 2000, carried out by the authors.

3.2 Nomenclature

The plant species were determined by using the five volumes of "Flora of New Zealand" (ALLAN 1982, EDGAR & CONNOR 2000, MOORE & EDGAR 1976, HEALY & EDGAR 1980 and WEBB et al. 1988). In the case of *Avicennia resinifera*, *Cotula dioica* and *Leptocarpus similis* we follow the revisions by DUKE (1991), LLOYD & WEBB (1987) and BRIGGS & JOHNSON (1998) who suggest the new names *Avicennia marina*, *Leptinella dioica* and *Apodasmia similis*, respectively.

4. Floristic aspects

The New Zealand salt-marsh vegetation consist of some 74 species of vascular plants. Seven of them (*Carex litorosa*, *Lachnagrostis littoralis*, *Leptinella dioica*, *Apodasmia similis*, *Plagianthus divaricatus*, *Poa cita*, and *Puccinellia walkeri*) are endemic to the New Zealand region.

WARDLE (1991) noted that almost half of the higher plant species in New Zealand are not native (Tab. 1). In salt-marshes of New Zealand the proportion of introduced plant species is with 49 % somewhat higher as shown in Table 1. This applies to an assessment of all the three islands together. A separate examination of North and South Island shows that the proportion of introduced plants sinks under the values given by WARDLE (1991) and can be explained by the fact that many introduced plant species have become established only locally. This corresponds to ESLER (1991), who emphasized that intertidal communities have a degree of immunity from invaders because of the few introduced species able to occupy this habitat.

The introduction of plants and animals to New Zealand began with the Maori (approx. AD 900), but was accelerated by the European settlers. The presence of introduced species leads to a series of communities comprising a mixture of indigenous and adventive elements (HEALY 1973). This applies for example to *Parapholis incurva* which cannot be seen as posing a threat to native communities (BRIDGEWATER & KAESHAGEN 1979). But also stands consisting of only introduced plant species have become established. This is particular the case for monospecific stands of cord grasses (*Spartina anglica* and *S. alterniflora*). Both species were used in foreshore protection

Table 1. Proportion of introduced and native land plants in salt-marshes in the two main islands of New Zealand compared to Wardle (1991)

	Wardle		salt-marshes					
	New Zealand absolute	%	North Island absolute	%	South Island absolute	%	New Zealand absolute	%
introduced species	ca. 1860	45	25	43	22	42	36	49
native species	ca. 2300	55	33	57	31	58	38	51
total	ca. 4160	100	58	100	53	100	74	100

and the reclamation of estuarine areas. The earliest planting in New Zealand was in 1913 at Foxton, in the North Island (Lee & Partridge 1983). The reason for such plantings were the higher sedimentation rates caused by *Spartina* compared with native salt-marshes or mangrove swamps. This leads to a change of the original morphology of the estuary and causes a loss of tidal flat areas as it is pointed out for the Aramoana estuary, Otago (Partridge & Wilson 1975). As a consequence, Esler (1991) regards *Spartina anglica* as the greatest threat for New Zealand's salt-marshes.

Due to its extreme flooding tolerance, Adam (1981) suggested a probable threat of invasion to the uppermost part of eel-grass beds by *Spartina*, but the species spreads also more quickly even through elevated regions of salt-marshes and causes a shift in salt-marsh zonation.

About 88 % of all the introduced species come from the Holarctic (comprising North-America, Eurasia and North-Africa) the remainder (each about 6 %) from the tropics and South-Africa. The introduction of plant species has changed the floristic composition and physiognomy of New Zealand's salt-marshes considerably (Figs. 2 and 3).

Apart from drainage and reclamation for housing and industrial uses, grazing has the most severe impact on the native salt-marsh vegetation. New Zealand's flora evolved in the absence of browsing mammals, so that many plant species proved to be palatable and susceptible for browsing (Johnson 1993). The spread of certain plant species and stands are enhanced by trampling. This is the case for *Cotula coronopifolia*, as noted by Wardle (1977). Other species such as *Samolus repens* and *Selliera radicans* can cope with the impact of grazing animals. On the other hand, species like *Sarcocornia quinqueflora*, *Suaeda novae-zelandiae*, *Puccinellia* spp., and *Mimulus repens* can become severely damaged by nibbling and trampling and are hardly found in intensely grazed salt-marshes.

The comparison between salt-marshes consisting of native and introduced plant species reveals a much higher proportion of Asteraceae, Juncaceae, and Poaceae within salt-marshes dominated by introduced plant species. Five families (Fabaceae, Gentianaceae, Iridaceae, Plantaginaceae, and Polygonaceae) do not occur in salt-marshes free from introduced species. In salt-marshes composed of native species there is a higher proportion of Apiaceae, Chenopodiaceae and Cyperaceae as well as other 14 families characteristic of these salt-marshes (Tab. 2). The lack of dominance of

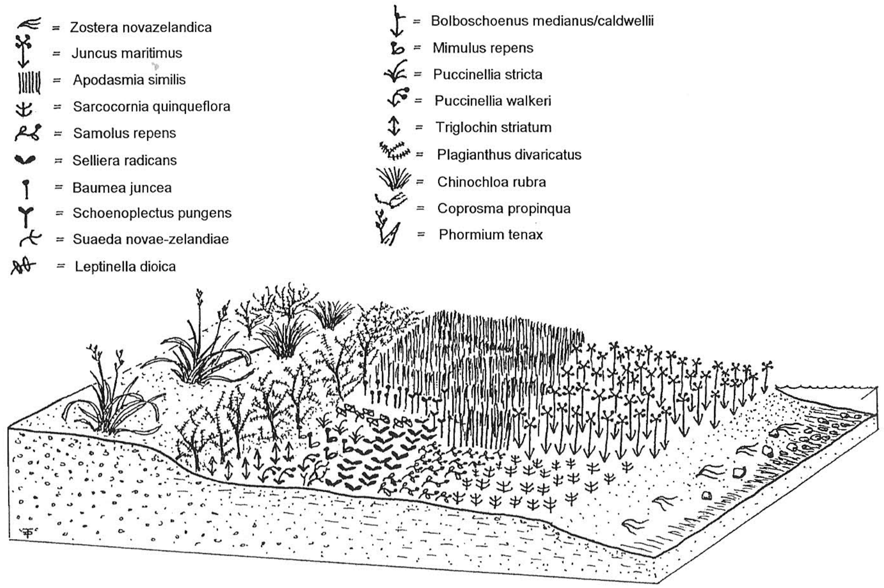

Fig. 2. Idealised block profile with vegetation spread in salt-marshes of New Zealand at the beginning of the 19th century.

grasses both in terms of their proportion as well as in terms of their cover prevents a meadow-like character of the saline vegetation – a typical view of many Northern Hemisphere salt-marshes. The same applies also to the salt-marshes of Australia (Adam 1981, Haacks & Thannheiser 2000, Thannheiser 2001).

4.1 Species richness

Along the 13 degrees of latitude spanned by New Zealand the species richness of vascular plant species was investigated. For that purpose plant species of salt-marshes recorded in the relevés, were assigned to the single latitudes, separated in native and introduced species. Due to their specialised character, the number of species within azonal communities is usually smaller than in zonal communities (Grabherr et al. 2000).

Such statements are available for salt-marshes of Australia, which in general resemble very much the salt-marshes of New Zealand. According to Saenger et al. (1977) the number of species within the Australian salt-marshes increases from the equator to the south. That applies also to salt-marshes in New Zealand, where an increase of species richness from north to south is evident. The reason for that is that in the north of New Zealand the area of salt-marshes is limited by mangroves. Furthermore, some areas of salt-marsh towards the north comprise species-poor *Juncus maritimus*

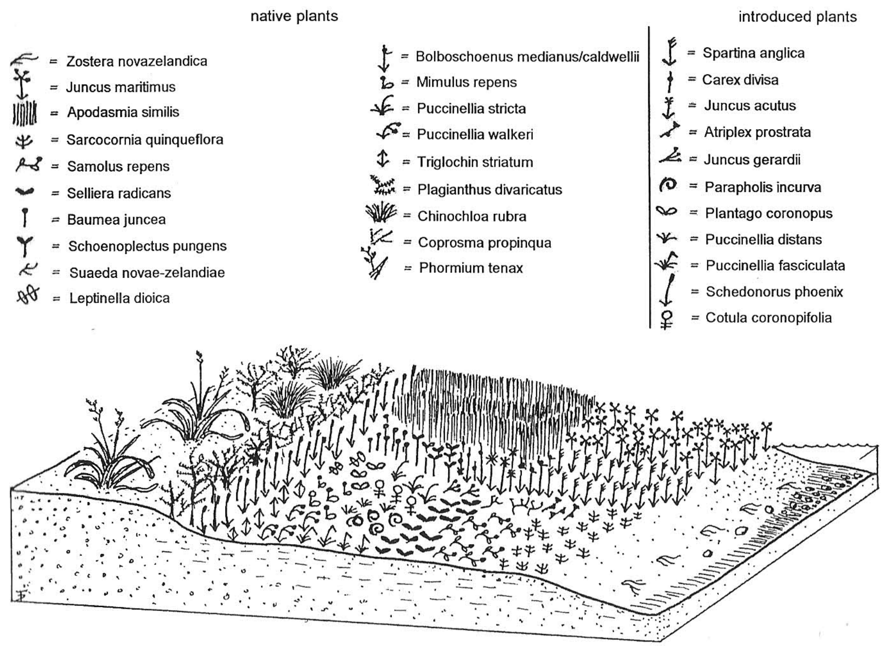

Fig. 3. Idealised block profile with vegetation spread in salt-marshes of New Zealand at the end of the 20th century.

Table 2. Comparison of the family composition between native and introduced salt-marsh species in New Zealand.

family	native species	introduced species
Apiaceae	2	1
Asteraceae	1	3
Caryophyllaceae	1	1
Chenopodiaceae	2	1
Cyperaceae	11	1
Juncaceae	1	4
Poaceae	5	19
Polygonaceae	0	2
Scrophulariaceae	2	0
other families (only one record)	13	4

and *Apodasmia similis* stands, respectively. That is the case for both native and introduced species, in which the former outnumbers the latter (Fig. 4). A Spearman rank-correlation test revealed a highly significant correlation between the number of native plant species and introduced plant species in the salt-marshes ($r_s = 0.962$, $n = 13$, $p_{two\text{-}tailed} = 0.001$). That means salt-

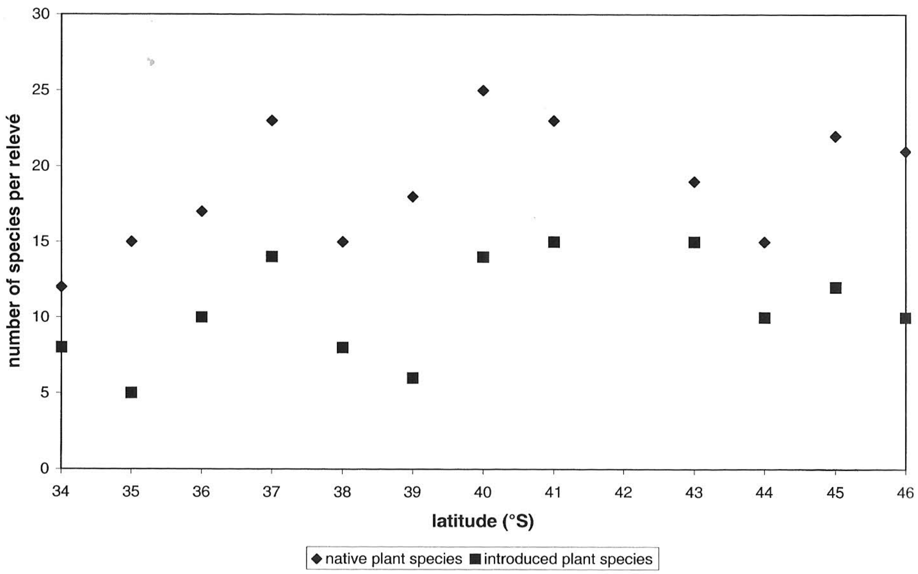

Fig. 4. Number of species along the degrees of latitude in the salt-marshes of New Zealand.

marshes with a high or low species number showed them for both native and introduced species.

5. Plant communities

27 vegetation units were distinguished of which 18 were considered as associations. They are depicted in constancy tables (Tabs. 3–5).

In spite of the generally low species richness of New Zealand's salt-marshes the high number of vegetation numbers is explained by the fact that stands consist mainly of one or few species and are distributed mosaic-like.

A zonation as it is known from salt-marshes of the Wadden Sea (Dijkema 1983), hardly applies to salt-marshes of New Zealand. On the tidal flats of bays and lagoons the small scale differentiation of low stands alternates with high stands which is a notable characteristic. Only at the margins of salt-marshes where an elevation and salinity gradient become apparent, is a zonation in lower, middle, and upper salt-marsh recognizable as noted by Wardle (1991).

The communities already described by Chapman & Ronaldson (1958) are classified with regard to their ecological requirements following the Tansley-Clements School and are not described following Braun-Blanquet (1964). In the works by Doak (1931), Partridge & Wilson (1988, 1989) and Wardle (1977, 1991) stands are named – partly after having performed a cluster analysis – by the one or two dominating species but not according to the International Code of Phytosociological Nomenclature (Weber et al. 2000).

In the following, a short description of characteristic plant communities of the New Zealand salt-marshes is given. A detailed revision of the salt-marsh communities of New Zealand is found in Haacks (2003).

Zosteretum novazelandicae

The eel-grass, *Zostera novazelandica*, is confined to the sublittoral and eulittoral zone. *Zostera novazelandica* grows on both muddy and slightly sandy substrates. It is not found on substrates consisting predominantly of sand. The species is regularly found along the coastline, however, it is dependent on bays with an accumulation of fine marine sediments and small ocean current velocity. Monospecific stands of this species resemble closely related associations of the Northern Hemisphere and were described by Partridge & Wilson (1988) as the Zosteretum novazelandicae but were not proofed by a phytosociological table.

Ruppietum megacarpae

In small lagoons behind spits *Ruppia megacarpa* is found. This community is also monospecific and can be regarded as an association Ruppietum megacarpae Haacks 2003, because it corresponds with related *Ruppia* associations of the Holarctic.

Juncetum kraussii and Apodasmia similis-community

The outer edge of the salt-marshes is characterised by high growing rushes, restiads as well as sedges and grasses. The big harbours and inlets of the North Island are dominated by extensive stands of *Juncus maritimus* (syn. *J. kraussii*) and *Apodasmia similis* in particular. *Juncus* normally represents the frontal fringe and is followed by *Apodasmia*, but in some places the order is reversed (Chapman 1974). Furthermore, both species can grow together and form mixed stands (Chapman & Ronaldson 1958).

Apodasmia similis grows predominantly on clayish substrates, whereas *Juncus maritimus* prefers coarse substrate, and shows greater salt tolerance than *Apodasmia similis*.

The stands dominated by *Juncus maritimus* were classified as the Juncetum kraussii Bridgewater 1982. The restiad *Apodasmia similis* is very salt tolerant, but no definite halophyte. Important for its thriving is a variable water table which is characteristic for tidal areas. Large stands of *Apodasmia similis* are also found in dune slacks, in freshwater marshes and at lakes edges as well as saline habitats further inland (Moore & Edgar 1976, Wilson 1994). For the time being phytosociological data of stands of this plant species are only available for salt-marshes but not for the other habitats. Due to the insufficient data, the stands of *Apodasmia similis* remain rankless.

Spartinetum anglicae

A further plant of this zone is the cord grass *Spartina anglica*, of which monospecific stands occur on both sandy and clayish substrate. It seems appropriate to regard the unit as the Spartinetum anglicae Corrillon 1953.

Schoenoplectetum pungentis

At the edges of the tidal flat zone grow – usually in a girdle-like arrangement – stands of the sedge *Schoenoplectus pungens*. In contrast to Chapman & Ronaldson (1958) who combined stands of this species together with *Bolboschoenus* spp. into the *Scirpus* association, Wardle (1991) mentioned monospecific stands of *Schoenoplectus pungens*. Thannheiser & Holland (1994) regarded such stands, due to insufficient data, not as an association. In the framework of further investigations in the years 1999 and 2000 the predominantly monospecific stands can be regarded as Schoenoplectetum pungentis Haacks 2003.

Sarcocornietum quinqueflorae and Samoletum repentis

The perennial glasswort *Sarcocornia quinqueflora* and the Primulaceae *Samolus repens* are of importance as pioneers. Both species form by their stolons dense carpets. The stands are either composed of one or only a few species. The stands of glasswort were classified as the Salicornietum quinqueflorae by Bridgewater (1982), whereas stands of the *Samolus repens* were classified as the *Samolus repens*-community by Adam et al. (1988). Based upon recent phytosociological studies it seems reasonable to classify such stands as Samoletum repentis Haacks 2003. According to Chapman & Ronaldson (1958) the occurrence of the Sarcocornietum and the Samoletum, respectively, is substrate dependent; better drainage of coarse material favours the Samoletum. According to our investigations both phytocoenoses occur on both pure sandy and clayish substrates. The Samoletum repentis prefers finer substrates.

Communities of the middle marsh

The associations mentioned above are followed by the middle-marsh communities according to Partridge & Wilson (1975) which belong also to the low salt-marsh. Extensive stands dominated by *Selliera radicans* were described as the *Selliera*-community by Thannheiser (1994) and as the Sellieretum radicantis by Haacks (2003). The Leptinelletum dioicae Haacks 2003 is found relatively seldom. This endemic association is characterised by *Leptinella dioica* (syn. *Cotula dioica*) as well as one or two other species, and its stands cover only small areas. On the South Island that marsh is also dominated by stands of different salt grasses. The Puccinellietum strictae as well as the *Puccinellia fasciculata*-community were described by THANNHEISER (1994). In the salt-marshes of Otago (south-east coast of the South Island) and in those of Stewart Island species-poor stands of *Puccinellia walkeri* are found. These were described as Puccinellietum walkeri by HAACKS (2003).

Transition to the non-saline vegetation

The salt-marsh is demarcated phytosociologically on the North Island by four, on the South Island by three associations.

Countrywide, the limit of the saline vegetation is marked by a dense girdle of the endemic *Plagianthus divaricatus*, a shrub 1–2 m high. Such stands are classified as the Plagianthetum divaricati Haacks 2003 and are usually found on embankments of tidal river mouths. Stands of the introduced *Plantago coronopus* form, at the transition to the non-saline vegetation, a *Plantago coronopus*-community. This community is also distributed countrywide.

Stands of the tussock grass *Austrostipa stipoides* (syn. *Stipa stipoides*) were described as the Stipetum stipoides by BRIDGEWATER (1982). The Stipetum is characteristic for the North Island; on the South Island the grass is found only in the Nelson region (EDGAR & CONNOR 2000).

Additionally, stands of *Baumea juncea* are found in the transition to the non-saline vegetation. Such stands were regarded as the *Baumea juncea*-community by ADAM et al. (1988). In New Zealand the distribution is restricted to the North Island.

6. Vegetation complexes

6.1 Sigmeta of the salt-marshes

The sigmasociological approach provides a spatial view of the vegetation because the vegetation complexes are regarded as spatial units. The specifity of vegetation complexes in large-scale assessments is not sufficiently well depicted in medium-scale maps (SCHWABE 1997). The vegetation units (associations, communities, stands) were unified to sigmeta (vegetation complexes) based on their physiognomy and ecology. Vegetation complexes can only be defined by clearly differentiated phytocoenoses and combined aspects of biology and geography (SCHWABE 1997). Furthermore, the rankless vegetation units (communities, sub-communities, stands) are better represented by applying the sigmasociological approach than by the phytosociological approach following BRAUN-BLANQUET.

The whole inventory of associations and communities found in salt-marshes of New Zealand was assessed sigmasociologically. Four sigmeta (Zosteretum novazelandicae Sigmetum, Avicennietum marinae Sigmetum, Sarcocornietum quinqueflorae Sigmetum, and Juncetum kraussii Sigmetum) were distinguished. Because of the lack of extensive salt-marsh areas on Stewart Island, only salt-marshes on North and South Island were investigated.

Table 3. Constancy table of low salt-marsh communities dominated by native species.

	1 Zosteretum novazelandicae	*2* Mimuletum repentis	*3* Sarcocornietum quinqueflorae	*4* Samoletum repentis	*5* Puccinellietum strictae	*6* Puccinellietum walkeri	*7* Triglochinetum striati	*8* Leptinelletum dioicae	*9* Sellieretum radicantis	*10* Lilaeopsis novae-zelandiae-comm
Number of relevés	16	16	107	76	5	5	37	6	68	7
Average of plant species	1	3	3	3	4	2	3	4	5	4
Characteristic species of associations and communities										
Zostera novazelandica	V$^{4-5}$	.	.	.	.	.	.	.	.	.
Mimulus repens	.	V$^{3-5}$	+$^{2a-3}$	+^{2a}	.	II^{1-2a}	+$^{+}$	.	.	I^{2b}
Sarcocornia quinqueflora	.	I^{2a-3}	V$^{3-5}$	II^{+-3}	V$^{1-3}$	II^{1-2a}	I^{1-2a}	.	III^{+-3}	.
Samolus repens	.	I^{1}	II^{+-3}	V$^{3-5}$	.	.	I^{1-2b}	III$^{1-3}$	IV^{+-3}	II^{1-2m}
Puccinellia stricta	.	.	I$^{1-3}$	I^{r-1}	V$^{3-5}$	.	.	.	.	.
Puccinellia walkeri	.	.	.	.	.	V$^{4-5}$	.	.	.	.
Triglochin striatum	.	I^{2m}	I^{1-2b}	I^{1-2b}	I^{2m}	.	V^{2m-5}	I^{1}	III^{+-2b}	I^{2m}
Leptinella dioica	.	.	.	+^{1}	.	.	.	V$^{3-5}$	+$^{+-2a}$	I^{2a}
Selliera radicans	.	I^{1}	I^{1-2b}	II$^{1-3}$	III^{2m-2a}	.	+^{1}	I^{2m}	V$^{3-5}$	.
Lilaeopsis novaezelandica	.	I^{2m-2b}	.	.	.	.	I^{1-2b}	II^{2m}	+$^{2a-2m}$	V^{2b-5}
Accompaning species										
Avicennia marina	I^{1}	.	I^{r-2a}	I^{+-2a}	.	.	I^{1}	.	I^{+-2a}	.
Isolepis cernua	.	I^{2m-2a}	+ 1	II^{1-2b}	.	.	III$^{1-5}$	IV^{2m-3}	I^{1-2b}	III^{2m-2a}
Cotula coronopifolia	.	III^{+-1}	I^{+-2a}	+$^{+}$	.	.	III^{+-2b}	I^{2a}	+$^{+-1}$	II^{+-1}
Puccinellia fasciculata	.	I^{1-2m}	I^{1-2b}	+^{2a}	.	.	+ 2a	II^{1}	I^{+-2m}	.
Schoenoplectus pungens	.	I^{1-2a}	+^{1}	I^{2m-2b}	.	.	I^{+-2b}	.	+^{2m}	.
Atriplex prostrata	.	I^{+-2b}	I^{+-2b}	+$^{+}$	III^{+-2m}	.	.	.	I^{+-2a}	I^{2b}
Juncus maritimus	.	.	I^{+-2b}	I^{1-2b}	.	.	II^{+-2b}	.	II^{+-2b}	.
Apodasmia similis	.	.	+^{1}	+^{2m}	.	.	I^{+}	.	I^{+-2m}	.
and others										

Both on the North Island and on the South Island the salt-marsh is preceded by the Zosteretum novazelandicae Sigmetum (Tab. 6). This vegetation complex shows only scattered phytocoenoses of typical salt-marshes.

The Avicennietum marinae Sigmetum is found only on the North Island as a girdle in front of the salt-marsh vegetation but is partly meshed with it (Tab. 7). The Avicennietum marinae Sigmetum is geographically restricted to the 38° latitude due to the susceptibility of the mangrove (*Avicennia marina*) to frost. However, that applies only to the east coast but on the west coast the limit of distribution lies somewhat north and does not reach Kawhia and Aotea Harbour at latitude 38° (GODLEY 1975).

The salt-marsh vegetation of New Zealand was differentiated into the two vegetation complexes, such as the Sarcocornietum quinqueflorae Sigmetum and the Juncetum kraussii Sigmetum according to the dominance of the name-giving communities (Tables 8 and 9). Particularly extens-

Table 4. Constancy table of low salt-marsh communities dominated by introduced species.

	1 Paspalum vaginatum-community	2 Cotula coronopifolia-community	3 Puccinellia fasciculata-community	4 Juncus gerardii-community	5 Plantago coronopus-community	6 Carex divisa-community
Number of relevés	12	7	10	5	14	5
Average of plant species	3	4	4	2	5	3
Characteristic species of associations and communities						
Paspalum vaginatum	V^{3-5}	.	.	.	.	.
Cotula coronopifolia	.	V^{3-5}	I^{1}	.	II^{+-2a}	.
Puccinellia fasciculata	.	.	V^{3-5}	.	I^{2m}	.
Juncus gerardii	.	.	I^{1}	V^{5}	.	.
Plantago coronopus	.	.	I^{+}	.	V^{4-5}	II^{2a-3}
Carex divisa	.	.	.	.	.	V^{3-5}
Accompaning species						
Samolus repens	II^{+-2b}	III^{1-2a}	I^{2a}	II^{+-1}	III^{1-2b}	II^{2a}
Triglochin striatum	I^{2m}	IV^{1-2b}	.	.	.	.
Sarcocornia quinqueflora	II^{1-2b}	III^{1-2a}	III^{1-3}	.	I^{2a}	I^{2a}
Juncus maritimus	I^{+}	I^{1}	.	II^{2a}	II^{+-2a}	.
Atriplex prostrata	II^{+-1}	.	III^{+-2m}	I^{2m}	I^{2m}	I^{1}
Selliera radicans	I^{2a}	.	II^{1-2a}	I^{2b}	III^{1-2b}	.
Avicennia marina	II^{+-2a}	.	.	.	.	.
Isolepis cernua	.	III^{2a-2b}	I^{2a}	.	I^{1-2m}	.
Schoenoplectus pungens	.	III^{1-2ba}	.	.	I^{2m}	.
and others						

ive stands of *Juncus maritimus* and *Apodasmia similis* grow in the muddy inlets and harbours, although representatives of low growing salt-marsh communities are also found. The latter dominate in areas with sandy substrate. North and South Island each show typical units within the vegetation complexes and therefore a further structuring in subsigmeta was carried out.

The Sarcocornietum quinqueflorae Sigmetum (Tab. 8) is characterised by units such as the Sarcocornietum quinqueflorae, the Samoletum repentis, the *Plantago coronopus*-community, and the Sellieretum repentis. The higher number of vegetation units is notable for the South Island.

The Juncetum kraussii Sigmetum (Tab. 9) is characterized by the Juncetum kraussii and *Apodasmia similis*-community found on both North and South Island. On the North Island in particular, the Juncetum

Table 5. Constancy table of high salt-marsh communities.

	1 Spartinetum anglicae	2 Spartina alterniflora-community	3 Schoenoplectetum pungentis	4 Juncetum kraussii	5 Apodasmia similis-community	6 Ruppietum megacarpae	7 Bolboschoenetum caldwellii	8 Bolboschoenus medianus-community	9 Plagianthetum divaricati	10 Stipetum stipoides	11 Baumea juncea-community
Number of relevés	9	5	38	95	102	13	6	11	35	8	6
Average of plant species	1	1	3	2	2	1	2	3	5	6	3
Characteristic species of associations and communities											
Spartina anglica	V^{4-5}	.	$+^{1}$	$+^{2a}$	$+^{+}$	.	.	.	.	.	.
Spartina alterniflora	.	V^{3-5}	.	.	.	.	.	.	.	.	.
Schoenoplectus pungens	.	.	V^{3-5}	$+^{2m-2a}$	$+^{+-2m}$	I^{1}	I^{2m}	I^{2m}	$+^{1}$	.	.
Juncus maritimus	.	.	I^{1}	V^{3-5}	II^{+-3}	.	I^{1}	I^{1}	III^{1-3}	IV^{2m-2b}	III^{1-2a}
Leptocarpus similis	.	.	.	II^{1-3}	V^{3-5}	.	.	I^{2a}	III^{2a-3}	II^{1-2b}	II^{2m-2a}
Ruppia megacarpa	.	.	$+^{2a}$	.	.	V^{2b-5}	.	.	.	.	.
Bolboschoenus caldwellii	.	.	.	.	$+^{1}$	.	V^{4-5}	.	.	.	.
Bolboschoenus medianus	.	.	.	$+^{+-2a}$	$+^{1}$	.	.	V^{3-5}	I^{1-2b}	.	.
Plagianthus divaricatus	.	.	.	I^{+-3}	I^{+-3}	.	.	.	V^{3-5}	III^{1-2b}	I^{2b}
Austrostipa stipoides	.	.	.	.	.	.	.	.	$+^{+}$	V^{3-5}	.
Baumea juncea	.	.	$+^{2m}$	$+^{+-2m}$	.	.	.	I^{2m}	I^{1-2a}	I^{2a}	V^{4-5}
Accompaning species											
Puccinellia fasciculata	I^{2a}	.	.	.	.	.	.	.	.	.	.
Triglochin striatum	.	.	I^{2m-2b}	I^{2m-2a}	$+^{+-2m}$	.	II^{2m-2b}	II^{2m-2b}	I^{2m-2a}	.	.
Samolus repens	.	.	I^{+-2b}	II^{1-2a}	I^{1-2b}	.	I^{1}	.	I^{1}	II^{2m-2a}	.
Cotula coronopifolia	.	.	I^{+-1}	$+^{1-2m}$	$+^{1}$	.	.	I^{2m-2a}	$+^{1}$	.	.
Avicennia marina	.	.	I^{+}	I^{+-2a}	I^{+-2a}	.	.	.	$+^{1}$	II^{1}	.
Sarcocornia quinqueflora	.	.	I^{1-2a}	I^{+-2b}	$+^{1-3}$	.	.	I^{1}	I^{1-2a}	II^{2m-2a}	I^{+}
Selliera radicans	.	.	I^{1-2a}	I^{1-2b}	I^{+-3}	.	.	I^{1}	I^{1-2a}	II^{1-2a}	.
Isolepis cernua	.	.	$+^{+}$	$+^{1-2m}$	$+^{2m}$	.	.	I^{2m-2a}	.	.	.
and others											

Table 6. Constancy table of the Zosteretum novazelandicae Sigmetum.

Number of Sigma relevés	9
Average number of vegetation units	2
Zosteretum novazelandicae	$V^{(4-5)}$
Juncetum kraussii	$III^{(1-2)}$
Schoenoplectetum pungentis	$III^{(1-2)}$
Apodasmia similis-community	$I^{(1)}$

kraussii Sigmetum is very frequent. *Juncus maritimus* is distributed through the whole North Island whereas its limit of distribution on the South Island is around Okarito on the west coast and around Banks Peninsula on the east coast, respectively (Godley 1975). In addition, there is an extensive area dominated by *Juncus maritimus* in the Purakanui Estuary, north of Dunedin (Partridge & Wilson 1988).

Table 7. Constancy table of the Avicennietum marinae Sigmetum.

Number of Sigma relevés	10
Average number of vegetation units	4
Avicennietum marinae	V $^{(4)}$
Juncetum kraussii	III $^{(1-2)}$
Apodasmia similis-community	III $^{(+-2)}$
Sarcocornietum quinqueflorae	II $^{(+-2)}$
Paspalum vaginatum-community	II $^{(+-2)}$
Plagianthetum divaricati	II $^{(+-1)}$
Zosteretum novazelandicae	I $^{(+-2)}$
Samoletum repentis	I $^{(+-1)}$
Sellieretum radicantis	+ $^{(+)}$
Atriplex prostrata-community	+ $^{(+)}$
Schedonorus phoenix-community	+ $^{(+)}$

6.2 Juncetum kraussii geosigmetum

The vegetation complexes described in chapter 6.1 are unified to form a geosigmetum of the halosere which occur repeatedly over extensive areas in more or less the same combination (Tab. 10). For example, the xerosere of the French dune coast was sigmasociologically assessed by GÉHU (1977, 1991).

The salt-marsh geosigmetum on the North and South Island can be divided in four and three vegetation complexes, respectively. As shown by Table 9, the Zosteretum novazelandicae Sigmetum and the Avicennietum marinae Sigmetum are only sparsely distributed.

The Sarcocornietum quinqueflorae Sigmetum is in New Zealand not as common as the Juncetum kraussii Sigmetum, but the former has its main distribution on the South Island. Distinctive differences of the Sarcocornietum quinqueflorae Sigmetum between North and South Island justify the formation of two sub-sigmeta, namely the North Island Subsigmetum and the South Island Subsigmetum, respectively. The South Island Subsigmetum is characterised by four units, which consist predominantly of introduced species, which have become established. The communities in question are those dominated by *Festuca rubra*, *Juncus gerardii*, *Puccinellia fasciculata*, and *Spergularia marina*.

The Juncetum kraussii Sigmetum is very similar on both Islands. The *Bolboschoenus medianus*-community, the *Spartina alterniflora*-community, the *Baumea juncea*-community as well as the *Juncus acutus*-community were only found on the North Island.

Connected to the salt-marsh sigmeta is the transition zone to the non-saline hinterland (Fig. 5). However, the limit of the upper salt-marsh is difficult to define as pointed out also for Australian salt-marshes by ADAM (1981). In most cases a definite topographic boundary is missing and the transition zone is determined by bordering vegetation and land-use (CHAPMANN 1974). Adjacent to salt-marsh vegetation *Leptospermum scoparium* woodlands are sometimes found or salt-marshes changes gradually to a reed zone with *Typha orientalis*. Most frequently, the adjacent hinterland was cleared and subsequently grazed.

Table 8. Constancy table of the Sarcocornietum quinqueflorae Sigmetum.

	North Island	South Island
Number of Sigma relevés	9	16
Average number of vegetation units	6	7
Sarcocornietum quinqueflorae	V $^{(+-5)}$	V $^{(1-4)}$
Juncetum krausii	V $^{(1-2)}$	III $^{(+-3)}$
Samoletum repentis	III $^{(+-4)}$	III $^{(+-4)}$
Plantago coronopus-community	III $^{(+-2)}$	III $^{(+-2)}$
Sellieretum radicantis	II $^{(+-4)}$	IV $^{(+-3)}$
Triglochinetum striati	II $^{(1-2)}$	I $^{(+-1)}$
Plagianthetum divaricati	II $^{(+-1)}$	I $^{(+-2)}$
Atriplex prostrata-Gesellschaft	II $^{(+)}$	.
Apodasmia similis-community	I $^{(2)}$	III $^{(+-2)}$
Isolepis nodosus-community	I $^{(1)}$	I $^{(+-1)}$
Agrostis stolonifera-community	I $^{(1)}$	I $^{(+-2)}$
Mimuletum repentis	I $^{(+)}$	II $^{(+-3)}$
Paspalum vaginatum-community	I $^{(+)}$	I $^{(+-1)}$
Ruppietum megacarpae	+ $^{(3)}$	I $^{(+-2)}$
Schoenoplectetum pungentis	+ $^{(1)}$	+ $^{(+)}$
Schedonorus phoenix-community	+ $^{(+)}$	IV $^{(+-2)}$
Spartinetum anglicae	I $^{(1)}$	+ $^{(1)}$
Suaedetum novae-zelandiae	I $^{(+)}$	I $^{(1-2)}$
Cotula coronopifolia-community	I $^{(+-2)}$	II $^{(+-1)}$
Zosteretum novazelandicae	+ $^{(+)}$	+ $^{(2)}$
Spergularia media-community	+ $^{(1)}$	+ $^{(2)}$
Parapholis incurva-community	+ $^{(1)}$	+ (1)
Leptinelletum dioicae	I $^{(+)}$	+ (+)
North Island Subsigmetum		
Avicennietum marinae	II $^{(1-2)}$	.
Carex divisia-community	+ $^{(+-2)}$	.
Lilaeopsetum noveazelandiae	+ $^{(1)}$	.
South Island Subsigmetum		
Puccinellietum strictae	.	II $^{(+-4)}$
Puccinellietum walkeri	.	I $^{(4)}$
Elytrigia repens-community	.	I $^{(1-2)}$
Puccinellia fasciculata-community	.	+ $^{(2)}$
Apium prostrata-community	.	+ $^{(+)}$
Festuca rubra-community	.	+ $^{(1)}$
Juncus gerardii-community	.	+ $^{(+-2)}$
Spergularia marina-community	.	+ $^{(2)}$

Table 9. Constancy table of the Juncetum kraussii Sigmetum.

	North Island	South Island
Number of Sigma relevés	69	18
Average number of vegetation units	5	6
Juncetum kraussii	V $^{(+-5)}$	V $^{(2-5)}$
Apodasmia similis-community	V $^{(+-5)}$	IV $^{(+-4)}$
Sarcocornietum quinqueflorae	II $^{(+-3)}$	IV $^{(+-3)}$
Samoletum repentis	II $^{(+-3)}$	IV $^{(+-2)}$
Plagianthetum divaricari	III $^{(+-2)}$	I $^{(+-1)}$
subcommunity of Apodasmia similis-community with Juncus kraussii	II $^{(1-3)}$	III $^{(1-4)}$
Sellieretum radicantis	II $^{(+-3)}$	III $^{(+-2)}$
subassociation of Juncetum kraussii with Apodasmia similis	II $^{(1-3)}$	II $^{(1-3)}$
Schedonorus phoenix-stand	II $^{(+-1)}$	II $^{(+-2)}$
Mimuletum repentis	2 $^{(+-2)}$	+ $^{(+)}$
Zosteretum novazelandicae	+ $^{(2)}$	II $^{(2-4)}$
Schoenoplectum pungentis	+ $^{(+-5)}$	II $^{(1-3)}$
Cotula coronopifolia-community	+ $^{(+-1)}$	II $^{(+)}$
Stipetum stipoides	I $^{(+-3)}$	+ $^{(+-2)}$
Plantago coronopus-community	+ $^{(+)}$	I $^{(+-1)}$
Lilaeopsetum noveazelandia	+ $^{(1)}$	I $^{(+)}$
Spartinetum anglicae	+ $^{(2-5)}$	+ $^{(2)}$
Ruppietum megacarpae	+ $^{(+)}$	+ $^{(2)}$
Bolboschoenetum caldwellii	+ $^{(+-2)}$	+ $^{(+-1)}$
Isolepis nodosus-stand	+ $^{(+-1)}$	+ $^{(+)}$
Ulex europaeus-stand	+ $^{(+-1)}$	+ $^{(1)}$
Triglochinetum striati	+ $^{(+-3)}$	+ $^{(+)}$
Leptinelletum dioicae	+ $^{(+)}$	+ $^{(+)}$
North Island Subsigmetum		
Avicennietum marinae	III $^{(1-2)}$	.
Paspalum vaginatum-community	I $^{(+-2)}$	.
Atriplex prostrata-community	+ $^{(+-1)}$	.
Cortaderia spec.-stand	+ $^{(+-1)}$	.
Phormium tenax-stand	+ $^{(+-1)}$	.
Parapholis incurva-community	+ $^{(1)}$	.
Elytrigia repens-community	+ $^{(1)}$	.
South Island Subsigmetum		
Juncus gerardii-community	.	I $^{(1)}$
Agrostis stolonifera-community	.	I $^{(+-1)}$
Poa cita-community	.	I $^{(+-1)}$
Puccinellietum strictae	.	+ $^{(1)}$
Puccinellia fasciculata-community	.	+ $^{(+)}$

Table 10. Constancy table of the Juncetum kraussii Geosigmetum of New Zealand salt-marshes.

	North Island	South Island
Number of Geosigma relevés	**45**	**66**
Average of vegetation units	**5**	**5**
Zosteretum novazelandicae-Sigmetum		
Zosteretum novozelandicae	+ $^{(+)}$	I $^{(+-3)}$
Avicennietum marinae-Sigmetum		
Avicennietum marinae	II $^{(1-3)}$	.
Sarcocornietum quinqueflorae-Sigmetum		
Sarcocornietum quinqueflorae	II $^{(+-4)}$	III $^{(1-5)}$
Sellieretum radicantis	II $^{(+-3)}$	III $^{(+-4)}$
Samoletum repentis	II $^{(+-3)}$	III $^{(1-4)}$
Triglochinetum striati	II $^{(+-3)}$	I $^{(+-3)}$
Plantago coronopus-community	I $^{(+-3)}$	I $^{(+-3)}$
Paspalum vaginatum-community	I $^{(+-3)}$	I $^{(+-1)}$
Cotula coronopifolia-community	I $^{(+-2)}$	I $^{(+-2)}$
Atriplex prostrata-community	I $^{(+-1)}$	+ $^{(+-1)}$
Mimuletum repentis	+ $^{(1)}$	I $^{(+)}$
Suaedetum novae-zelandiae	+ $^{(+)}$	I $^{(1-2)}$
Spergularia media-community	+ $^{(1)}$	+ $^{(1)}$
Parapholis incurva-community	+ $^{(1)}$	+ $^{(1)}$
Leptinella dioica-community	+ $^{(+)}$	+ $^{(+)}$
North Island Subsigmetum		
Carex divisa-community	+ $^{(1-3)}$	.
Lilaeopsetum noveazelandiae	+ $^{(1)}$	.
South Island Subsigmetum		
Puccinellia fasciculata-community	.	I $^{(1-2)}$
Elytrigia repens-community	.	I $^{(1-2)}$
Festuca rubra-community	.	+ $^{(2-4)}$
Puccinellietum strictae	.	+ $^{(+-2)}$
Puccinellietum walkeri	.	+ $^{(1)}$
Juncus gerardii-community	.	+ $^{(+-2)}$
Spergularia marina-community	.	+ $^{(2)}$
Juncetum kraussii-Sigmetum		
Juncetum kraussii	V $^{(+-4)}$	IV $^{(1-5)}$
Apodasmia similis-community	IV $^{(1-4)}$	IV $^{(+-5)}$
Plagianthetum divaricati	III $^{(1-3)}$	II $^{(1-3)}$
subcommunity of Apodasmia similis-community with Juncus kraussii	I $^{(1-3)}$	II $^{(1-4)}$
Schoenoplectetum pungi	II $^{(+-4)}$	I $^{(+-4)}$
subassociation of Juncetum kraussii with Apodasmia similis	I $^{(1-3)}$	I $^{(1-3)}$
Spartinetum anglicae	I $^{(+-3)}$	I $^{(+-3)}$
Stipetum stipoides	I $^{(+-3)}$	+ $^{(+-2)}$
Ruppietum megacarpae	I $^{(+-3)}$	+ $^{(2)}$
Bolboschoenetum caldwellii	I $^{(+-5)}$	+ $^{(+-1)}$
Bolboschoenus medianus-community	I $^{(1-3)}$	.
Juncus acutus-community	+ $^{(+-2)}$	.
Spartina alterniflora-community	+ $^{(2)}$	.
Baumea juncea-community	+ $^{(+)}$	.
transition-zone to non-saline vegetation		
Schedonorus phoenix-stand	I $^{(+-2)}$	I $^{(1-2)}$
Leptospermum scoparium-stand	+ $^{(+)}$	+ $^{(1)}$
Phormium tenax-stand	.	+ $^{(1)}$
Ulex europaeus-stand	.	+ $^{(1)}$
Agrostis stolonifera-stand	.	+ $^{(2)}$
bare of vegetation	V $^{(1-3)}$	V $^{(1-3)}$

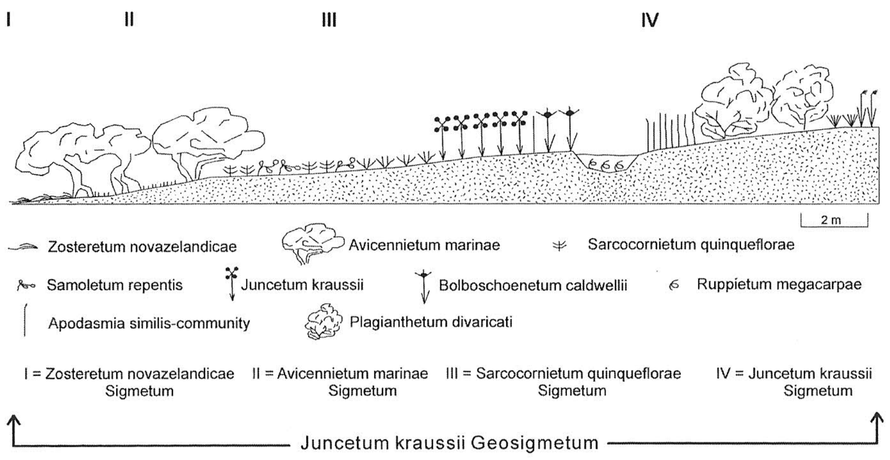

Fig. 5. Diagram showing the Juncetum kraussii Geosigmetum of New Zealand salt-marshes.

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