SALT-MARSH COMMUNITIES

INTRODUCTION TO SALT-MARSH COMMUNITIES

The sampling and analysis of salt-marsh vegetation

The herbaceous vascular vegetation on the intertidal silts and sands of salt-marshes is one of the most frequently used illustrations of ecological pattern but there are considerable difficulties in producing an adequate national classification of the plant communities of this distinctive habitat.

First, much salt-marsh vegetation is species-poor. There is little problem in sampling and sorting monospecific stands but, in many cases, a small number of species occur with varying abundance in a wide variety of combinations on salt-marshes. Early accounts of this vegetation (e.g. Tansley 1911, 1939) relied heavily on dominance in an attempt to make sense of such variation, but, as Dalby (1970) noted, this may obscure patterning among less conspicuous species that it is sensible to try and interpret. Furthermore, there has been a tendency in Britain to lump more complex vegetation, less susceptible to analysis, into a 'general salt-marsh' community. This term has sometimes been applied in its original, broad sense (Tansley 1911) to vegetation 'not dominated by any single species, except locally' and varying 'from place to place according to local conditions and to the accidents of colonisation by different species'; on other occasions (e.g. Chapman 1934), it has been used to denote a more clearly-defined community.

Second, on many salt-marshes there is a site-related element in the floristic variation among the communities which reflects particular local histories of marsh use or unique combinations of environmental conditions. Detailed studies of limited areas of salt-marsh (e.g. Yapp & Johns 1917, Chapman 1934, Dalby 1970, Packham & Liddle 1970, Gray & Bunce 1972) can be particularly valuable in elucidating such local patterns of variation but the use of a single suite of salt-marshes as a reference point for interpreting floristic variation throughout the country can be misleading. The especially attractive and varied salt-marshes of the north Norfolk coast have been frequently employed in such a way and this has bequeathed to us a perspective in which the salt-marshes of the north and west tend to be underrated. On the other hand, to treat all local variation on an equal level would produce a very cumbersome national classification.

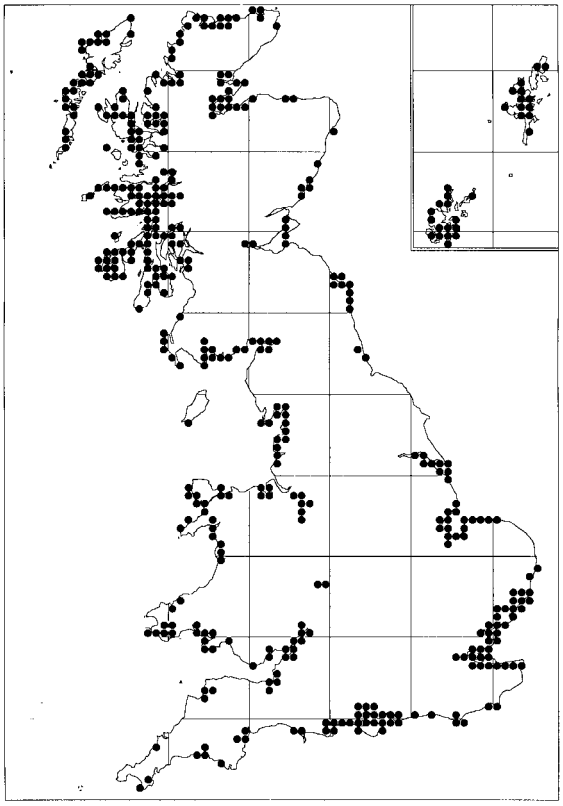
A third point is that 'salt-marsh' is as much a habitat as a group of plant communities and, although the vegetation itself plays some part in salt-marsh development, the physiographic boundaries of the habitat do not exactly coincide with a well-circumscribed range of communities. The salt-marsh flora has two major components: a halophyte element more or less confined to this particular kind of saline environment and an element comprising species which are widespread in inland, non-saline habitats. The latter species are commonly referred to as glycophytes, although it is possible that they include some distinct ecotypes which differ markedly from their inland counterparts in their physiological tolerances. Communities consisting predominantly or entirely of halophytes can sensibly be termed salt-marsh vegetation types but, towards the upper marsh limit and, in some areas (like the grazed marshes of the north and west) more extenstively, communities consisting mainly or exclusively of glycophytes also occur in the salt-marsh habitat. These may extend well into the zone of tidal influence but they are often far from the common conception of salt-marsh vegetation. Some are perhaps best seen as highly modified forms of more typical salt-marsh communities produced by specialised treatments. Others probably reflect coincidences of environmental conditions which, though not especially coastal, occur only on salt-marshes. Deciding whether a particular vegetation type is more closely related to a mainstream salt-marsh community or a predominantly inland community is sometimes very difficult.

Finally, algae are often a conspicuous feature of salt-marsh vegetation and a decision has to be taken about whether or not to record them with the vascular flora and employ them in the analysis of data. Although there are some difficulties of identification with these taxa,

especially among the microscopic species, a number of schemes have been proposed for the classification of algal communities on salt-marshes (e.g. Cotton 1912, Carter 1932, 1933*a*, *b*, Chapman 1974, Polderman 1979, Polderman & Polderman-Hall 1980). These suggest that the concordance of algal assemblages with vascular plant communities may not be precise. In addition, algal communities appear to be subject to greater seasonal changes and, at least where the smaller species are concerned, to be organised on a finer scale. For the most part, therefore, vascular communities appear to be superimposed upon a distinct, more changeable and finer pattern of algal vegetation.

In an attempt to take account of such difficulties, Adam (1976, 1981) collected almost 3000 new samples of vegetation from British salt-marshes and his classification forms the basis of the scheme presented here. Adam's geographical coverage was extensive but some stretches of coastline were sparsely sampled (the Hampshire coast and south-west England) and others unvisited by him (the Thames estuary, the Humber and eastern Scotland). Where possible, this under-representation has been rectified by our own sampling programme and by the generous donation of external data, most notably from Birse & Robertson (1976), Hilliam (1977) and Birse (1980), which considerably extended coverage, particularly in eastern Scotland, Orkney and Shetland (Figure 4).

Figure 4. Distribution of samples available from salt-marshes.



Adam did not include the *Zostera* vegetation of flats in his survey but some very limited sampling by the survey team and a good deal of qualitative information forms the basis of an outline description included here. The work of Lee (1975, 1977) has also enabled a fuller account to be given of those communities represented in inland saline habitats. It has been possible, too, to integrate Adam's data with samples of swamps, mires and mesotrophic grasslands widely distributed inland and so produce a coherent account of some of the communities of the upper salt-marsh. However, the vegetation of brackish pools and ditches and the grassy sea-banks and walls characteristic of many reclaimed sites (Beeftink 1975, Gray 1977, Adam & Akeroyd 1978) remains under-sampled.

As with other sections of the National Vegetation Classification, floristic data alone were used to characterise the vegetation types, any available environmental or site information being employed afterwards to help provide an ecological interpretation to the various sample groups distinguished.

The description of salt-marsh communities

Adam warned about the difficulty of generalising from a national scheme to a particular local situation and the same caution should be applied to this expanded and modified classification. Two of the communities distinguished are especially problematic in this respect: the *Puccinellia maritima* salt-marsh (SM13, *Puccinellietum maritimae* (Warming 1906) Christiansen 1927) and the *Festuca rubra* salt-marsh (SM16, *Juncetum gerardi* Warming 1906). These both encompass a very wide range of floristic variation, the internal differences between the sub-communities being almost as great as those features which distinguish these vegetation types from other salt-marsh communities. Although the sub-communities characterised should be useful in discussing national variation, they may well be of less value in local small-scale studies and, in certain cases, it might be appropriate to devise *ad hoc* classifications within these major types for particular sites.

Although Adam's approach was phytosociological, it was an important feature of his work that he classified the samples without prior reference to existing schemes devised for salt-marshes in other parts of Europe (e.g. Beeftink 1962, 1965, 1966, Géhu 1975). Nevertheless, there is a striking similarity between many of his final groups and the salt-marsh associations of Continental classifications and much British vegetation of this kind can be seen as extending the known distribution of

previously-described communities. It is less easy to relate the vegetation types characterised here to those in earlier descriptive accounts of British salt-marshes where floristic definition was sometimes vague and units often rather heterogeneous.

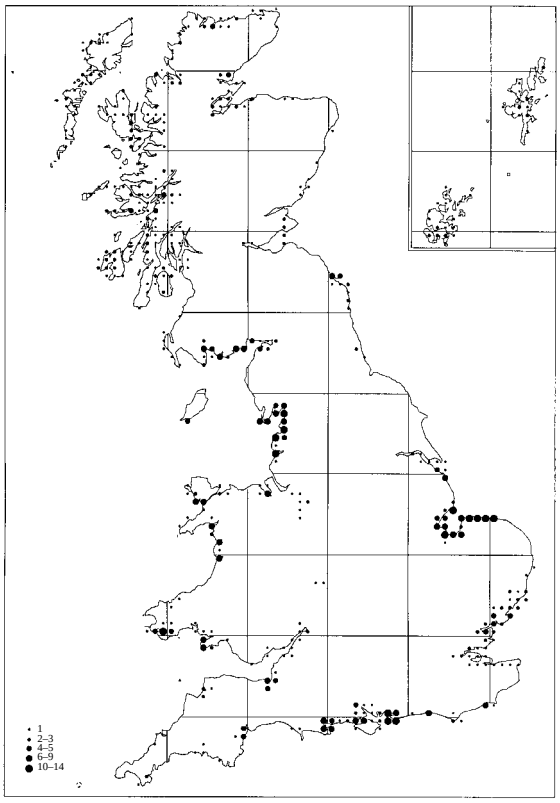
A total of 28 communities of salt-marsh vegetation has been characterised from the available data (Figure 5). These can be conveniently reviewed under four main heads: eel-grass and tassel-weed communities of tidal flats, pools and ditches (3 communities), communities of the lower salt-marsh (13), communities of the middle salt-marsh (9) and communities of the upper salt-marsh (3). Brief mention is also made below of vegetation types that are treated in other volumes but which sometimes figure prominently on salt-marshes.

Eel-grass and tassel-weed communities of tidal flats, pools and ditches

Our three native species of *Zostera* (*Z. marina*, *Z. angustifolia* and *Z. noltii*) are prominent, usually with very few other vascular species but often with abundant algae, in vegetation that occurs on the eu-littoral and sub-littoral zones of sand and silt flats. Without extensive floristic data, separate communities have not been defined here but these vegetation types are the British representatives of the eel-grass communities of the Mediterranean, west European and Baltic coasts placed in the alliance Zosterion Christiansen 1934 of the class Zosteretea marinae.

Ruppia maritima and the much rarer *Eleocharis parvula* can each occur prominently in communities of brackish pools, pans, and creeks and, in certain parts of their ranges in Britain, on the open surface of salt-marshes. Comparable vegetation elsewhere in Europe has been characterised as a *Ruppietum maritimae* Hocquette 1927 (SM2) and an *Eleocharetum parvulae* (Preuss 1911/12) Gillner 1960 (SM3) and grouped in the alliance Ruppion maritimae Br.-Bl. 1931 of the class Ruppietea maritimae J. Tüxen 1960.

Figure 5. Distribution of vegetation types characterised from salt-marshes.



Lower salt-marsh communities

Although the distinction between low, mid- and upper marsh is not a simple one, it is convenient to group together thirteen communities in which either *Spartina* spp., annual *Salicornia* spp., *Suaeda maritima* and/or *Puccinellia maritima* generally form a prominent component of the vegetation with, more unevenly, *Aster tripolium* and *Halimione portulacoides*.

Three communities dominated by *Spartina* spp. occur in Britain. By far the commonest is the *Spartina anglica* salt-marsh (SM6, *Spartinetum townsendii* (Tansley 1939) Corillion 1953), dominated by *S. townsendii sensu lato* (generally the fertile amphidiploid *S. anglica* but also occasionally with its male sterile F_1 precursor *S.* × *townsendii*). Although *S. anglica* can be found as a scattered associate in almost every salt-marsh community, the spread over the last 100 years of dense stands of this species is one of the most spectacular recent changes in the vegetation of the maritime zone of Britain. Communities dominated by its presumed parents, the native *S. maritima* (SM4, *Spartinetum maritimae* (Emb. & Regn. 1926) Corillion 1953) and the naturalised alien *S. alterniflora* (SM5, *Spartinetum alterniflorae* Corillion 1953), appear to be declining and are now much restricted in their distribution. Cord-grass vegetation of these types through western Europe and on the east coast of North America has been placed in the alliance Spartinion Conrad 1933 of the class Spartinetea maritimae R.Tx. 1961.

Annual *Salicornia* spp., *Suaeda maritima* and *Puccinellia maritima* occur together in various combinations as colonising vegetation towards the lower limit of salt-marshes and in open and disturbed areas at higher levels. Three communities have been distinguished according to the balance of the various components: the annual *Salicornia* salt-marsh (SM8, *Salicornietum europaeae* Warming 1906), *Suaeda maritima* salt-marsh (SM9, *Suaedetum maritimae* (Conrad 1935) Pignatti 1953) and

the transitional *Puccinellia-Salicornia-Suaeda* salt-marsh (SM10). Predominantly low-marsh vegetation of these kinds in which annual chenopods are prominent is grouped in the alliance Thero-Salicornion strictae Br.-Bl. 1933 *emend*. R.Tx. 1950 of the class Thero-Salicornietea Pignatti 1953 *emend*. R.Tx. in R.Tx. & Oberdorfer 1958.

The perennial relative of *Salicornia*, now termed *Arthrocnemum perenne*, occurs occasionally in Britain in a variety of salt-marsh communities but locally forms dense stands which are best treated as a distinct vegetation type similar to the *Salicornietum radicantis* Br.-Bl. 1931, traditionally separated off from the annual chenopod communities into the Salicornion fruticosae Br.-Bl. 1931 alliance of the Salicornietea fruticosae.

The five remaining low-marsh communities are all richer and more varied vegetation types than these, composed largely of perennial halophytes and, among these, the grass *Puccinellia maritimae* is of prime importance with, less frequently and more unevenly throughout, *Aster tripolium*, *Halimione portulacoides*, *Glaux maritima*, *Plantago maritima*, *Limonium* cf. *vulgare*, *Triglochin maritima*, *Armeria maritima* and *Spergularia media*.

The general relationship of these communities to phytosociological units defined from mainland Europe is fairly clear. They fall within the class Juncetea maritimae R.Tx. & Oberdorfer 1958 which also takes in much perennial mid-marsh and sea-cliff vegetation extending from the Arctic to the Mediterranean. West European salt-marsh communities are assigned to the order Glauco-Puccinellietalia Beeftink & Westhoff 1962 but, in Britain, the floristic distinction between the two major alliances, the Puccinellion maritimae Christiansen 1927 of the low-marsh and the Armerion maritimae Br.-Bl. & de Leuuw 1936 of the mid-marsh, is not as clear as on the Continent. In this country, *Armeria maritima* and, to a lesser extent, *Glaux maritima*, both considered good diagnostic species for the Armerion elsewhere in Europe, extend on to the low marsh and, indeed, are important components of some of the Puccinellion communities. Within Britain, a better general distinction between low- and mid-marsh vegetation types is the separation between the dominant role of *Puccinellia maritima* on the one hand and *Festuca rubra* and *Juncus gerardii* on the other, although, in particular situations, this too may be an unclear criterion.

In this scheme, the bulk of this remaining low-marsh vegetation is included in a single large and varied community, the *Puccinellia maritima* salt-marsh (SM13, *Puccinellietum maritimae* (Warming 1906) Christiansen 1927). This is the most widespread of all British salt-marsh vegetation types and it spans swards which grade, in one direction, to the Thero-Salicornion through an increased representation of annual chenopods and, in another, to the Armerion communities with a switch in dominance to *F. rubra*, *J. gerardii* and *Agrostis stolonifera*. As well as some rather species-poor *Puccinellia*-dominated swards, it also includes a variety of richer vegetation types, some previously considered within the ambit of a 'general salt-marsh' community and others representing local variation in which individual species attain prominence.

A second major community, especially on ungrazed sites to the south and east, is the *Halimione portulacoides* salt-marsh (SM14, *Halimionetum portulacoidis* (Kuhnholtz-Lordat 1927) Des Abbayes & Corillion 1949). This shares many species with the *Puccinellietum* and grades floristically to it, but it is generally distinct in the partial or total dominance of *H. portulacoides*. Also predominantly on ungrazed south-eastern sites, though somewhat more restricted in its distribution, is the *Aster tripolium* var. *discoideus* salt-marsh (SM11, *Asteretum tripolii* Tansley 1939). Like the *Halimionetum*, this community is often prominent on creek-sides, though it is also frequent low down on salt-marshes and shows some floristic overlap with Thero-Salicornion vegetation. Variation within *A. tripolium* is complex but a provisional community has been erected to contain stands dominated by the rayed form (SM12, cf. Sociatie van *Aster tripolium* Beeftink 1962). This is of local distribution and it shows some affinities with vegetation of brackish waters but further sampling is needed to establish its exact status and relationships. With a similar range and also showing close floristic relationships to the *Halimionetum* is vegetation with a striking local dominance of *Inula crithmoides* (SM26), a plant more geographically confined on salt-marshes than its occurrences on sea cliffs in Britain.

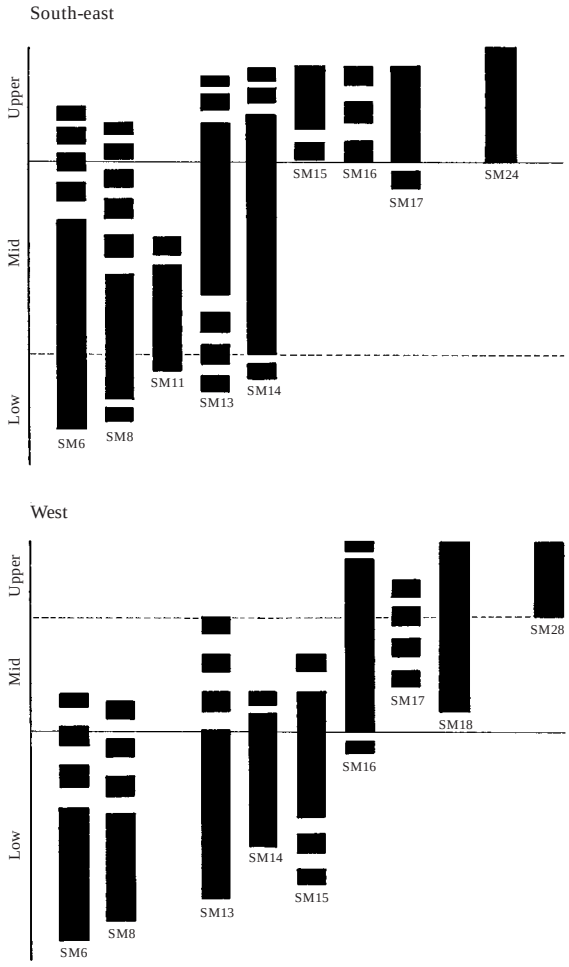
Finally, Puccinellion species form an understorey to one of the British salt-marsh communities in which *Juncus maritimus* is a physiognomic dominant. The classification of these vegetation types is problematic (Adam 1977): *J. maritimus* is dominant in certain mid-marsh communities as well as in sub-communities of the *Halimionetum* and the upper-marsh *Atriplici-Elymetum pycnanthi* (see below). However, the *Juncus maritimus-Triglochin maritima* salt-marsh (SM15) is a distinct type floristically, is the most widespread of all British *J. maritimus* communities and satisfactorily incorporates those stands in which *J. maritimus* reaches its lowest limit around our coasts. Vegetation of this type has sometimes been separated off into a separate alliance, the Halo-Scirpion (Dahl & Hadač 1971) den Held & Westhoff 1969 *nom. nov*.

Middle salt-marsh communities

Eight communities are distinguished from the middle salt-marsh zone (Figure 6). Three have a generally high frequency of *Festuca rubra*, *Juncus gerardii* and *Agrostis*

stolonifera with *Glaux maritima* and *Plantago maritima* and, more unevenly, *Armeria maritima* and *Triglochin maritima*. *Cochlearia officinalis*, *Plantago coronopus*, *Carex extensa* and *C. distans* occur patchily throughout

Figure 6. Generalised salt-marsh zonations in the south-east and west of Britain. The figure shows the relative extent of the major communities with an indication of the clarity of distinctions between low, mid and upper marsh.
SM6 *Spartinetum townsendii*
SM8 *Salicornietum europaeae*
SM11 *Asteretum tripolii*
SM13 *Puccinellietum maritimae*
SM14 *Halimionetum portulacoidis*
SM15 *Juncus maritimus-Triglochin maritima* salt-marsh
SM16 *Juncetum gerardi*
SM17 *Artemisietum maritimae*
SM18 *Juncus maritimus* salt-marsh
SM24 *Atriplici-Elymetum pycnanthi*
SM28 *Elymetum repentis*



and a variety of glycophytes, notably *Trifolium repens*, *Potentilla anserina*, *Holcus lanatus* and *Leontodon autumnalis*, attain prominence in some communities. Thero-Salicornion species such as *Puccinellia maritima*, *Halimione portulacoides* and *Limonium* cf. *vulgare* are infrequent. These communities correspond approximately to the Armerion alliance within the Glauco-Puccinellietalia.

The *Festuca rubra* salt-marsh (SM16, *Juncetum gerardi* Warming 1906) is, like the *Puccinellietum*, a large and varied vegetation type with a wide distribution, especially on the grazed marshes of the north and west of Britain. It includes swards which, on the one hand, grade to the *Puccinellietum* and, on the other, show diverse affinities with brackish and freshwater inundation communities of the Elymo-Rumicion crispi, Cynosurion pastures and Caricion davallianae mires. These reflect its considerable vertical range on salt-marshes, its widespread use for grazing and turf-cutting and the disturbance and freshwater flushing which it often experiences at higher levels.

Juncetum gerardi species form an understorey to a second community, the *Juncus maritimus* salt-marsh (SM18) which includes the bulk of those mid-marsh stands in which *J. maritimus* is dominant, often with abundant *Oenanthe lachenalii* and Elymo-Rumicion species such as *Elymus repens*, *Rumex crispus* and *Atriplex prostrata*. An *Artemisia maritima* salt-marsh (SM17, *Artemisietum maritimae* Hocquette 1927) has not traditionally been characterised in British accounts but it is a distinct vegetation type which shows affinities with both the Armerion communities (especially the *F. rubra*-dominated form of the *Juncetum gerardi*) and the Puccinellion (particularly the *Halimionetum*).

The six remaining mid-marsh communities are rather specialised vegetation types of either widespread but local occurrence or restricted geographical distribution. Two are dominated by colonial members of the Cyperaceae and are especially characteristic of damp depressions and brackish sites, especially to the north and west. The *Blysmus rufus* salt-marsh (SM19, *Blysmetum rufi* (G. E. & G. Du Rietz 1925) Gillner 1960) and the *Eleocharis uniglumis* salt-marsh (SM20, *Eleocharitetum uniglumis* Nordhagen 1923) are sometimes accommodated within a distinct alliance, the Eleocharion uniglumis, and they represent a phytogeographical affinity with predominantly north European salt-marsh communities.

Two further communities are unique to Britain, and within the country confined to north Norfolk and Sussex, and are characterised by the occurrence of Mediterranean plants in highly distinctive salt-marsh/sand-dune/shingle transitions. The *Suaeda vera-Limonium binervosum* salt-marsh and the *Halimione portulacoides-Frankenia laevis* salt-marsh (SM22, perhaps equivalent

to the *Limonio vulgaris-Frankenietum laevis* Géhu & Géhu-Franck 1975) can be seen as the northernmost outpost of the vegetation of the Frankenio-Armerenion, proposed as a sub-alliance of the Armerion.

Also, within the Glauco-Puccinellietalia is the *Spergularia marina-Puccinellia distans* salt-marsh (SM23, *Puccinellietum distantis* Feekes (1934) 1945), a community which is especially characteristic of the hypersaline conditions developing in drying pans and depressions on salt-marshes, in inland saline sites and, increasingly now, along the edges of inland roads which have received heavy applications of rock-salt in frosty weather. This kind of vegetation is usually placed in the alliance Puccinellio-Spergularion salinae Beeftink 1965. Finally, among the mid-marsh communities, it is sensible to include ephemeral vegetation with *Sagina maritima, S. nodosa* and various local annuals which finds a place in turf-cuttings and other breaks in the salt-marsh swards of the *Puccinellietum* and *Juncetum gerardi* as an early stage in recolonisation. We have not characterised any separate communities here but referred the assemblages (SM27) more generally to the Saginion maritimae Westhoff, van Leeuwen & Adriani 1962, an alliance placed in its own class.

Upper salt-marsh communities

Of the considerable variety of vegetation types which occur on salt-marshes towards the upper limit of tidal influence, three are described in this volume. They are characterised by the general prominence of *Elymus pycnanthus* and/or *E. repens*, patchy representation of Puccinellion and Armerion species and the scattered occurrence throughout of nitrophilous weeds and plants of fresh-water inundation communities. Predominantly perennial vegetation of this kind, characteristic of European drift-lines, has been variously placed in the alliance Elymion pycnanthi of the Elymetea pycnanthi or the Elymo-Rumicion crispi Nordhagen 1940 of the Molinio-Arrhenatheretea.

Two of the communities are grass-dominated. The *Elymus pycnanthus* salt-marsh (SM24, *Atriplici-Elymetum pycnanthi* Beeftink & Westhoff 1962) is the vegetation type which commonly terminates the salt-marsh zonation in the south and east. To the north and west, it is replaced by the *Elymus repens* salt-marsh (SM28, *Elymetum repentis maritimum* Nordhagen 1940) which has a less conspicious representation of salt-marsh species and which shows more obvious floristic affinities with the halophyte forms of Elymo-Rumicion vegetation. On drift-lines on the salt-marsh/sand-dune transition at scattered localities in the south-east, a third vegetation type, the *Suaeda vera* community (SM25, *Elymo pycnanthi-Suaedetum verae* (Arènes 1933) Géhu 1975), is characteristic.

Other vegetation types on salt-marshes

A variety of vegetation types described fully in other sections of *British Plant Communities* occurs on salt-marshes where there is a combination of little tidal influence and low soil salinity with either some influence of fresh-water or types of treatment and/or disturbance characteristic of other habitats (Figure 9).

Three mesotrophic grasslands occur commonly on salt-marshes (see Rodwell 1992). Both the *Festuca rubra-Agrostis stolonifera-Potentilla anserina* inundation community (MG11) and the *Festuca arundinacea* coarse grassland (MG12, *Potentillo-Festucetum arundinaceae* Nordhagen 1940) have distinct halophyte sub-communities and are found at scattered localities, mainly on the west coast, the former sometimes extensively on the grazed open marsh, the latter more patchily on ungrazed sites and on ditch-banks where there is some brackish influence. The *Agrostis stolonifera-Alopecurus geniculatus* inundation grassland (MG13) is also widespread as small stands in areas where there is some brackish influence and poaching by stock.

Swamp vegetation may occur in estuaries and in salt-marsh ditches and pools where there is slow-moving or standing brackish water and is also occasionally encountered on the open surface of salt-marshes and around saline springs inland (Rodwell 1994*a*). Two such communities are largely confined to such situations: the *Scirpus maritimus* swamp (S21, *Scirpetum maritimi* (Br.-Bl. 1931) R.Tx. 1937), which is widespread and sometimes extensive and the *Scirpus lacustris* ssp. *tabernaemontani* swamp (S20, *Scirpetum tabernaemontani* Passarge 1964) which is more local. The *Phragmites australis* swamp (S4, *Phragmitetum australis* Gams (1927) Schmale 1939), the *Typha latifolia* swamp (S12, *Typhetum latifoliae* Soó 1927) and the *Phalaris arundinacea* tall-herb fen (S28, *Phalaridetum arundinaceae* Libbert 1931) are much more widely distributed in fresh-water habitats and salt-marsh stands are often only marginally halophyte in character.

Finally here, the *Iris pseudacorus-Filipendula ulmaria* tall-herb fen (M28, *Filipendulo-Iridetum pseudacori* Adam 1976) is a very conspicuous feature of the upper-marsh and some raised beaches on the west coast of Scotland where stands may be extensive and rich around freshwater flushes.

KEY TO SALT-MARSH COMMUNITIES

With something as complex and variable as vegetation, no key can pretend to offer an infallible short cut to diagnosis. The following should thus be seen as simply as a crude guide to identifying the types of vegetation found on salt-marshes and must always be used in conjunction with the data tables and community descriptions. It relies on floristic (and, to a lesser extent, physiognomic) features of the vegetation and demands a knowledge of the British vascular flora. It does not make primary use of any habitat features, though these may provide a valuable confirmation of a diagnosis.

Because the major distinctions between the vegetation types in the classification are based on inter-stand frequency, the key works best when sufficient samples of similar composition are available to construct a constancy table. It is the frequency values in this (and, in some cases, the ranges of abundance) which are then subject to interrogation with the key.

Samples should always be taken from homogeneous stands and be 2×2 m or 4×4 m according to the scale of the vegetation or, where stands are irregular, of identical size but different shape.

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1 Open or closed vegetation of, or overwhelmingly dominated by, a single species 2

Vegetation with two or more co-dominants or, if with a single dominant, then some other species with cover values of Domin 4–7 3

2 Open or closed vegetation of, or overwhelming dominated by:

Zostera marina, *Z. angustifolia* or *Z. noltii* on sub- or eulittoral flats, often with no other vascular plants but commonly with some fucoids and green algae

SM1 *Zostera* communities
Zosterion Christiansen 1934

Ruppia maritima, sometimes with *Potamogeton pectinatus*, *Zannichellia palustris* and/or *Ranunculus baudotii* as submerged vegetation in brackish pools, in dried-up pans or, more rarely, on open flats

SM2 *Ruppia maritima* salt-marsh
Ruppietum maritimae Hocquette 1927

Suaeda maritima in usually somewhat open vegetation and often in small stands

SM9 *Suaeda maritima* salt-marsh
Suaedetum maritimae (Conrad 1935) Pignatti 1953

Aster tripolium var. *discoideus*

SM11 *Aster tripolium* var. *discoideus* salt-marsh
Asteretum tripolii Tansley 1939

Rayed *Aster tripolium*

SM12 Rayed *Aster tripolium* stands

Variation within *Aster tripolium* is complex and the phytosociological relationships of the forms are unclear.

Puccinellia maritima in low, open or closed vegetation or occasionally in dense, tall swards but with no extensive understorey of turf fucoids

SM13 *Puccinellia maritima* salt-marsh
Puccinellietum maritimae (Warming 1906) Christiansen 1927
Puccinellia maritima dominated sub-community

In hot dry summers on the upper marsh, when the shoots of *Glaux maritima* may become shrivelled, some stands of the *Puccinellietum maritimae*, *Glaux maritima* sub-community may key out here.

Eleocharis parvula in a very diminutive sward, sometimes obscured by algae or freshly-deposited silt

SM3 *Eleocharis parvula* salt-marsh
Eleocharetum parvulae (Preuss 1911/12) Gillner 1960

Spartina maritima in isolated clumps or as extensive stands

SM4 *Spartina maritima* salt-marsh
Spartinetum maritimae (Emb. & Regn. 1926) Corillion 1963

Spartina alterniflora in a dense cover with a little *S. anglica*, *Puccinellia maritima* and *Aster tripolium*

SM5 *Spartina alterniflora* salt-marsh
Spartinetum alterniflorae Corillion 1953

Spartina anglica, sometimes with *S.* × *townsendii*, often in very extensive stands

SM6 *Spartina anglica* salt-marsh
Spartinetum townsendii (Tansley 1939) Corillion 1953

Arthrocnemum perenne in dense pure stands or as open mosaic with *Halimione portulacoides*, *Puccinellia maritima* and *Suaeda maritima*

SM7 *Arthrocnemum perenne* stands

Annual *Salicornia* spp. in usually somewhat open vegetation

SM8 Annual *Salicornia* spp. salt-marsh
Salicornietum europaeae Warming 1906

Puccinellia maritima or *Plantago maritima* with an extensive understorey of diminutive turf fucoids

SM13 *Puccinellietum maritimae*
Puccinellia maritima-turf fucoid sub-community

Glaux maritima in often small and fragmentary stands

SM13 *Puccinellietum maritimae*
Glaux maritima sub-community

Halimione portulacoides as an even-topped bushy canopy or discrete hemispherical bushes in species-poor vegetation without *Juncus maritimus*

SM14 *Halimione portulacoides* salt-marsh
Halimionetum portulacoidis (Kuhnholtz-Lordat 1927) Des Abbayes & Corillion 1949
Halimione portulacoides-dominated sub-community

Halimione portulacoides with some *Juncus maritimus* as scattered shoots or small dense patches

SM14 *Halimionetum portulacoidis*
Juncus maritimus sub-community

Small but discrete patches of these two sub-communities of the *Halimionetum* may occur in mosaics with the *Puccinellietum maritimae* and these should be distinguished from the intimate mixtures of *H. portulacoides* and *P. maritima* that characterise the *Puccinellia maritima* sub-community of the *Halimionetum*.

Juncus maritimus as small dense patches within a ground of *Halimione portulacoides*

SM14 *Halimionetum portulacoidis*
Juncus maritimus sub-community

Juncus maritimus as tall dense patches with little or no *Halimione portulacoides*

SM15 *Juncus maritimus-Triglochin maritima* salt-marsh

Juncus maritimus may also be locally dominant in the *Juncus maritimus* salt-marsh but the consistent presence there of *Festuca rubra*, *Agrostis stolonifera* and *Juncus gerardii* as an often thick understorey usually serves to separate this vegetation from the two above. *J. maritimus* may also be locally abundant in the *Atriplici-Elymetum pycnanthi* but there *Elymus pycnanthus* is consistently dominant.

Juncus gerardii as generally small and often roughly circular patches of sometimes tall vegetation

SM16 *Festuca rubra* salt-marsh
Juncetum gerardi Warming 1906
Juncus gerardii-dominated sub-community

Juncus gerardii may also be locally abundant in other sub-communities of the *Juncetum gerardi*.

Festuca rubra as a thick springy mattress of tall and dense vegetation

SM16 *Juncetum gerardi*
Sub-community with tall *Festuca rubra* dominant

Festuca rubra may also be locally abundant in the shorter swards of other sub-communities of the *Juncetum gerardi*.

Blysmus rufus in often small stands of sometimes open vegetation

SM19 *Blysmus rufus* salt-marsh
Blysmetum rufi (G. E. & G. Du Rietz 1925) Gillner 1960

Eleocharis uniglumis in often small stands of sometimes open vegetation

SM20 *Eleocharis uniglumis* salt-marsh
Eleocharitetum uniglumis Nordhagen 1923

Suaeda vera as an open bushy canopy with one or more of *Limonium binervosum*, *L. bellidifolium* or *Frankenia laevis* beneath

SM21 *Suaeda vera-Limonium binervosum* salt-marsh

Suaeda vera as a more or less closed canopy in strandline vegetation without the above species

SM25 *Suaeda vera* salt-marsh
Elymo pycnanthi-Suaedetum verae (Arènes 1933) Géhu 1975

Spergularia marina or *Puccinellia distans* in often small stands of usually somewhat open vegetation

SM23 *Spergularia marina-Puccinellia distans* salt-marsh
Puccinellietum distantis Feekes (1934) 1945

Elymus pycnanthus as stiff clumps, usually without any *Suaeda vera* or *Inula crithmoides*

SM24 *Elymus pycnanthus* salt-marsh
Atriplici-Elymetum pycnanthi Beeftink & Westhoff 1962

Elymus repens in a closed grassy sward

SM28 *Elymus repens* salt-marsh
Elymetum repentis maritimum Nordhagen 1940

Inula crithmoides, usually with some *Halimione portulacoides*

SM26 *Inula crithmoides* stands

Sagina maritima or *Plantago coronopus* in often open or fragmentary vegetation in breaks within swards of other communities, especially the *Juncetum gerardi*

SM27 Ephemeral *Sagina maritima* vegetation
Saginion maritimae Westhoff, van Leeuwen & Adriani 1962

Potentilla anserina as small stands colonising breaks within swards of other mid- and upper-marsh vegetation

SM16 *Juncetum gerardi* phase of sward regeneration in turf-cuttings

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Vegetation dominated by swamp species such as *Scirpus maritimus*, *S. lacustris* ssp. *tabernaemontani*, *Phragmites australis*, *Typha latifolia* and *Phalaris arundinacea* may be encountered on salt-marshes but these communities are included in Rodwell (1994*a*).

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3 Low swards, sometimes rather open, dominated by various mixtures of annual *Salicornia* spp., *Suaeda maritima* and *Puccinellia maritima* 4

Annual *Salicornia* spp. and *Suaeda maritima* not dominant or co-dominant 5

4 *Suaeda maritima* and annual *Salicornia* spp. co-dominant with less than 10% *Puccinellia maritima*

SM9 *Suaedetum maritimae*

Annual *Salicornia* spp., *Suaeda maritima* and *Puccinellia maritima* co-dominant in various proportions, often with a little *Aster tripolium*

SM10 Transitional low-marsh vegetation

Vegetation of this kind frequently occurs as mosaics between the *Salicornietum europaeae* and the *Puccinellietum maritimae*, *Spartinetum maritimae* and, especially in the south-east, the *Asteretum tripolii* and *Halimionetum portulacoidis*.

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5 *Aster tripolium* var. *discoideus* or rayed *Aster tripolium* dominant 6

Aster tripolium absent or present in small amounts 7

6 *Aster tripolium* var. *discoideus* dominant

SM11 *Asteretum tripolii*

Rayed *Aster tripolium* dominant

SM12 Rayed *Aster tripolium* stands

Variation within *Aster tripolium* is complex and the phytosociological relationships of the different forms are unclear.

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7 *Arthrocnemum perenne* co-dominant with *Halimione portulacoides* and some *Puccinellia maritima*

SM7 *Arthrocnemum perenne* stands

Arthrocnemum perenne absent or present in small amounts 8

8 *Puccinellia maritima* a major constituent of the vegetation 9

Puccinellia maritima absent or present in small amounts 16

9 Any of *Festuca rubra*, *Agrostis stolonifera* and *Juncus gerardii* present in more than a trace and often co-dominant with *Puccinellia maritima*

SM16 *Juncetum gerardi*
Puccinellia maritima sub-community

Above species usually comprising less than 10% of the sward 10

10 *Limonium binervosum* and/or *Frankenia laevis* present with *Halimione portulacoides* 11

Neither *Limonium binervosum* nor *Frankenia laevis* present 12

11 *Suaeda vera* present as a conspicuous component

SM21 *Suaeda vera-Limonium binervosum* salt-marsh

Suaeda vera absent

SM22 *Halimione portulacoides-Frankenia laevis* salt-marsh
Limonio vulgaris-Frankenietum laevis Géhu & Géhu-Franck 1975

12 *Puccinellia maritima* dominant or co-dominant with *Plantago maritima* and/or *Armeria maritima* with a conspicuous understorey of diminutive turf fucoids

SM13 *Puccinellietum maritimae*
Puccinellia maritima-turf fucoid sub-community

Turf fucoids absent or with low cover 13

13 *Spartina maritima* present

SM13 *Puccinellietum maritimae*
Puccinellia maritima-Spartina maritima sub-community

Spartina maritima absent 14

14 *Halimione portulacoides* co-dominant with *Puccinellia maritima* in intimate mixtures in which shoots of the latter emerge through an open network of shoots of the former; *Festuca rubra* rare and never abundant

SM14 *Halimionetum portulacoidis*
Puccinellia maritima sub-community

Prostrate *Halimione portulacoides* is also sometimes abundant in the *Limonium vulgare-Armeria maritima* sub-community of the *Puccinellietum maritimae* but other dicotyledons are usually co-dominant there and *P. maritima* itself rarely comprises more than 10% of the swards. Intimate mixtures of *Halimione portulacoides* and *Puccinellia maritima* such as are included here should be distinguished from mosaics of discrete patches of the *Halimionetum portulacoidis* and the *Puccinellietum maritimae*.

Halimione portulacoides infrequent and never co-dominant 15

15 *Puccinellia maritima* and *Glaux maritima* co-dominant in species-poor vegetation usually in small stands

SM13 *Puccinellietum maritimae*
Glaux maritima sub-community

Puccinellia maritima dominant in open vegetation with *Spergularia marina* and/or *Puccinellia distans*

SM23 *Puccinellietum distantis*

16 Varied swards dominated by mixtures of dicotyledons including *Armeria maritima*, *Triglochin maritima* and *Plantago maritima* with usually less than 10% *Puccinellia maritima* and without *Frankenia laevis*, *Limonium binervosum*, *L. bellidifolium* and *Suaeda vera* 17

Vegetation not dominated by mixtures of the listed dicotyledons or, if so, then some of *Frankenia laevis*, *Limonium binervosum*, *L. bellidifolium* and *Suaeda vera* also present 18

17 *Limonium vulgare* (or, locally, *L. humile*), *Halimione portulacoides* and annual *Salicornia* spp. present and sometimes abundant

SM13 *Puccinellietum maritimae*
Limonium vulgare-Armeria maritima sub-community

Glaux maritima and rayed *Aster tripolium* constant and sometimes abundant with no *Limonium vulgare* and little *Halimione portulacoides*

SM13 *Puccinellietum maritimae*
Plantago maritima-Armeria maritima sub-community

18 *Suaeda vera* and *Limonium binervosum* present and/or *Frankenia laevis* 19

Not as above 21

19 *Frankenia laevis* present 20

Frankenia laevis absent

SM21 *Suaeda vera-Limonium binervosum* salt-marsh
Typical sub-community

20 *Suaeda vera* present

SM21 *Suaeda vera-Limonium binervosum* salt-marsh
Frankenia laevis sub-community

Suaeda vera absent

SM22 *Limonio vulgaris-Frankenietum laevis*

21 *Artemisia maritima* prominent in usually small stands of somewhat variable vegetation ranging from rank grassy swards with much *Festuca rubra* to open bushy canopy of *A. maritima* over low *Halimione portulacoides*

SM17 *Artemisietum maritimae*

Artemisia maritima absent or inconspicuous 22

22 Grassy swards in which *Festuca rubra*, *Agrostis stolonifera* and *Juncus gerardii* are generally important components in the absence of *Juncus maritimus* 23

Juncus maritimus an important component of the vegetation 25

23 *Trifolium repens*, *Leontodon autumnalis* and *Potentilla anserina* present and often abundant in various combinations, sometimes with *Carex distans* and/or *C. flacca* 24

Short swards of very variable composition but usually dominated by *Festuca rubra* and *Agrostis stolonifera* with some *Juncus gerardii*, *Glaux maritima*, *Triglochin maritima*, *Armeria maritima* and *Plantago maritima* and with the above species absent or at less than 10% cover

SM16 *Juncetum gerardi*
Festuca rubra-Glaux maritima sub-community

On heavily-grazed marshes, especially in north-west England, swards lacking *Trifolium repens*, *Leontodon autumnalis* and *Potentilla anserina* may also have a very low cover of either *Festuca rubra* or *Agrostis stolonifera* or *Juncus gerardii*. These are best considered as derivatives of the *Festuca-Glaux* sub-community of the *Juncetum gerardi*.

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24 *Carex flacca* constant and sometimes abundant

SM16 *Juncetum gerardi*
Carex flacca sub-community

Carex flacca infrequent

SM16 *Juncetum gerardi*
Leontodon autumnalis sub-community

On heavily-grazed marshes, especially in north-west England, swards lacking *Carex flacca* but also poor in *Leontodon autumnalis* and *Potentilla anserina* may be encountered. *Trifolium repens* remains a conspicuous component and such swards are best considered as derivatives of the *Leontodon autumnalis* sub-community of the *Juncetum gerardi*.

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25 *Oenanthe lachenalii* constant and often abundant 26

Oenanthe lachenalii rare and never abundant but *Plantago maritima* and rayed *Aster tripolium* often conspicuous

SM18 *Juncus maritimus* salt-marsh
Plantago maritima sub-community

26 *Festuca arundinacea* constant and often co-dominant with *Juncus maritimus*

SM18 *Juncus maritimus* salt-marsh
Festuca arundinacea sub-community

Festuca arundinacea infrequent and never abundant

SM18 *Juncus maritimus* salt-marsh
Oenanthe lachenalii sub-community

A variety of other vegetation types encountered on salt-marshes may fail to key out here. These are most likely to be certain kinds of driftline vegetation, of mires and of mesotrophic grasslands. The mesotrophic grasslands are likely to be the most troublesome to distinguish as they often grade into forms of the *Juncetum gerardi* which have been much altered by agricultural treatment or into the communities of brackish pools with an increase in soil water salinity.

COMMUNITY DESCRIPTIONS

SM1
Zostera communities
Zosterion Christiansen 1934

In Britain, three species of eel-grass, *Zostera marina*, *Z. angustifolia* and *Z. noltii*, form distinctive stands in the sub-littoral and eu-littoral zones of sand and mud flats. Very few samples of this vegetation were taken and the following account relies heavily on published and unpublished material relating in particular to The Solent (C. R. & J. M. Tubbs), the Thames estuary and Essex (Wyer & Waters 1975; Charman 1975, 1977*b*, 1979), north Norfolk (Ranwell & Downing 1959, Charman & Macey 1978), Lindisfarne (D. O'Connor), the Moray Firth (Rae 1979), and the west coast of Scotland (A. Currie). There are two difficulties in making use of existing information. First, *Z. angustifolia* is not consistently distinguished from narrow-leaved forms of *Z. marina*: this partly reflects the long-standing discussion on the taxonomic status of plants variously described as *Z. marina* var. *angustifolia*, *Z. hornemanniana* or *Z. angustifolia*. Second, eu-littoral stands have often been described simply as '*Zostera*' irrespective of whether they comprise *Z. angustifolia*, *Z. noltii* or both these species. This has been particularly true of accounts of the grazing of *Zostera* spp. by wildfowl and a separate note on this important aspect of the conservation value of the vegetation has therefore been appended.

Zostera marina stands
Zosteretum marinae Harmsen 1936

Zostera marina forms stands with a cover of trailing leaves up to 1 m long. Algae, especially *Enteromorpha* spp., are usually the sole associates. *Z. marina* is essentially a sub-littoral species, extending from 1–4 m below to just above low water of spring tides, although it also occurs in lagoons. The lower salinity limit for the species is about 35 g l^{-1} (chloridity 24 g l^{-1}) but the exact limits of its distribution may be controlled by light requirement below and susceptibility to dessication above. Around The Solent, plants are exposed for only 1½ hours even at low water of spring tides.

Z. marina shows considerable morphological variation with a decrease in leaf size and density upshore. Narrow-leaved plants from the lower eu-littoral have been described as *Z. marina* var. *angustifolia* or confused with *Z. angustifolia*. There also appears to be some variation in phenology in relation to the position of the plants on the shore. *Z. marina* shows considerable leaf loss in autumn and early winter but this may be much more apparent in eu-littoral plants than in those which are permanently submerged where a dense cover is maintained throughout the winter. Regrowth occurs in all plants in spring and early summer. Flowering seems to be most frequent in eu-littoral plants and in those sheltered from wave action with larger sub-littoral plants reproducing vegetatively.

In Britain, *Z. marina* always grows on a firm substrate, usually sand or sandy mud, though sometimes with an admixture of fine gravel.

Where their ranges overlap, as in The Solent, *Z. marina* passes upshore to *Z. noltii*; elsewhere *Z. marina* stands may be separated by a considerable expanse of bare substrate from salt-marsh vegetation proper. In The Solent, *Z. marina* may have a potential competitor in the sub-littoral brown alga *Sargassum muticum*, a native of Japan which has colonised some sites once occupied by *Z. marina*.

Z. marina was much reduced in the early 1930s by a wasting disease which seems to have been a combination of attack by a protozoan and an ascomycete fungus. Butcher (1934, 1941) catalogued the most substantial decrease on the East Anglian and north Kent coasts and around The Solent. In recent years, the species has certainly reappeared in abundance in The Solent but seems to have remained rare elsewhere in the south-east. Butcher (1934) did not examine changes on the Scottish coast but *Z. marina* is now abundant down the western coast of the mainland and the Outer Hebrides and also in the Moray Firth. The map shows the distribution of the species in Perring & Walters (1962) with modifications.

Zosteretum marinae has been widely reported from throughout Europe though its exact status following the 1930s disease and subsequent erosion of substrates is uncertain. In The Netherlands, Beeftink (1962) records the association as rare; in France it appears to have recovered somewhat (Géhu 1975).

***Zostera angustifolia* stands**

Zostera angustifolia forms stands with a cover of trailing leaves up to about 25 cm long. It may occur pure, though it is often mixed with the smaller *Z. noltii* and with a variety of algae among which species of *Ulva*, *Chaetomorpha* and *Enteromorpha* are often abundant. The table lists some samples of mixed *Zostera* vegetation from the Exe estuary, Devon. On the extensive estuarine flats of the Cromarty Firth, it occurs with *Ruppia maritima* and annual *Salicornia* spp.

Z. angustifolia can behave as a short-lived perennial. Around the Moray Firth, Rae (1979) noted that few plants lasted longer than two years and, throughout its British range, the species seems to suffer heavy leaf loss in autumn and early winter by a combination of natural shedding, storm damage and wildfowl grazing. Regrowth in spring can be largely by seedling germination (Ranwell & Downing 1959, Wyer & Waters 1975, Rae 1979) though good regeneration from existing rhizomes has also been reported.

Z. angustifolia is a plant of the lower and middle eulittoral zone, extending to well above low water of neap tides and sometimes to high water of neap tides. Its optimal salinity is about 25–34 g l^{-1} (chloridity 16–20 g l^{-1}; Proctor 1980) and, as with *Z. marina*, its exact limits seem to be controlled by light requirement below and susceptibility to desiccation above. In The Solent, it is exposed for a maximum of about 6½ hours on the spring tides. It certainly grows best in sites which are never deeply submerged at high tide nor ever fully dry at low tide and is particularly characteristic of shallow depressions on tidal flats, often with some standing water at low tide. In such situations, it may form distinctive mosaics with *Z. noltii* which prefers the drier tops of low marsh ridges (Tutin, 1942, Wyer & Waters 1975, Rae 1979). It also occurs in the wet bottoms of deep marsh creeks (Chapman 1959).

Z. angustifolia is most characteristic of muds and muddy sands. These may be quite firm and contain some fine gravel but the species is typically associated with very sloppy mud on which even duck boards are an unsuccessful aid to sampling.

Z. angustifolia may pass upshore to stands of *Z. noltii* through mosaics of the two species; elsewhere it may give way to salt-marsh vegetation proper with an expanse of bare substrate between or through *Salicornietum europaeae*. In the Exe estuary, *Z. angustifolia* is replaced upshore by *Spartinetum townsendii* (Proctor 1980).

The disease of the 1930s seems to have left *Z. angustifolia* largely untouched and, at present, the species is widespread along the south and east coasts of England and the east coast of Scotland (Perring & Walters 1962). It is all but absent from the west coast of Scotland. There are very extensive stands in the Cromarty Firth (Figure 7) and also along the Essex and north Kent coasts.

In Europe, the equivalent community *Zosteretum marinae stenophyllae* Harmsen 1936 has been recorded from The Netherlands (Beeftink 1962) and France (Géhu 1975).

***Zostera noltii* stands**

Zosteretum noltii Harmsen 1936

Zostera noltii forms stands with a cover of delicate trailing narrow leaves up to about 20 cm long. It may occur pure or with *Z. angustifolia* (see table) and occasional plants of lower salt-marsh species such as annual *Salicornia* spp. or *Spartina anglica*. *Ruppia maritima* occurs with *Z. noltii* on the estuarine flats of the Cromarty Firth (Rae 1979).

Like *Z. angustifolia*, *Z. noltii* experiences considerable leaf loss in autumn and early winter through natural shedding, storm damage and wildfowl grazing but plants towards the lower limit may remain winter-green (Wyer & Waters 1975, Rae 1979). Unlike *Z. angustifolia*, expansion in spring seems to occur more consistently by the regrowth of existing rhizomes (Wyer & Waters 1975, Rae 1979) as well as by the germination of seed, production of which may be prolific, especially at higher levels.

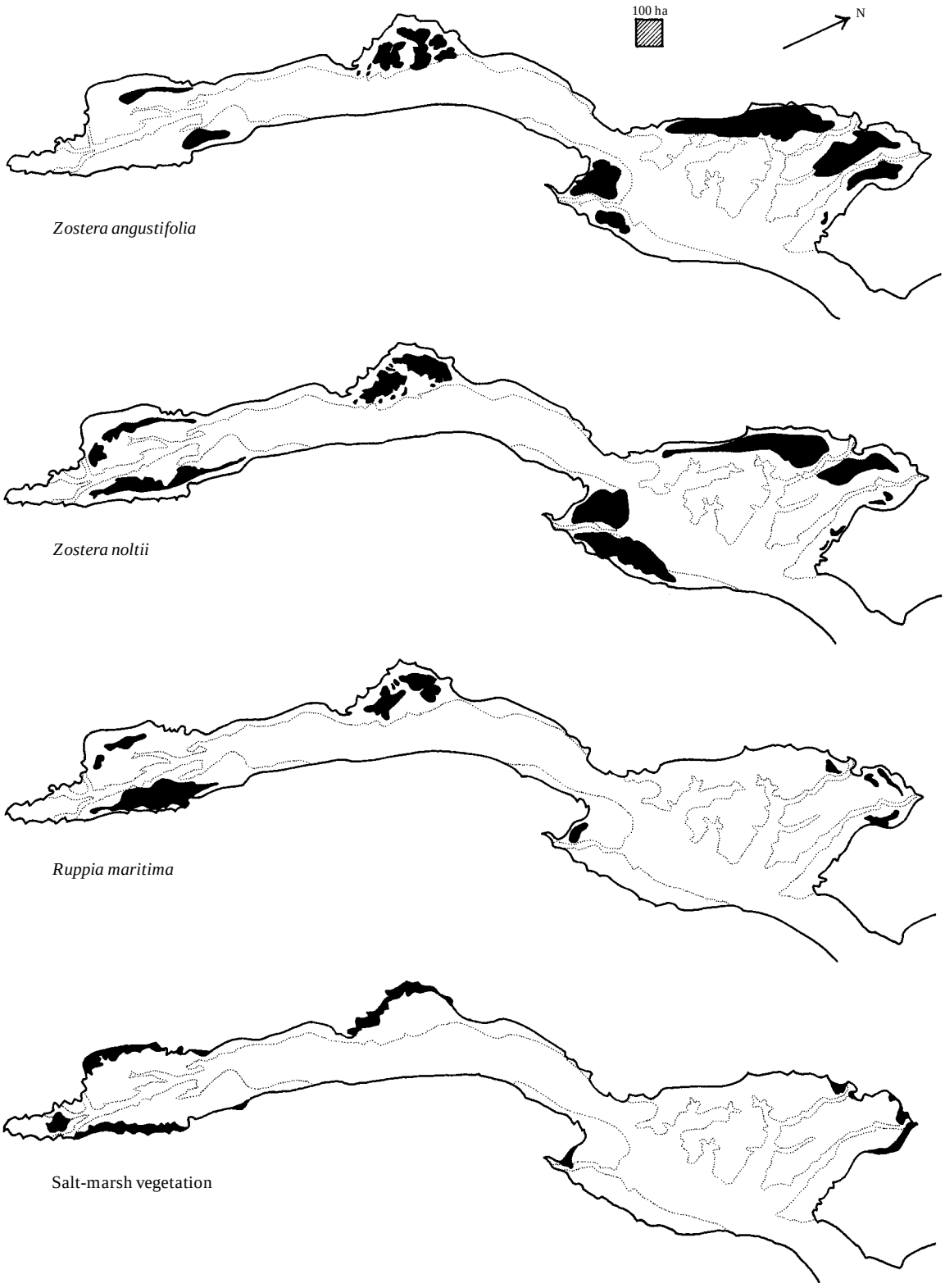
In general, *Z. noltii* is a species of the middle and upper eu-littoral zone and its lower salinity limit is about 15 g l^{-1} (chloridity 9 g l^{-1}; Mathiesen & Nielsen 1956). It occurs on mud/sand mixtures of a variety of consistencies from very soft to quite firm. It is most characteristic of situations where the substrate dries out somewhat on exposure and on flats with a gentle bar/hollow topography it forms distinctive mosaics with *Z. angustifolia*. It can also occur in shallow standing water.

Stands of *Z. noltii* pass downshore to *Z. angustifolia* and above may grade to communities of the lower salt-marsh, notably the *Salicornietum europaeae*. *Spartina anglica* is known to have invaded stands of *Z. noltii* at various sites (Chapman 1959, Goodman *et al*. 1959, Bird & Ranwell 1964, Hubbard & Stebbings 1968).

The British distribution of *Z. noltii* is similar to that of *Z. angustifolia* (Perring & Walters 1962) and there are particularly extensive stands in the Cromarty Firth (Rae 1979: Figure 7) and along the Essex and north Kent coasts (Wyer & Waters 1975).

In Europe the *Zosteretum noltii* is widespread in similar situations to those in Britain (e.g. Beeftink 1962, Géhu 1975).

Figure 7. Distribution of mud-flat and salt-marsh vegetation in the Cromarty Firth, Scotland.



Zostera and wildfowl grazing

Zostera spp. provide an important source of food for certain wildfowl, notably in Britain for overwintering brent goose (*Branta bernicla*) and wigeon (*Anas penelope*) and, to a lesser extent, of mute swan (*Cygnus olor*) and whooper swan (*Cygnus cygnus*).

The early wildfowling literature and some recent studies (e.g. Charman 1977*a*) consider *Z. marina* to have been the species most frequently eaten by brent in the past but it seems likely that, at the present time at least, *Z. angustifolia* and *Z. noltii* account for the bulk of the *Zostera* consumed. There is some suggestion (e.g. Ranwell & Downing 1959; Charman 1977*a*, 1979) that of these *Z. noltii* is the preferred species for brent. This may reflect its generally longer periods of exposure on flats but *Z. noltii* appears to reach its standing crop maximum later in the year than *Z. angustifolia*, around September/October (Wyer & Waters 1975, Rae 1979) just when brent are beginning to gather in their winter haunts. *Z. angustifolia* may be preferentially grazed by wigeon: its standing crop peak, in July/August, coincides with the gathering of that species.

A number of studies (Ranwell & Downing 1959; Charman 1975, 1977*a*, *b*, 1979; Charman & Macey 1978) have demonstrated a distinctive sequential exploitation of flat and salt-marsh food sources by brent. The accumulating birds begin feeding on *Zostera* in September/October and only when their numbers reach a peak and the *Zostera* is largely consumed do they move on, first to *Enteromorpha*, then to salt-marsh vegetation and sometimes to arable and pasture. This timing coincides to some extent with the maximum availability of nutritious food, though Charman (1979) has suggested that, among the various foods, only *Zostera* can provide an adequate daily energy requirement for brent.

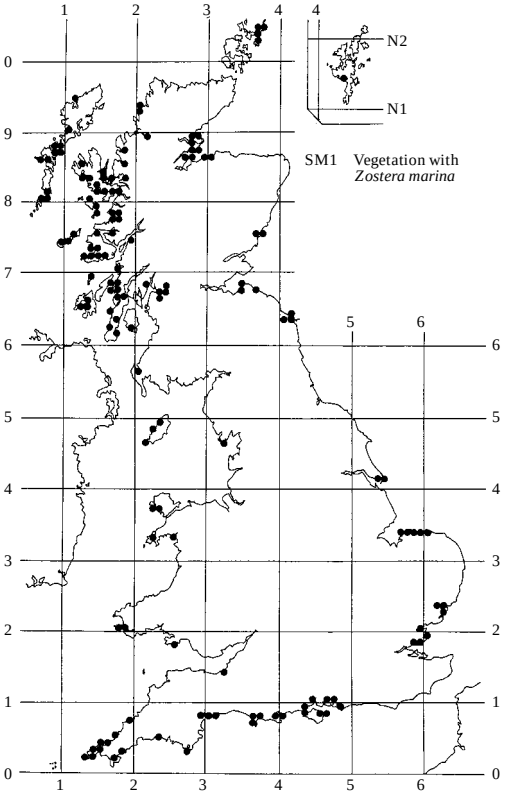
Zostera stands therefore provide what seems to be an indispensible resource for some wintering wildfowl and vast numbers of birds exploit the larger beds. The 820 ha of *Zostera* along the coasts of south Suffolk, Essex and north Kent (Wyer & Waters 1975) receive about 30000 dark-bellied brent (*Branta bernicla bernicla*) (Ogilvie 1978), the expanding stands of The Solent foreshore and harbours about 23000 (figure for 1979/80), north Norfolk about 5000 and The Wash about 6000 (Ogilvie 1978), in total about half of the world population of this race. Smaller numbers of light-bellied brent (*Branta bernicla hrota*), between 200 and 1100, winter at Lindisfarne NNR. What is probably the largest total area of *Z. noltii* and *Z. angustifolia* in Britain, the 1200 ha in the Cromarty Firth, is outside the winter range of the brent goose but the estuary is visited by enormous numbers of wigeon.

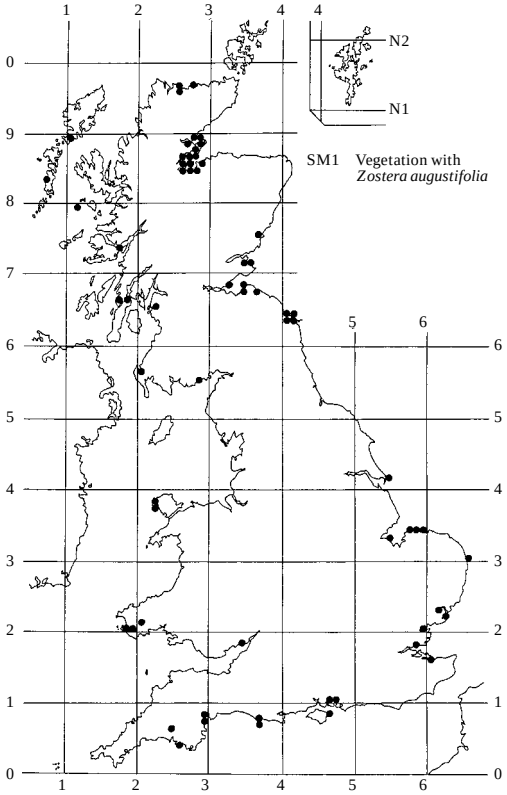
Although wildfowl sometimes uproot *Zostera* while feeding they seem mostly to eat the leaves and flowering shoots. Beds appear able to recover even from very heavy grazing and the resource to renew itself adequately from year to year by vegetative expansion and/or seed germination.

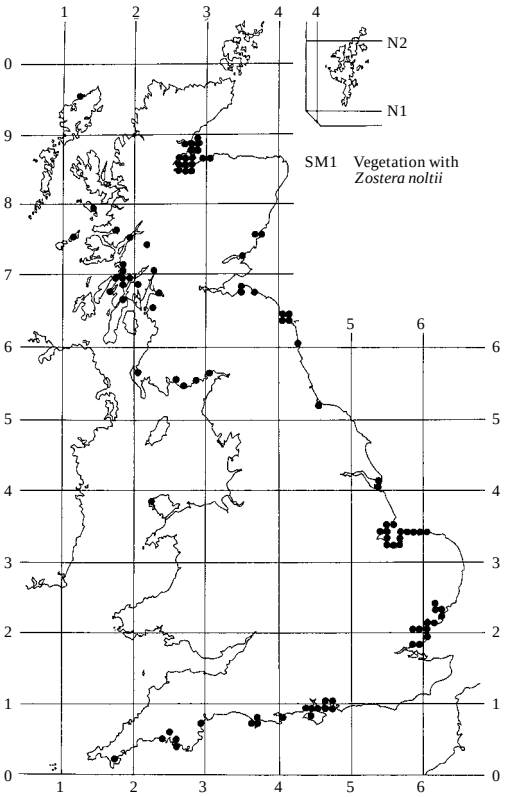
Floristic table SM1

Zostera angustifolia	V (2–8)
Zostera noltii	V (4–10)
Fucus spiralis	IV (1–4)
Enteromorpha cf. *E. marginata*	IV (1–7)
Ulva lactuca	III (1–4)
Chaetomorpha linum	II (1–6)
Polysiphonia cf. *P. insidiosa*	I (2)
Ceramium rubrum	I (1–2)
Polyneura gmelinii	I (1)
Fucus vesiculosus	I (1–2)
Cladophora sp.	I (4)
Chondria dasyphylla	I (1)
Polysiphonia cf. *P. nigrescens*	I (1)
Enteromorpha intestinalis	I (1–2)
Ectocarpus sp.	I (1)
Chaetomorpha cf. *C. tortuosa*	I (2)
Porphyra umbilicalis	I (2)
Spartina anglica	I (4)
Number of samples	15

Shells of the cockle (*Cerastoderma edule*) and common periwinkle (*Littorina littorea*) and casts of the lugworm (*Arenicola marina*) occasional to very abundant in the samples; spire shell (*Hydrobia ulvae*), mussel (*Mytilus edulis*) and shore crab (*Carcinus maenas*) recorded less frequently.


N2
N1
SM1 Vegetation with
Zostera marina


N2
N1
SM1 Vegetation with
Zostera augustifolia


N2
N1
SM1 Vegetation with
Zostera noltii

SM2

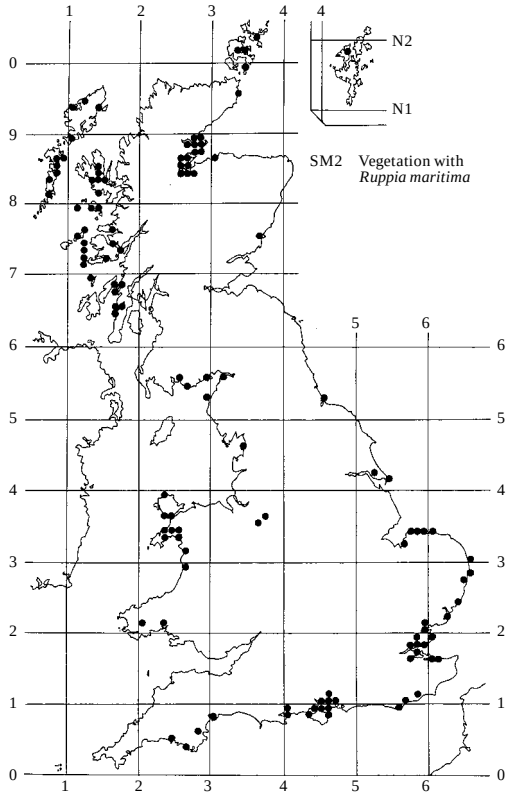
Ruppia maritima salt-marsh community

Ruppietum maritimae Hocquette 1927

Ruppia maritima is a monocotyledonous perennial which can occur as the dominant in a submerged aquatic community with *Zannichellia palustris*, *Potamogeton pectinatus*, *Ranunculus baudotii* and, within its rather restricted range, *Ruppia spiralis*. The community occurs locally in permanently-filled pans and creeks on coastal salt-marshes, at some inland saline sites (Lee 1977) and also in brackish counter-dykes behind sea walls (Rose & Géhu 1964, Jermyn 1974). In the tidal portion of the outlet stream of the Loch of Wester in Caithness there is a zonation from *R. maritima*-dominated vegetation through *Potamogeton pectinatus* to *Hippuris vulgaris* at the tidal limit.

R. maritima can also occur as a plant of estuarine flats and it is particularly abundant in this habitat in the Cromarty Firth (A. Currie, P. Steele, pers. comm.: Figure 7) where it forms a belt of varying width between the salt-marsh proper, sometimes overlapping with *Salicornietum europaeae*, and stands of *Zostera noltii*. Here *R. maritima* seems to behave as an annual (P. Steele, pers. comm.), disappearing very rapidly from September onwards. It is known to be a food source for wigeon (*Anas penelope*) but frost sensitivity may also play a part in its behaviour.

The *Ruppietum maritimae* has been described from The Netherlands (Beeftink 1962) and from France (Géhu 1975) and in the latter it occurs on coastal flats.



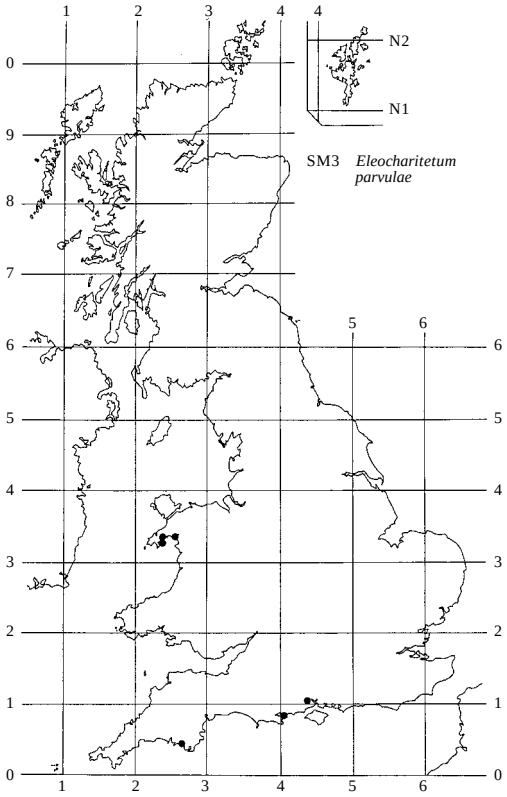
SM3

Eleocharis parvula salt-marsh community

Eleocharitetum parvulae (Preuss 1911/12) Gillner 1960

Eleocharis parvula occurs as a short open sward which is 'physiognomically the least conspicuous of all sea-shore communities' (Tyler 1969*b*). The diminutive shoots, only 1–2 cm tall, are frequently matted with (mainly green) algae and obscured by freshly-deposited silt (cf. Praeger 1934). At Beaulieu in Hampshire, stands occur at the limit of tidal influence with some input of fresh-water from land drainage at low tide (Géhu 1973*a*) but in Ireland the species may extend further downshore (Praeger 1934; C. D. Pigott, pers. comm.).

E. parvula is a very rare species in Britain with records for Beaulieu, Poole Harbour in Dorset, Bigbury Bay in Devon and Tremadoc Bay in Gwynedd. It has a similarly disjunct distribution throughout much of Europe (Beeftink 1972) but the *Eleocharitetum parvulae* has been recorded from the Biscay coast of France and Spain, from northern Portugal and the Mediterranean and Black Seas. The association is widespread in the Baltic where it frequently contains *Ruppia maritima* and *Zannichellia palustris* (Gillner 1960, Tyler 1969*a*). This led Gillner (1960) to place the association alongside the *Ruppietum maritimae* in the Ruppion maritimae, a view which is now generally accepted.



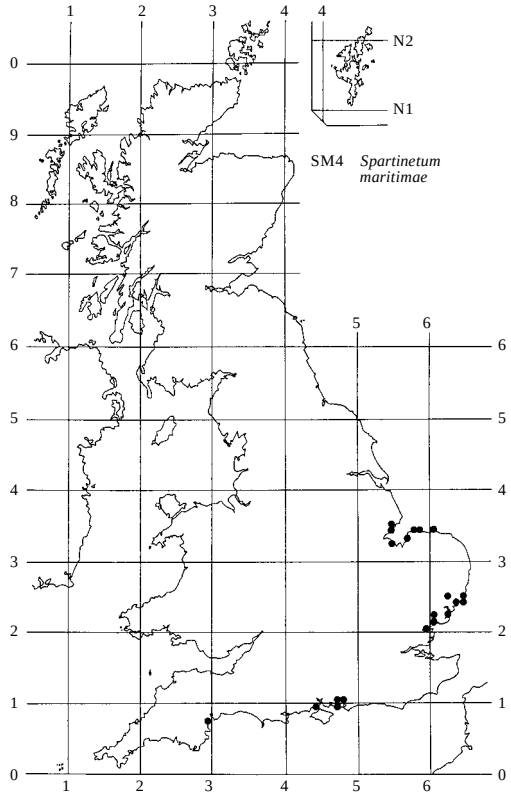
SM4

Spartina maritima salt-marsh community

Spartinetum maritimae (Emb. & Regn. 1926) Corillion 1953

Spartina maritima is a native species which seems to have reached a peak of abundance in the late nineteenth and early twentieth centuries when it grew in every harbour between Beaulieu in Hampshire to Chichester in Sussex and plentifully along the coasts of Kent, Essex and south Suffolk and around The Wash (Marchant & Goodman 1969*a*). It declined rapidly thereafter and now survives often as isolated clumps around The Solent and on the north Isle of Wight coast (Marchant & Goodman 1969*a*) though extensive stands remain in parts of Essex (Jermyn 1974, Boorman & Ranwell 1977). The population at Scolt Head Island in Norfolk (Deighton & Clapham 1925, Chapman 1934) is now extinct.

S. maritima grows as clumps of stiff shoots and at Wittering in Sussex it has some *Spartina anglica* and a little *Arthrocnemum perenne*, *Puccinellia maritima*, *Suaeda maritima* and *Salicornia* agg. (Géhu & Delzenne 1975). It is a pioneer community throughout its European range which runs south from The Netherlands to Portugal (Beeftink & Géhu 1973). The cause of its demise in Britain is not fully understood. It may partly be due to competition with *S. anglica*: Some former *S. maritima* sites are now occupied by *S. anglica* and the former seems to survive best where the latter is least aggressive, on drier sites above mean high water of spring tides (Marchant & Goodman 1969*a*). However, *S. maritima* is at the northern limit of its range in Britain and small climatic fluctuations may have played a part in its reduction (Marchant 1967). Certainly, little viable seed is produced at the present time (Marchant & Goodman 1969*a*).



SM5

Spartina alterniflora salt-marsh community
Spartinetum alterniflorae Corillion 1955

Spartina alterniflora is a naturalised alien in Europe first recorded in Britain in 1829 from the river Itchen, Hampshire (Marchant & Goodman 1969*b*). By the turn of the century, it had spread to occupy extensive areas of Southampton Water and occurred as far east as Chichester Harbour in Sussex (Rankin in Tansley 1911, Marchant & Goodman 1969*b*). Since then it has declined, at least partly in response to land reclamation (Marchant 1967) though perhaps also as a result of invasion by *Spartina anglica*, the fertile amphidiploid which arose from hybridisation between *S. alterniflora* and *S. maritima*.

S. alterniflora now survives only at Marchwood, Hampshire, and as transplanted clumps in the *Spartina* Garden in Poole Harbour, Dorset (Marchant & Goodman 1969*b*). The natural stand comprises a dense cover of *S. alterniflora* shoots with some *Spartina anglica*, *Puccinellia maritima* and *Aster tripolium* (Beeftink & Géhu 1973, Géhu & Delzenne 1975). The association occurs in scattered localities down the Atlantic coast of western Europe and is characteristic of situations with a lower and more variable salinity than other *Spartina*-dominated communities (Beeftink & Géhu 1973). The Marchwood stand has been placed in the sub-association *asteretosum tripolii* which has also been recorded from Brittany and Spain (Beeftink & Géhu 1973, Géhu & Delzenne 1975, Kortekaas *et al.* 1976).

SM6

Spartina anglica salt-marsh community

Spartinetum townsendii (Tansley 1939) Corillion 1953

Constant species

Spartina townsendii sensu lato comprises the male sterile F_1 hybrid *S.* × *townsendii* and the much commoner fertile amphidiploid from the same cross, *S. anglica*. The latter alone was recorded in our samples and is the sole constant of the community.

Rare species

Arthrocnemum perenne

Physiognomy

S. anglica always dominates as scattered tussocks, coalescing clumps or a continuous sward up to 1 m in height. The community is species-poor though the associates are somewhat varied. *Puccinellia maritima* and annual Salicornias occur frequently and may account for up to 50% cover and beneath them there is often an algal mat. Free-living fucoids such as *Fucus vesiculosus* ecad *caespitosus* and ecad *volubilis* may be locally abundant. *S.* × *townsendii* may be recognised within *S. anglica* swards by its denser tussocks of shorter shoots. It sometimes forms extensive swards as at Hythe and Poole (Marchant 1967) and may occur as a landward fringe to *S. anglica* (Hubbard 1965). In such cases the associates of *S.* × *townsendii* are the same as in the community as a whole.

Sub-communities

Beeftink & Géhu (1973) and Kortekaas *et al*. (1976) have characterised a variety of sub-communities within the European *Spartinetum townsendii*. Some corresponding distinction could be made within the British stands but their general species poverty, their capacity for rapid floristic change and the unchallenged dominance of *S. anglica* throughout argue for retaining a single community at national level. Sub-division may be more appropriate in detailed studies of particular marshes: a few sites, for example, have a distinctive phase with *Atriplex hastata* and *Suaeda maritima* conspicuous.

Habitat

Although scattered plants of *S. anglica* can be found in almost every salt-marsh community, the distinctive situations of the community are towards the seaward fringes of marshes, on creek sides, colonising old pans in the upper-marsh zone and, more rarely, in brackish seepage areas behind sea walls. The *Atriplex hastata-Suaeda maritima* phase is characteristic of tidal drift.

A wide variety of substrates is colonised, from extremely soft mud to shingle. There is some evidence of more rapid vegetative spread through finer material (Chater & Jones 1957). The pH is generally above 7.0 and loss-on-ignition varies from 0.2% to 36.3% (Adam 1976). The sediment is generally strongly reduced although there may be a narrow zone of oxidation around the roots. *S. anglica* is extremely tolerant of tidal submergence. In general, its lower limit seems to be around mean high water of neap tides, which implies about 6 hours' submersion/day at spring tides (Goodman *et al*. 1969, Dalby 1970, Morley 1973, Proctor 1980) but in exceptional situations, as in the shelter of Poole Harbour with its narrow tidal range, the community may extend down to mean low water of neap tides, with as much as 23½ hours' submersion/day at neap tides (Hubbard 1969). The lower limit of colonisation is therefore probably controlled by factors other than submersion tolerance and it appears most likely that exposure to the physical effects of wave or tidal action is responsible. Goodman *et al*. (1959) and Goodman (1960) have shown how *S. anglica* may become dwarfed by such a process where the maximum fetch is short. Such stunted plants resume normal growth under culture (Goodman *et al*. 1969) and should be distinguished from the dwarf brown mutants described from certain sites (e.g. Chater 1965). It is also possible that the nature of the substrate may influence the seaward limit of the species but data are lacking. The landward limit of extension may be controlled by the juxtaposition of existing communities up the shore. *S. anglica* can tolerate up to about 2.5% chloridity

(Ranwell *et al*. 1964, Proctor 1980) and this may give it more competitive advantage in the hypersaline conditions when dry weather follows high tides on the upper marsh.

The community occurs on both grazed and ungrazed marshes. Although less heavily exploited than some marsh communities, it appears to be eaten by rabbits, sheep and cattle and *S.* × *townsendii* may actually be encouraged or maintained by grazing (Hubbard 1965) and its growth favoured against invasion by *S. anglica* where the two species occur contiguously. Hubbard & Ranwell (1966) showed that cut and ensilaged *S. anglica* had a similar intake, digestibility and crude protein content to medium quality hay when fed *ad libitum* to Halfbred × Suffolk wethers, though they recognised that marsh physiography would usually militate against its widespread exploitation as a crop. Despite its dramatic spread, *S. anglica* rarely seems to pose a navigational hazard though its presence in coastal resorts or nature reserves may be undesirable. Some control has been achieved by helicopter spraying with dalapon (Ranwell 1967) though assiduous digging is usually necessary to ensure eradication.

Zonation and succession

S. × *townsendii* was first noticed around Southampton Water in the 1870s and is presumed to be a natural hybrid between the native *Spartina maritima* and the introduced *S. alterniflora* (Marchant 1967). Its slow natural spread was quickly overtaken by the much more vigorous fertile amphidiploid *S. anglica* which, in the 20 years after its first appearance in Southampton Water and The Solent probably around 1890, had colonised every estuary and salt-marsh between Chichester and Poole (see, for example, Goodman *et al*. 1959, 1969, Hubbard 1965, Ranwell 1967, Hubbard & Stebbings 1967). Widespread planting for reclamation after 1910 extended the distribution of *S. anglica* in Britain and natural spread from these centres has filled many gaps.

S. × *townsendii* appears to have been transmitted to a number of scattered localities by inclusion of sterile material in transplant consignments but this species probably accounted for less than 20 ha out of a total of over 12000 ha of marsh dominated by *S. townsendii s. l.* in Great Britain at the last detailed survey (Hubbard & Stebbings 1967).

Once established, the plants perennate and reproduce naturally by rhizome fragmentation, especially where the tidal run is fast, as at Bridgwater Bay (Ranwell 1964*a*) and, in the case of *S. anglica*, by seed, the set of which is regular though variable in quantity (Goodman *et al*. 1969). Spread from such fragments or seedlings can be rapid in *S. anglica* with clonal patches expanding and coalescing into clumps and then closing to a sward; in other cases discrete patches may persist for long periods.

In many places *S. anglica* has become established on previously bare substrates and initiated the development of new marshes. Accretion of material has been found to vary between 0.5 and 10 cm/year (Ranwell 1964*a*, Bird & Ranwell 1964); at the higher rates something like 500 cm/ha/year of material is deposited. Accretion rate may depend on local climate, the tidal pattern and perhaps the seasonal microflora (Ranwell 1964*a*) and the subsequent marsh drainage pattern may be influenced by the slope, tidal range and substrate type (Braybrooks & J. M. Lambert, unpublished). Accretion eventually raises the marsh surface to a level at which other species can theoretically compete with the *S. anglica* but, although species from *Puccinellietum maritimae* and *Juncetum gerardi* communities occur occasionally within swards, they are never particularly abundant and competition with the tall and vigorous *S. anglica* may prevent overtopping and the replacement of the community. Litter accumulation or frost action (Hubbard & Stebbings 1967, Ranwell 1972) and grazing (Ranwell 1961, Goodman *et al*. 1969) may initiate the opening up of the *S. anglica* sward and allow the spread of *Puccinellia maritima*.

On the higher parts of ungrazed marshes there is evidence of invasion by a variety of plants. At Bridgwater Bay, a short-period sub-seral alternation of *S. anglica* and *Atriplex hastata* has been observed on accumulated drift with sand (Ranwell 1961, 1964*b*). *A. hastata* has also invaded the upper part of a *S. anglica* marsh at Lytham on the Ribble estuary. At Keysworth in Poole Harbour, *Elymus pycnanthus* has invaded (Hubbard & Stebbings 1968). There and at Bridgwater, *Scirpus maritimus* and *Phragmites australis* have also appeared at higher levels and replaced about 50% of the *S. anglica* sward in 12 years. Ranwell (1972) has suggested that such a process is favoured by the development of less saline conditions consequent upon land-drainage seepage but this has not been widely investigated. *Halimione portulacoides* can establish itself along creek margins within *S. anglica* marshes (Goodman *et al*. 1959).

S. anglica has also become established on existing marshes. Invasion of *Zostera noltii* swards has been recorded on the south and east coasts (Goodman *et al*. 1959; Bird & Ranwell 1964; Hubbard & Stebbings 1968) and Chapman (1959) mapped such a process in North Cockle Bight at Scolt Head between 1932 and 1959. At that site, *Z. angustifolia* on very soft mud was not invaded; neither is there any evidence that *S. anglica* has anywhere replaced *Z. marina* which occurs at lower levels than *Z. noltii*. At Keysworth in Poole Harbour, a *Ruppia maritima-Potamogeton pectinatus* community has been replaced by *S. anglica* (Hubbard & Stebbings 1968). *S. anglica* can flourish at the same level as the *Salicornietum europaeae* and, as a result, pioneer vegetation

of this kind is now of local occurrence throughout south-east England.

The extent to which *S. anglica* invades other existing marsh communities is uncertain. Pans and creeks in vegetation higher up the marsh may be grown over and scattered plants are widespread throughout marshes, but the wholesale replacement of other communities is not well documented. Chater & Jones (1957) provide some evidence for a slow advance into *Puccinellietum maritimae* and *Juncetum gerardi* in the Dovey estuary but this is not apparent at many sites. Similarly there is little evidence as to how much invasion into *S. anglica* swards takes place from contiguous communities. On grazed marshes in the Dovey, creek levees have become colonised by *Festuca rubra* which has eventually ousted *S. anglica*; because of the frequency of creeks there, the total area of marsh affected is considerable (Chater 1973). Heavily grazed and poached upper levels of *S. anglica* have elsewhere been invaded by *Puccinellia maritima*. It is not known how far the development of a *S. anglica* community to seaward of an existing marsh complex affects the overall nature of the marsh but it might be expected that alterations in drainage would be of prime importance.

In general, *S. anglica* has consolidated its early initial spread but the patchy degeneration of sward which became known as 'die-back' was noticed as early as 1928 and in some sites has made a considerable impression. It is still mainly restricted to Channel coast marshes and its exact cause remains unknown. Pathogens and pollution have been ruled out (Goodman *et al*. 1959) and it seems possible that the process is caused by a toxic reduced inorganic ion (perhaps sulphide) produced in anaerobic waterlogged root environments (Goodman & Williams 1961). Alternatively, the switch from accretion to ablation under *S. anglica* may be responsible for its demise.

Distribution

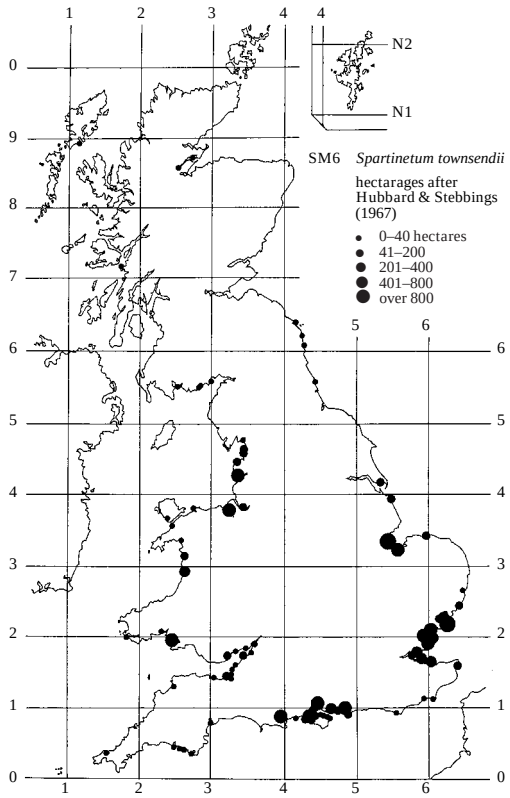
Spartinetum townsendii is widespread around the English and Welsh coasts and is still expanding vigorously at a number of sites along the Scottish shore of the Solway. *S.* × *townsendii* in itself present in abundance only below Hythe in Southampton Water (Hubbard & Stebbings 1967) though there is F_1 material scattered through *S. anglica* swards from Poole to Wittering and on the Isle of Wight. This natural limit is probably set by the slow vegetative spread of the species. There are also small quantities, probably transmitted with *S. anglica* for transplant, in Norfolk, Somerset, Merioneth and Dublin. The limit of *S. anglica* and of the association as a whole, may be related to temperature: in the northern hemisphere, really successful plantings occur south of the 13–18 °C July isotherms (Goodman *et al*. 1969). The far northern stations of the species in Argyll and Harris (Hubbard & Stebbings 1967) have not been checked but it is known that growth in these localities is very slow and seedling establishment poor because of winter storms, cold and bird damage (Shaw, *pers. comm*. in Goodman *et al*. 1969). The European distribution of the community is discussed by Beeftink (1972), Géhu (1972) and Beeftink & Géhu (1973).

Affinities

The association is easily defined floristically by the dominance of *S. anglica* and in phytosociological schemes the community has been placed in a separate class, the Spartinetea, with other communities based on *S. maritima* and *S. alterniflora*.

Floristic table SM6

Spartina anglica	V (5–10)
Algal mat	III (2–9)
Puccinellia maritima	III (1–7)
Salicornia agg.	III (1–7)
Suaeda maritima	II (1–5)
Aster tripolium var. *discoideus*	I (1–7)
Aster tripolium (rayed)	I (2–6)
Aster tripolium	I (1–5)
Atriplex prostrata	I (2–7)
Limonium cf. *L. vulgare*	I (1–3)
Plantago maritima	I (3–5)
Fucus vesiculosus ecad *caespitosus*	I (2–5)
Fucus vesiculosus ecad *volubilis*	I (2–6)
Catenella repens	I (2)
Cochlearia anglica	I (2–5)
Spergularia media	I (1–5)
Halimione portulacoides	I (2–6)
Number of samples	136
Mean number of species/sample	3 (1–10)
Mean vegetation height (cm)	34 (8–10)
Mean total cover (%)	84 (25–100)


N2
N1
SM6 *Spartinetum townsendii*
hectarages after Hubbard & Stebbings (1967)
0–40 hectares
41–200
201–400
401–800
over 800

SM7
Arthrocnemum perenne stands

Arthrocnemum perenne is a perennial halophyte with a restricted distribution in Britain: it occurs around the coast of south-east England from The Wash to Poole Harbour with isolated records from North Wales and Teesmouth (Perring & Walters 1962). It is encountered as an occasional in a variety of communities from both low and high marsh and only very locally is it an important constituent of salt-marsh vegetation.

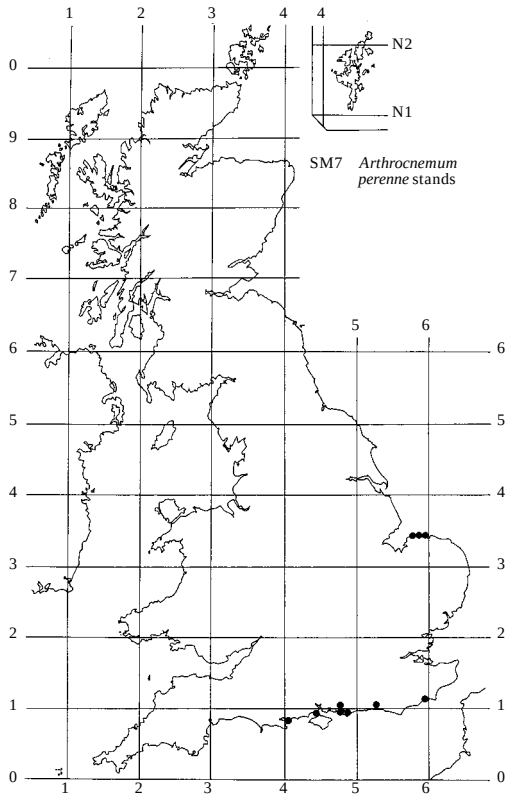
At a number of sites in north Norfolk, *A. perenne* forms an open mosaic with *Halimione portulacoides*, *Puccinellia maritima* and *Suaeda maritima* at the lower limit of *Halimionetum* on sand or firm silt with abundant gravel and shell fragments. A similar community occurs very locally on firm clays with shell fragments elsewhere in south-east England.

Dense pure stands of *A. perenne* are found on drift litter over shell banks at a few sites, particularly around Chichester Harbour, Hampshire. Scattered bushes of *A. perenne* are associated with local erosion within low-marsh communities, especially where these occur on gravel-rich substrates (Beeftink 1965, 1977*a*; Beeftink & Géhu 1973).

Although Beeftink (1965, 1977*a*) recognises the occurrence of *Salicornietum radicantis* Br.-Bl. 1931 in Britain we have insufficient data to characterise a community. The *A. perenne-Halimione portulacoides* mosaics could perhaps be regarded as an extreme form of *Halimionetum*.

Floristic table SM7

Arthrocnemum perenne	V (2–9)
Halimione portulacoides	V (2–9)
Puccinellia maritima	V (2–6)
Suaeda maritima	IV (2–4)
Salicornia agg.	III (2–6)
Algal mat	III (4–8)
Limonium cf. *L. vulgare*	III (2–5)
Aster tripolium var. *discoideus*	III (2–7)
Aster tripolium	I (1–3)
Bostrychia scorpioides	I (4–5)
Spergularia media	I (1)
Number of samples	12
Mean number of species/sample	6 (3–9)
Mean vegetation height (cm)	19 (8–30)
Mean total cover (%)	76 (40–100)


N2
N1
SM7 *Arthrocnemum perenne* stands

SM8

Annual *Salicornia* salt-marsh community
Salicornietum europaeae Warming 1906

Constant species
Several distinct taxa can be recognised among the British annual Salicornias but diagnosis below the level of the three groups *S. europaea*, *S. procumbens* and *S. pusilla* is difficult for non-specialists. Here, all annual taxa encountered are described under *Salicornia* agg. and this is the sole constant of the community.

Rare species
Arthrocnemum perenne.

Physiognomy
The community comprises ephemeral stands of annual Salicornias sometimes with no other species. The vegetation is invariably somewhat open and though *Salicornia* agg. is always conspicuous, the density of plants is variable: around The Wash, for example, *Salicornia* agg. cover is high whereas at sites with sandier substrates the density can be very low. There is often an algal mat over the substrate surface but vascular companions are usually very few. Scattered plants of *Puccinellia maritima*, *Suaeda maritima* and *Spartina anglica* occur frequently with occasional records for a variety of other lower marsh species. At a few sites (Blakeney Point, for example), *Fucus vesiculosus* ecad *caespitosus* is abundant.

Sub-communities
With careful identification of distinct taxa, it may be possible to define a range of communities within this broad general unit as a number of Continental authors have done (see, for example, Géhu & Delzenne 1975). Ball & Tutin (1959) recommend collecting a dozen specimens from populations in September/October when the characteristic colours have developed. Where particular taxa have been ascribed distinct ecological preferences *in litt*. these have been noted below.

Habitat
Annual Salicornias germinate in May from seeds widely dispersed over whole marsh surfaces. The lower limit of establishment appears to be set by the time necessary for the seedlings to become firmly anchored: Wiehe (1935) showed that, in the Dovey estuary, two to three days' exposure between tidal flooding was necessary for sufficient root growth to take place. The speedier radical growth of *Salicornia dolichostachya* over *S. europaea sensu stricto* may give the former an establishment advantage in such situations: in the Dee estuary, *S. dolichostachya* is certainly the commoner species in the open habitats of the lower marsh (Ball & Brown 1970; see also Ball & Tutin 1959).

Salicornia agg. is tolerant of frequent tidal submersion, enduring around 600 flooding tides/year at its lower limits where it forms the familiar pioneer stands. The community is also characteristic of other bare marsh habitats such as creek sides, borrow pits and other disturbed areas in the upper marsh. Here seedlings grow rapidly and by August the plants are bushy, green and up to 15–20 cm high. Although certain taxa, *S. europaea s. s.* for example, appear less susceptible than others to competition from perennial grasses (Ball & Brown 1970), growth in the upper marsh is generally slow and the restrictions may be due to the lack of competition for sediment nutrients, especially nitrogen, with established perennials (Pigott 1969, Stewart *et al*. 1972). Addition of nutrients to *Salicornia* plants within the other high marsh communities stimulates growth to levels characteristic of the lower marsh stands, though a lag in response is suggestive of a determinate growth pattern genetically adapted to an environment with a cyclical but delayed suitability: such sites are not flooded again after *Salicornia* germination until the autumn equinox (Jefferies *et al*. 1979).

Within suitable sites, the community can flourish on a variety of substrates from hard clay to shelly sand, occasionally even on shingle but only rarely are very soft sediments colonised. Where *Spartina anglica* has become well established, the low-marsh *Salicornia* stands tend to be restricted to thin gravels or shingles over hard clay (Perraton 1953). Where wind-blown sand is abundant,

plants tend to adopt a decumbent habit and can survive virtual burial for most of the summer (Tüxen 1974). In brackish areas behind sea walls, which we have not examined closely but where annual Salicornias may flourish, *S. ramosissima* and *S. prostrata* appear to be the common taxa (Ball & Tutin 1959).

Annual *Salicornia* stands occur on both grazed and ungrazed marshes. All species are highly susceptible to oil and refinery effluent spills being killed by a single inundation (Baker 1979). On a few marshes in south-east England (principally around The Wash) Salicornias are harvested as 'samphire' for human consumption.

Zonation and succession

Salicornia stands may form a distinct zone in the lower marsh, sometimes hundreds of metres deep. At some sites, particularly those on sandy substrates, patches of *Salicornia* may be separated from the main marsh front by several hundred metres of bare flat. The community can also occur in a mosaic with the *Puccinellietum maritimae* or with the *Spartinetum townsendii*. The expansion of the latter has much reduced the area of lower marsh available for pioneer *Salicornia* establishment especially in south-east England.

Although the annual *Salicornietum* is generally the lowest marsh community proper it may rarely initiate a succession because summer accretion can be offset by ablation after the stands have disappeared in the winter. Chapman (1957) has, however, produced a cartographic record of changes in the distribution of *Salicornia* marsh at Scolt Head, Norfolk with ageing of open and closed marshes.

Distribution

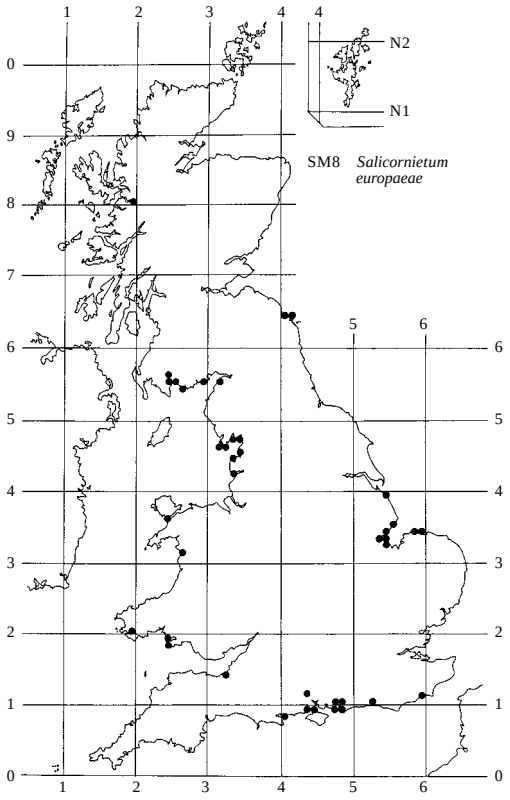
The community is widely distributed around the British coastline. On the sandy marshes of the west coast occurrences are local, though extensive open stands occur in some estuaries. The very local distribution in western Scotland is largely a reflection of the lack of suitable habitats: many loch-head marshes are fronted by cobble beaches rather than sand flats and these carry a dense cover of free-living fucoids.

Affinities

Equivalent communities have a widespead distribution in Europe. Although various divisions have been made with the *Salicornietum europaeae*, the general composition and habitat relationships of the vegetation types accord with the British community (see, for example, Beeftink 1962, 1965, 1972, 1977*a*).

Floristic table SM8

Salicornia agg.	V (4–9)
Algal mat	III (3–8)
Puccinellia maritima	III (1–7)
Suaeda maritima	II (1–5)
Spartina anglica	II (1–5)
Halimione portulacoides	I (1–3)
Aster tripolium var. *discoideus*	I (1–4)
Aster tripolium (rayed)	I (1–3)
Number of samples	81
Mean number of species/sample	3 (1–7)
Mean vegetation height (cm)	7 (2–20)
Mean total cover (%)	53 (5–95)



SM9

Suaeda maritima salt-marsh community
Suaedetum maritimae (Conrad 1935) Pignatti 1953

Synonymy
Suaeda maritima nodum Adam 1976; *Salicornietum auct. p.p.*

Constant species
Suaeda maritima is a variable taxon within which a number of distinct forms have been recognised. These are sometimes treated as varieties (e.g. Chapman 1947, Clapham *et al.* 1962) or as species. Ball (1964) has a single sub-species *S. maritima maritima* to include all British material. This is the only constant taxon of the community.

Physiognomy
This is a species-poor community, generally open, though always dominated by *Suaeda maritima* the density of which is normally high. There is sometimes a little annual *Salicornia*, *Puccinellia maritima*, *Spartina anglica*, *Halimione portulacoides* and *Aster tripolium* var. *discoideus*. An algal mat is quite common and Chapman (1947) lists seven different algal assemblages associated with abundant *Suaeda maritima*.

Sub-communities
Variation within the community is continuous, though the predominance in particular stands of different forms of *Suaeda maritima* has been used by some (e.g. Géhu 1975) to assign such stands to different communities. However, diagnosis is often difficult and there seem to be few consistent ecological differences between the taxa.

Habitat
Suaeda maritima is an annual and it is tolerant of a wide range of soil types subject to various submersion regimes: Chapman (1947) reported it dominant on Norfolk marshes with between 290 and 430 submergences/year. Like the annual Salicornias, its growth appears heavily dependent upon sediment nutrients, especially nitrogen (Pigott 1969, Stewart *et al.* 1972), and it is particularly characteristic of open situations free of competition from established perennials. On the lower marsh it is especially distinctive of rather gravelly mud where it forms mosaics with stands of annual Salicornias. Fragmentary stands are found around the base of the shell banks which occur at low levels in a few sites. Pure stands of *S. maritima* are a distinctive feature of disturbed situations such as the piles of sediment dumped on marshes during the construction of sea walls and drainage channels. Creek sides can also carry the community. Two further distinctive habitats are the accumulations of drift litter that occur at the foot of sea walls where dense stands can exploit the release of nutrients upon decomposition of the litter (see Beeftink 1966) and brackish areas behind sea walls where prostrate forms of *S. maritima* are common.

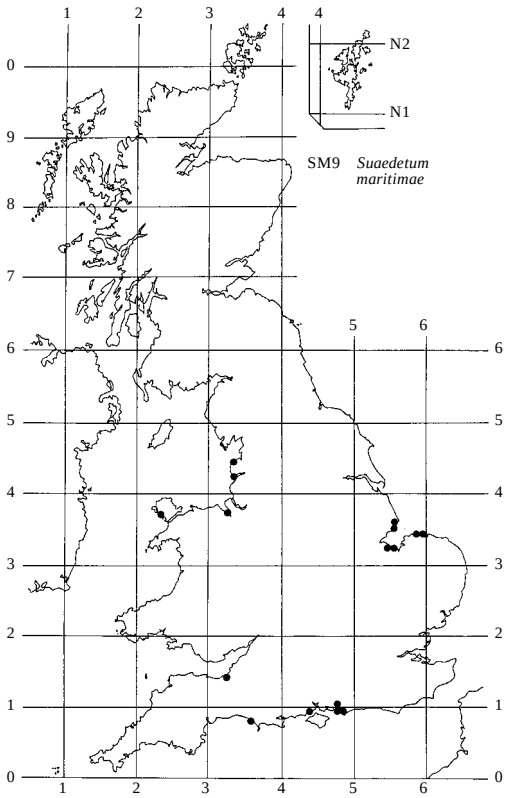
Zonation and succession
The habitat diversity of the community makes it difficult to generalise about the successional status of the community. In situations subject to repeated disturbance it can recur every year but increased stabilisation leads to replacement by the community appropriate for the particular level of the marsh.

Distribution
The community is widespread but many stands are fragmentary. It is most frequent in south-east England and very local in west Scotland.

Affinities
Although sometimes considered as part of a *Salicornietum*, stands dominated by *Suaeda maritima* are sufficiently distinctive to be worthy of considering as a separate community. Certain authors (e.g. Beeftink 1962, 1965, 1977*a*; Westhoff & den Held 1969) consider the nitrophilous character of the vegetation warrants placing the community with the ephemeral driftline associations of the Cakiletea but the floristic affinities to that class are few. The low-marsh occurrences are seen by others (e.g. Géhu 1975, Géhu & Delzenne 1975) as indicating a similarity to the communities of the Thero-Salicornieta which then becomes the class for all ephemeral chenopod-dominated vegetation types of the low marsh.

Floristic table SM9

Suaeda maritima	V (6–10)
Salicornia agg.	IV (2–7)
Puccinellia maritima	II (2–4)
Algal mat	II (5–8)
Spartina anglica	II (2–3)
Halimione portulacoides	II (1–4)
Aster tripolium var. *discoideus*	II (1–3)
Aster tripolium (rayed)	I (2)
Number of samples	18
Mean number of species/sample	3 (2–8)
Mean vegetation height (cm)	27 (8–50)
Mean total cover (%)	69 (30–100)



SM10

Transitional low-marsh vegetation with *Puccinellia maritima*, annual *Salicornia* species and *Suaeda maritima*

Adam (1976) recognised a number of vegetation types of the low marsh in which *Puccinellia maritima* was co-dominant with annual *Salicornia* species and/or *Suaeda maritima* during the growing season but which during the winter took on the appearance of very open *Puccinellia maritima* swards. Such transitional vegetation can be regarded as one extreme of variation within the *Puccinellietum maritimae* but, particularly in detailed studies of individual marshes, separate recognition might be appropriate. The description below refers to stands in which all three taxa are present.

Synonymy
Puccinellietum maritimae (Warming 1906), W. Christiansen 1927 *auct. p.p.*; *Puccinellia-Salicornia-Suaeda* nodum Adam 1976; *Suaedetum maritimae auct. p.p.*

Constant species
Puccinellia maritima, annual *Salicornia* spp., *Suaeda maritima*.

Rare species
Arthrocnemum perenne.

Physiognomy
Stands of the community are invariably species-poor and always dominated by complementary proportions of the three constants which during the growing season form a fairly low sward of rather variable total cover. Rayed *Aster tripolium* and *A. tripolium* var. *discoideus* are quite frequent though never abundant. There is sometimes an algal mat which can cover up to 50% of the substrate surface.

Habitat
At its lower limit the number of tides flooding the community is probably similar to that experienced by the lower part of the *Puccinellietum maritimae*. Soils vary from firm clays to coarse sands with a pH range of 7.0–8.0 and high levels of free calcium carbonate.

On sandy substrates, the community may occur as a pioneer. It is then rarely extensive, forming patches in a mosaic with the *Salicornietum europaeae*, the *Spartinetum townsendii* or the *Puccinellietum maritimae*. Where the lower marsh consists of a hummocky *Puccinellia maritima* community, a situation confined to sandy marshes which are normally heavily grazed, this transitional community may be found on the hummock tops (cf. Oliver 1907, Hill 1909, Tansley 1911).

On muddier marshes in south-east England, the community behaves in the contrary fashion, occurring in slight depressions within the *Puccinellietum maritimae*, *Spartinetum townsendii*, *Asteretum tripolii* and *Halimionetum portulacoidis*.

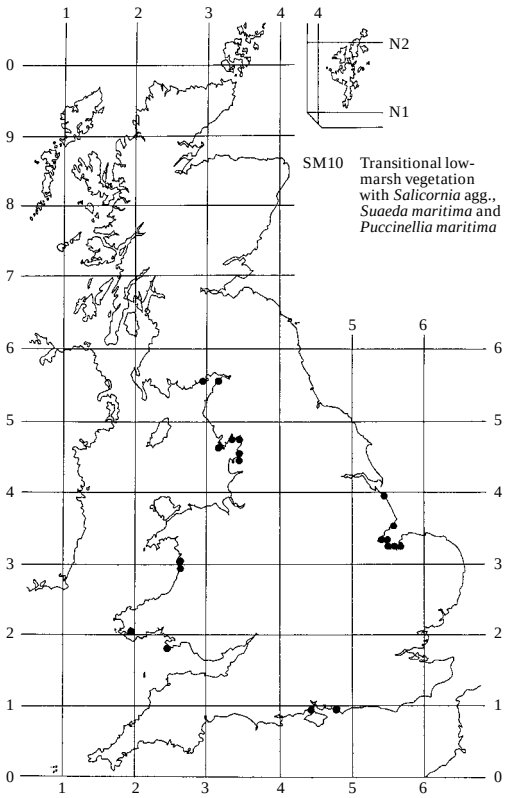
The community is also widespread on the sides of large creeks where it occupies a distinct zone above the *Salicornietum europaeae*. The majority of such occurrences are on ungrazed or cattle-grazed marshes; on sheep-grazed marshes, the community is confined to inaccessible creek sides.

Zonation and succession
In the low marsh, the community will be replaced by others as accretion progresses: in the south-east most probably by the *Puccinellietum maritimae* or the *Halimionetum portulacoidis*, in the west by the former or, more rarely, by the *Juncetum gerardi*. Creekside occurrences are part of what is probably a static zonation rather than a successional sequence.

Distribution
Apart from along the western Scottish coast, where occurrences are relatively rare, the community is widespread, although stands are often small.

Floristic table SM10

Puccinellia maritima	V (2–9)
Salicornia agg.	V (2–8)
Suaeda maritima	V (2–8)
Aster tripolium var. *discoideus*	III (2–5)
Aster tripolium (rayed)	III (1–4)
Algal mat	II (4–7)
Spartina anglica	I (1–4)
Halimione portulacoides	I (1–2)
Triglochin maritima	I (3–4)
Spergularia media	I (2–3)
Limonium cf. *L. vulgare*	I (2)
Armeria maritima	I (1–4)
Number of samples	50
Mean number of species/sample	5 (3–8)
Mean vegetation height (cm)	15 (4–40)
Mean total cover (%)	88 (30–100)



SM11

Aster tripolium var. *discoideus* salt-marsh community

Asteretum tripolii Tansley 1939

Synonymy

Asteretum and Creek *Asteretum* Chapman 1934; *Aster tripolium* var. *discoideus* nodum Adam 1976; descriptions of Great *Aster* marsh, Scolt Head, Norfolk.

Constant species

Aster tripolium var. *discoideus*, *Puccinellia maritima*, *Salicornia* agg.

Rare species

Arthrocnemum perenne.

Physiognomy

The association is dominated by the rayless *Aster tripolium* var. *discoideus* which is especially distinctive in the late summer–early autumn flowering season when its stems may attain a height of about 1 m; at other times the vegetation is 10–20 cm tall. The stands are generally rather species-poor though there is usually some *Salicornia* agg., *Puccinellia maritima* and *Suaeda maritima*. The substrate surface is frequently dissected by small drainage runnels threading between the *A. tripolium* rootstocks and locally may be carpeted by free-living fucoids, mainly *Fucus vesiculosus* ecad *caespitosus* and *Pelvetia canaliculata* ecad *libera*.

Although there is a floristic gradation between low-level stands with abundant *Salicornia* agg. and those at higher levels with abundant *Puccinellia maritima*, no sensible subdivisions can be made within the association. The floristic disinctions catalogued by Chapman (1934) between a low-marsh *Asteretum* and a Creek *Asteretum* are not borne out in the samples.

Habitat

The association occurs as an extensive zone in the low marsh or on creek sides at varying levels in the marsh. At its lower limits, the association seems able to tolerate upwards of 500 submergences/year (Chapman 1960*a*) with a maximum development around 350 submergences/year (Clapham *et al*. 1942). The sediments are predominantly firm clays or silts low in organic matter but with a high proportion of fine shell fragments and a pH between 7.0 and 8.0. Most of the sites are ungrazed or only lightly cattle-grazed.

Zonation and succession

In the low marsh the association forms a distinct zone above the *Salicornietum europaeae* or the *Spartinetum townsendii* or, occasionally, at the most seaward limit. Upwards it passes into the *Puccinellietum maritimae* or the *Halimionetum portulacoidis*. Landward boundaries are diffuse and patches of the association are frequently found in the lower part of the zone above.

Although *A. tripolium* var. *discoideus* can grow at lower levels on the shore than many salt-marsh species, it is not a successful primary coloniser. Gray (1971) has suggested that it has spread in recent years, possibly following *Spartina anglica* invasion of bare substrates, but the evidence for this is inconclusive. At Scolt Head, Norfolk, Chapman (1959) has shown the association developing from the *Salicornietum europaeae* in about 25 years.

Distribution

The association is predominantly south-eastern in its distribution, being frequent in The Wash, north Norfolk and Essex. Old records have *A. tripolium*-dominated communities on Canvey Island (Carter 1932) and in the Humber (Good & Waugh 1934). It is local on the south coast and in the Bristol Channel (but see Thompson 1922, 1930) and its general absence from the west may reflect climatic limitations, the scarcity of muddy marshes or the higher incidence of grazing there.

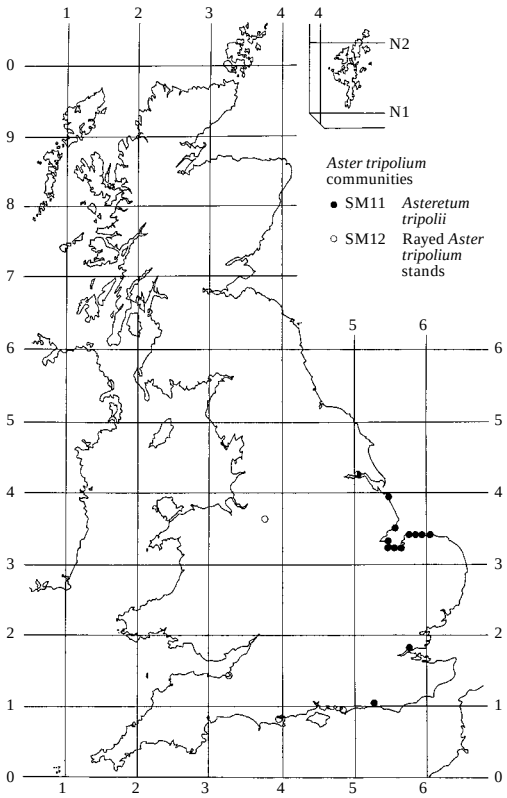
Affinities

The position of the association in the salt-marsh zonation places it between the annual communities of the Salicornietea and the perennial communities of the Asteretea but the perennial nature of *A. tripolium* var. *discoideus* itself suggests that it is best seen alongside the *Puccinellietum maritimae* and the *Juncetum gerardi* of the latter class.

Floristic table SM11 & SM12

	11	12a	12b
Aster tripolium var. *discoideus*	V (4–10)	III (4–7)	
Puccinellia maritima	V (1–9)	V (3–7)	
Salicornia agg.	V (3–9)	III (2–4)	
Suaeda maritima	III (2–8)	III (2–4)	
Algal mat	II (2–8)	I (6)	
Halimione portulacoides	II (1–5)		
Arthrocnemum perenne	I (1–5)		
Fucus vesiculosus ecad *caespitosus*	I (5–8)		
Pelvetia canaliculata	I (4–9)		
Bostrychia scorpioides	I (3–7)		
Aster tripolium (rayed)		V (5–8)	V (7–10)
Spartina anglica	II (1–6)	IV (2–3)	
Plantago maritima	I (4)	III (2–6)	
Spergularia media	I (3–4)	III (4–6)	
Triglochin maritima		II (5)	
Puccinellia distans			V (3–4)
Spergularia marina			III (1–3)
Atriplex prostrata		I (5)	III (2–3)
Scirpus lacustris tabernaemontani			II (2–7)
Juncus bufonius			II (2–3)
Number of samples	53	7	9
Mean number of species/sample	5 (3–8)	6 (4–9)	4 (2–6)
Mean vegetation height (cm)	28 (5–150)	43 (15–80)	68 (60–100)
Mean total cover (%)	80 (45–100)	81 (50–90)	99 (90–100)

11 *Aster tripolium* var. *discoideus* salt-marsh
12a Coastal stands of rayed *Aster tripolium*
12b Inland stands of rayed *Aster tripolium*


N2
N1
Aster tripolium communities
SM11 *Asteretum tripolii*
SM12 Rayed *Aster tripolium* stands

SM12
Rayed *Aster tripolium* on salt-marshes

Stands dominated by rayed *Aster tripolium* have been encountered in situations with some freshwater influence such as brackish ditches behind sea walls where *Spartina anglica* and *Puccinellia maritima* are frequent associates. Beeftink (1962, 1965) has described similar vegetation from sites with local freshwater flushing as a distinct *Aster tripolium* sociatie. Rayed *A. tripolium* is also abundant on periodically-flooded saline muds in inland salt-marshes with *Spergularia marina* and *Puccinellia distans* (see the *Puccinellietum distantis astereto-sum* of Lee 1977; also Edees 1972).

Although some floras note a certain habitat distinction between rayed forms of *A. tripolium* and the var. *discoideus* (e.g. Petch & Swann 1968, Jermyn 1974, Gibbons 1975), the situation is far from simple. The var. *discoideus* can also occur in brackish habitats and Jermy & Crabbe (1978) have recorded vegetation rich in dwarf rayed *A. tripolium* and *Suaeda maritima* from Salen Marsh, Mull, where there is little freshwater influence (cf. the intertidal *Suaedeto maritimae-Asteretum tripolii* Hocquette & Géhu 1965 in Ghestem 1972). Furthermore, even within the rayed form there appears to be a complex of genetically determined variation adapted to different environmental conditions (Gray 1971, 1974; Gray *et al*. 1979). Further sampling is needed to establish the ecological implications of this variation and to check the validity of erecting separate communities for the different forms.

SM13

Puccinellia maritima salt-marsh community

Puccinellietum maritimae (Warming 1906) Christiansen 1927

Synonymy

The *Puccinellietum maritimae* includes a considerable range of closely-related vegetation types. The limits of the association as a whole are similar to those adopted in recent Continental accounts (e.g. Beeftink 1965, Westhoff & den Held 1969) and, as such, would include all or part of a variety of salt-marsh types in earlier British descriptions. The synonmy of the communities is complex and, as many synonyms would be partial, a complete list is not attempted here. Where a particular sub-community has a clear counterpart *in litt*. a note is given below.

Constant species

Puccinellia maritima.

Rare species

The association does not provide the sole, or even major, context for any national rarity but the following occur occasionally: *Arthrocnemum perenne*, *Limonium bellidifolium*, *L. binervosum*, *Salicornia pusilla*, *Spartina maritima* and *Suaeda vera*.

Physiognomy

Mostly, the association occurs as a closed species-poor grassland but the complete range includes very open pioneer vegetation and herb-dominated stands in which *Puccinellia maritima* is of minor importance or even absent. The sward varies from a tight low turf 1–2 cm high to a rank mattress up to 50 cm tall. Although grazing is important in controlling the physiognomy (see below), a considerable range of genetically determined morphotypes of *P. maritima* is present in Britain (Gray & Scott 1977*a*; 1980). Although species from low- and high-marsh communities occur as associates, the *Puccinellietum maritimae* as a whole is differentiated from the low-marsh communities by the reduced frequency and cover/abundance of annual *Salicornia* species and *Spartina anglica* and from the high marsh by low levels of *Festuca rubra*, *Agrostis stolonifera* and *Juncus gerardii*. The most common associates throughout are *Triglochin maritima*, *Plantago maritima* and *Armeria maritima* and there is frequently an algal mat, often floristically varied and comprising a number of distinct species assemblages (Carter 1932, 1933*a*, *b*; Chapman 1934, 1937; Polderman 1979).

Sub-communities

Although the association is of widespread occurrence and individual stands are often great in extent and highly distinctive, the general species-poverty of the vegetation and the site-specific nature of much variation makes it difficult to attain an entirely satisfactory national subdivision. The sub-communities described below should be regarded as provisional and independent local schemes may sometimes be preferable. Alternative national classifications would also be possible: the scheme of Beeftink (1962, 1965) could, for example, be applied here with the addition of units to accommodate communities of northern and western Britain.

Sub-community with *Puccinellia maritima* dominant: *Puccinellietum* (*Glycerietum*) *maritimae* Tansley 1911. This is the most extensive and widespread perennial community of the lower salt-marsh in the British Isles. *P. maritima* is constant and dominant throughout forming a fairly closed sward in which other species are generally poorly represented. Adam (1976) recognised two noda, making a distinction between samples which are less and more species-rich but such a division is somewhat arbitrary and it is probably preferable to recognise a single rather diverse unit. The associate species vary with the level in the marsh and the geographical locality of the sub-community. At the lowest levels, annual *Salicornia* spp. and *Suaeda maritima* are most frequent: at higher levels, *Triglochin maritima*, *Plantago maritima* and *Aster tripolium* are found. *Limonium vulgare* is more frequent in the south and east and *Armeria maritima* in the west. *Glaux maritima* is virtually absent from this vegetation in south-east England. Locally, very dense stands of tall

Puccinellia maritima occur at relatively high levels in the marsh, most notably around The Wash; these stands are often monospecific but may have *Atriplex hastata*.

***Glaux maritima* sub-community:** *Glaucetum maritimae* Dahl & Hadač 1941; *Glaux maritima* isozion Dahlbeck 1945; *Glaux maritima* sociatie Beeftink 1962. Although *G. maritima* occurs at varying levels throughout the association, it is here constant and co-dominant with *Puccinellia maritima* in a low generally species-poor sward. The frequency and cover/abundance of *Triglochin maritima*, *Plantago maritima* and *Armeria maritima* stand between their low levels in the *Puccinellia*-dominated sub-community and the high values they attain in the *Limonium-Armeria* sub-community. *L. vulgare* itself and *Halimione portulacoides* are rare. Stands of this sub-community are often small and fragmentary but at some sites cover large areas. During hot dry summers, the shoots of *Glaux maritima* may become shrivelled by late July in upper-marsh sites. Further, although *G. maritima* is a perennial, its aerial parts die back completely in the winter when stands may appear virtually devoid of vegetation.

***Limonium vulgare-Armeria maritima* sub-community:** General Salt Marsh Tansley 1911 & Chapman 1934 (but not Chapman 1960); *Puccinellietum* (*Glycerietum*) *maritimae* Tansley 1911 *p.p.*; *Statice & Armeria* societies Marsh 1915; *Plagntag*(*in*)*etum* Chapman 1934 *p.p.*; *Limonietum & Armerietum* Tansley 1939 (but not *Armerietum* Yapp & Johns 1917); *Plantagini-Limonietum* Westhoff & Segal 1961; forb salt marsh Dalby 1970. This is one of the most distinctive communities of British salt-marshes with a varied sward dominated by herbaceous dicotyledons which present a colourful spectacle when flowering. *Limonium vulgare*, *Armeria maritima*, *Triglochin maritima*, *Plantago maritima*, *Halimione portulacoides* and annual *Salicornia* spp. (including locally the uncommon *S. pusilla*) are all constant and can be abundant. *Puccinellia maritima*, though also constant, rarely comprises more than 10% of the sward. There is often an algal mat and frequent scattered plants of *Spergularia media* and *Suaeda maritima*. *Limonium humile*, though of only occasional occurrence in this sub-community in south-east England, sometimes replaces *Limonium vulgare*, as in Milford Haven (Dalby 1970) and, to a lesser extent, in south-west Scotland. At the highest levels to which the sub-community extends, *Festuca rubra* and *Juncus gerardii* may occur.

The vitality of the common species is variable. Both *Limonium vulgare* and *Armeria maritima* flower profusely but *Aster tripolium* and, at some sites, *Plantago maritima* flower infrequently. *Halimione portulacoides* occurs not in shrubby form but as scattered prostrate shoots with small fleshy leaves which tend to be shed in late summer. Annuals, such as the *Salicornia* spp. and *Suaeda maritima*, persist as small plants which often turn red in early summer, possibly reflecting their inability to compete with established perennials for nutrients, particularly nitrogen.

***Plantago maritima-Armeria maritima* sub-community:** *Armerietum* Yapp & Johns 1917 *p.p.*; *Plantag*(*in*)*etum* Chapman 1934 *p.p.*; *Plantago maritima* isozion Dahlbeck 1945. This resembles the *Limonium-Armeria* sub-community in being dominated by herbaceous dicotyledons. *Plantago maritima*, *Armeria maritima* and *Triglochin maritima* are again constant and abundant and *Puccinellia maritima* is, as there, a relatively inconspicuous contributor to the sward. Here, however, *Halimione portulacoides* is rare and *Limonium vulgare* absent while *Glaux maritima* and rayed *Aster tripolium* are constant. Although always virtually closed, the vegetation exists in two physiognomic forms based on variation in *Plantago maritima* which sometimes has long leaves and an upright habit (Chapman 1934), sometimes short leaves appressed to the soil surface.

***Puccinellia maritima*-turf fucoid sub-community.** Turf fucoids occur at low levels in various types of *P. maritima* salt-marsh, but here they comprise an extensive dense understorey of diminutive plants beneath a sward often dominated by *Plantago maritima* but also with constant and abundant *Puccinellia maritima*, *Glaux maritima* and *Armeria maritima*. *Fucus vesiculosus* ecad *muscoides* is the principal fucoid and Cotton (1912) and Polderman & Polderman-Hall (1980) have both described the understorey as a discrete algal assemblage.

***Puccinellia maritima-Spartina maritima* sub-community:** *Puccinellietum maritimae typicum*, phase with *Spartina maritima* Beeftink 1962. Here, *P. maritima* dominates with variable amounts of *Spartina maritima*, annual *Salicornia* spp., *Limonium vulgare*, *Suaeda maritima* and *Aster tripolium* var. *discoideus*. Stands of this sub-community are generally a few tens of square metres in extent.

Habitat

The *Puccinellietum maritimae* is the most widespread and extensive perennial community of the lower salt-marsh in Britain. It occurs both as a discontinuous pioneer zone and as a continuous sward in the zonation above the pioneer vegetation. It is also common on slumped creek-sides, in old pans and on disturbed sites in the upper marsh. Fragmentary stands of the association are found infrequently on very exposed maritime cliffs, for example on the Butt of Lewis, Outer Hebrides. (see also Praeger 1911).

The association occurs on a wide range of substrates including various clays and silts, highly calcareous sands

and soils of high organic content; more rarely, it is found on gravel and shingle. Its importance as a colonising community is very much increased on sandier substrates: it is the most frequent pioneer on the sandy marshes of western England and Wales and commoner, for example, on the north-west as against the south-east shore of The Wash (Anon. 1976). The pH is usually basic with most soils in the range 6.0–8.5 (Adam 1976, Bridges 1977, Gray & Scott 1977*a*). Sediments in pioneer and lower marsh zones are generally higher in calcium content and lower in organic matter than those higher up the marsh (Gray & Bunce 1972, Adam 1976). Soils are often intermittently waterlogged and poorly aerated and share a moderate to high submergence rate and salinity. Data on submergence are limited but suggest that the lower limit of the *Puccinellietum* may experience more than 350 submergences/year; Gray & Scott (1977*b*) recorded a mean rate for their Morecambe Bay samples with *Puccinellia maritima* of 220 submergences/year while on Scolt Head, Norfolk, Chapman's General Salt Marsh extended from 150 to 225 submergences/year (Chapman 1960*b*). Proctor (1980) measured salinities of 12–30 g l^{-1} for *Puccinellia maritima* in the Exe estuary, Devon, but levels well in excess of those of sea-water may develop in the higher marsh because of evaporation in the absence of submersion.

Grazing is of undoubted importance in the maintenance of the association though its effect is complex and there is evidence that the response of species varies between sites. Many marshes are heavily used for pasturing stock, most frequently sheep but also cattle and horses; wildfowl, rabbit, hare and vole grazing may also be intensive. Grazing affects the species composition of the sward. It may be important in maintaining the dominance of perennial grasses as against herbaceous dicotyledons (Gray 1972) or in controlling the balance between *Puccinellia maritima* and *Festuca rubra* (Gray & Scott 1977*b*): *P. maritima* responds to grazing by the production of small, prostrate, short-leaved and rapidly tillering forms (Gray & Scott 1977*a*, 1980). With intensive grazing *Limonium* spp. and *Halimione portulacoides* may be reduced in abundance (Boorman 1967, Ranwell 1968, Rojanavipart & Kay 1977). On silt and clay marshes heavy cattle-trampling can lead to widespread poaching.

Moderate grazing helps maintain a sward which can support considerable populations of wintering wildfowl. There is evidence of a preference for *Puccinellia maritima* as against rank swards, such as those of the *Juncetum gerardi*, in wigeon (Cadwalladr *et al*. 1972, Cadwalladr & Morley 1974) and the brent goose (Charman & Macey 1978). For brent, the *Puccinellietum* provides a valuable food source after *Zostera* and *Enteromorpha* and there is heavy use in January–March (Ranwell & Downing 1959; Charman 1975, 1977*b*, 1979; Charman & Macey 1978).

Some of the species in the association are resistant to oil spillage by virtue of their underground storage organs, e.g. *Plantago maritima*, *Armeria maritima* and *Triglochin maritima*, but *Puccinellia maritima* itself declines rapidly with repeated oiling (Baker 1979).

The particular environmental relationships of the sub-communities are as follows. The *Puccinellia-Glaux* sub-community occurs in a number of different habitats all of which are open to rapid disturbance: old turf-cuttings, former pans, creeks, old cart tracks. It is also found in situations where the boundary between salt-marsh and dune becomes blurred: where sand is blown on to the upper marsh, where dune lows are subject to tidal flooding (see Lambert & Davis 1940) and where salt-marsh/dune interfaces are subject to disturbance by trampling or car-parking. There are small stands on gravel and shingle on the upper marsh at some sites and, at others, large stands in the open areas behind sea walls.

The *Limonium-Armeria* sub-community is found at relatively high levels in the salt-marsh zonation. Frequently it does not form a continuous belt but occurs as a series of small discrete stands separated from each other by creek levees. The soil in these inter-creek basins is normally a heavy clay with a considerable quantity of organic matter (loss on ignition >30%) in the upper few centimetres of the profile. The development of creek levees restricts the drainage in the basins (the concave stage of marsh development after Beeftink 1966): water may be retained there after submergence (Perraton 1953) and the soils are often strongly gleyed. On many salt-marshes in south-east England such stands have the maximum pan density within the sites (Pethwick 1974). The pan edges are often marked by a narrow fringe of more vigorous vegetation in which *Triglochin maritima* is particularly prominent.

At some sites, where salt-marsh abuts onto dunes, there is an unbroken zone of this sub-community. Here the sediments are sands or alternating bands of sand and clay and pans and creeks are relatively few; such creeks as do occur lack pronounced levees. At the higher parts of such stands *Festuca rubra* and *Juncus gerardii* occur. This habitat seems to be that described for the *Plantagini-Limonietum* Westhoff & Segal 1961.

The *Plantago-Armeria* sub-community is also found at comparatively high levels. The form with tall *Plantago maritima* occurs above the *Limonium-Armeria* sub-community and the form with short *P. maritima* in shallow depressions throughout the upper *Puccinellietum* and sometimes in the higher *Juncetum gerardi* of grazed salt-marshes. Extensive stands are found in some re-vegetated turf-cuttings in Morecambe Bay.

The *Puccinellia*-turf fucoid sub-community is rare or absent from sandy salt-marshes and is especially characteristic of loch-head sites in west Scotland where shallow soils (20–30 cm deep) develop over rock or shingle. Such

soils tend to have a high organic content, to be reddish in colour and to contain coarse gravel throughout the profile. Although high salinities can be attained during drought (Gillham 1957*b*), *Festuca rubra* may occur even at the lowest levels attained by this sub-community, perhaps reflecting the influence of high regional rainfall. Small stands of the sub-community are also widespread among coastal rocks in the lower splash zone.

The *Puccinellia-Spartina maritima* sub-community is very local but it has been recorded from mid-marsh depressions and upper-marsh borrow pits with soft mud. Beeftink (1962) considered the vegetation characteristic of mud-flat/salt-marsh transitions.

Zonation and succession

Where the *Puccinellietum* is a pioneer community, as on sandier substrates, it appears to establish itself mainly by the rooting of vegetative fragments of *P. maritima* uprooted from existing swards by grazing stock and carried by tides (Ranwell 1961, Brereton 1971, Adam 1976, Gray & Scott 1977*a*). *P. maritima* can set abundant seed (Gray & Scott 1977*a*) but it has no special dispersal mechanism and, though caryopses can be washed away, seedling establishment in the pioneer zone seems uncommon.

Once established, the scattered plants produce numerous radiating stolons and accrete sediment into a series of hummocks (see Plate 3 in Ranwell 1972). Hummock size varies from shore to shore: some hummocks never exceed 50 cm in height but others are taller and attain a diameter of several metres. The hummock tops may carry the transitional *Puccinellia-Salicornia-Suaeda* community. Yapp & Johns (1917) postulated that the intervening hollows developed into pans but Pethwick (1974) showed that such a model could not account for the majority of upper-marsh pans.

At some sites a narrow zone of very scattered hummocks gives way quickly to a continuous sward of the *Puccinellia*-dominated sub-community. In other cases the hummocky topography persists much higher upshore (see the striking photographs in Yapp & Johns 1917) and eventually passes to fairly smooth swards of some *Puccinellietum* vegetation or, in the mid- and upper marsh, to *Juncetum gerardi* which is the usual high level vegetation of the grazed marshes of the west coast (Figure 8). On ungrazed west coast sites, the *Limonium-Armeria* sub-community may occur in the upper marsh.

In the south-east, the *Puccinellietum* is rarely a pioneer community. Its position in the zonation varies, the *Puccinellia*-dominated sub-community appearing either below or above the *Halimionetum portulacoidis*. In this region, the *Puccinellietum* can be found right up to the tidal limit, either as the *Puccinellia*-dominated sub-community, as around The Wash, or as the very characteristic high marsh *Limonium-Armeria* sub-community.

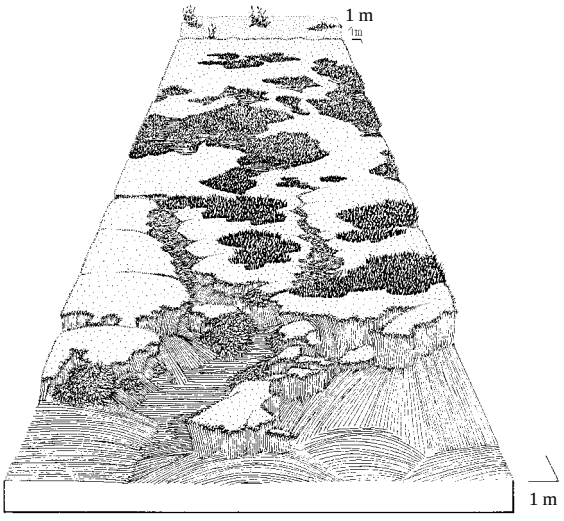
In the upper reaches of estuaries, where the soil salinity in the lower marsh is kept constantly low by freshwater dilution, an inversion of the normal zonation may be found with the *Puccinellietum* in upper marsh depressions where evaporation produces high salinities (Gillham 1957*a*, Adam 1976). Disturbance of upper marsh sites frequently results in the association appearing as a secondary pioneer, especially in the form of the *Puccinellia-Glaux* sub-community (cf. Beeftink 1962).

In the loch-head sites where the *Puccinellia*-turf fucoid sub-community is characteristic, it is frequently the lowest vegetation but it seems only rarely to be actively expanding. To seaward, there is usually a very low cliff or the vegetation cover is discontinuous with discrete patches on isolated rock or gravel plinths.

Distribution

The association is the most widespread community on British salt-marshes and probably no site lacks at least a fragmentary stand. The *Puccinellia*-dominated sub-community is the most widespread of the types, being frequent on all coasts except those of west Scotland and

Figure 8. Zonation on an eroding salt-marsh. The intact marsh carries various kinds of SM16 *Juncetum gerardi*, a ground of the *Armeria* variant of the *Festuca-Glaux* sub-community with patches of the *Juncus gerardii* sub-community. Running down below, on material slumped from the sides of the simple 'herring-bone' creeks, is a narrow zone of the SM13 *Puccinellietum maritimae*. The sequence terminates above in fragmentary SM24 *Atriplici-Elymetum pycnanthi*.



the northern Isles where it is largely replaced by the *Puccinellia*-turf fucoid sub-community. The *Plantago-Armeria* sub-community is also widespread, though local, and the *Puccinellia-Glaux* sub-community is commoner on the west coast. The *Limonium-Armeria* sub-community is widespread in the south-east but much less frequent on the west coast where it is confined to lightly grazed and ungrazed sites. *Spartina maritima* is declining throughout northern Europe and the *Puccinellia-S. maritima* sub-community is restricted to Essex (and perhaps north Kent?).

Affinities

The vegetation types within the *Puccinellietum maritimae* can be seen as a floristic transition between the open annual communities of the lower marsh dominated by *Salicornia* spp. and *Suaeda maritima* and the *Juncetum gerardi* swards of the mid- and high marsh. The association grades floristically to the former through the more species-poor forms of the *Puccinellia*-dominated sub-community and the transitional *Puccinellia-Salicornia-Suaeda* vegetation.

Floristic table SM13

	a	b	c	d	e	f	13
Puccinellia maritima	V (4–10)	V (2–10)	V (1–8)	III (2–7)	V (4–9)	V (9–10)	V (1–10)
Glaux maritima	II (1–7)	V (5–9)	I (2–5)	V (2–5)	V (3–6)		II (1–9)
Armeria maritima	II (1–7)	III (2–7)	IV (3–8)	V (3–8)	IV (2–8)	I (1–5)	II (1–8)
Plantago maritima	II (1–7)	III (2–5)	IV (3–9)	V (5–9)	V (4–7)		II (1–9)
Salicornia agg.	III (2–6)	III (2–6)	IV (2–8)	II (2–3)	II (2–4)	V (4–10)	II (2–10)
Algal mat	II (3–10)	II (5–8)	IV (3–9)	II (4–8)	IV (4–7)		II (3–10)
Triglochin maritima	II (1–8)	III (2–4)	V (2–8)	IV (2–7)	II (1–3)	II (1–6)	II (1–8)
Aster tripolium (rayed)	III (1–8)	II (2–6)	II (2–7)	IV (2–7)	II (2–3)		II (1–8)
Suaeda maritima	III (1–6)	I (1–3)	III (1–3)	I (2–3)		IV (1–10)	II (1–10)
Halimione portulacoides	II (1–5)	I (2)	IV (1–6)	I (2–4)		III (4–10)	II (1–10)
Limonium cf. *L. vulgare*	II (1–8)	I (3)	V (2–8)			V (1–10)	II (1–10)
Turf fucoids*	I (2–3)		I (3)		V (4–9)		I (2–9)
Spartina maritima						V (1–10)	I (1–10)
Aster tripolium var. *discoideus*	I (1–5)					IV (1–8)	I (1–8)
Spergularia media	II (1–5)	II (2–3)	III (1–4)	III (1–3)	II (2–4)	I (3–5)	II (1–5)
Spartina anglica	I (1–7)	I (3)	I (2)	I (1–2)		I (5)	I (1–7)
Festuca rubra	I (2–5)	II (2–5)	II (2–6)	III (2–6)	II (2–4)		I (2–6)
Agrostis stolonifera	I (3–5)	I (2–3)	I (3–4)	II (3–6)	I (3–4)		I (2–6)
Limonium humile	I (2–5)	I (1–3)	I (1–8)	I (1–3)		I (4)	I (1–8)
Cochlearia officinalis	I (1–3)	I (2)	I (1–4)		I (3)		I (1–4)
Juncus gerardii	I (2–3)		I (2–6)	II (2–6)	I (3–4)		I (2–6)
Bostrychia scorpioides	I (4–7)		I (3–8)	I (6)	I(3)	I (8)	I (3–8)
Arthrocnemum perenne	I (1–3)		I (1–4)			II (1–6)	I (1–6)
Aster tripolium	I (1–6)		II (1–5)	I (3–4)			I (1–6)
Cochlearia anglica	I (1–6)		I (1–4)	I (2–3)			I (1–6)
Atriplex prostrata	I (1–7)						I (1–7)

Number of samples	319	23	89	26	17	20	494
Mean number of species/sample	6 (1–13)	6 (3–12)	9 (3–14)	8 (5–11)	7 (5–12)	7 (4–10)	7 (1–14)
Mean vegetation height (cm)	11 (2–50)	6 (2–15)	11 (3–25)	6 (2–15)	5 (2–15)	no data	6 (2–50)
Mean total cover (%)	88 (20–100)	85 (45–100)	91 (50–100)	96 (90–100)	91 (75–100)	no data	90 (20–100)

* Includes *Ascophyllum nodosum* ecad *mackaii*, *Fucus vesiculosus* ecad *caespitosus* and ecad *volubilis* and *Pelvetia canaliculata*.

a Sub-community with *Puccinellia maritima* dominant

b *Glaux maritima* sub-community

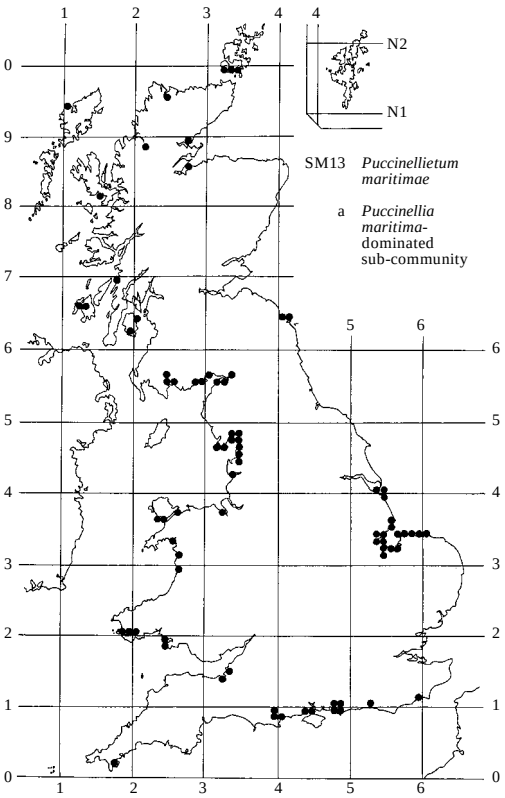
c *Limonium vulgare-Armeria maritima* sub-community

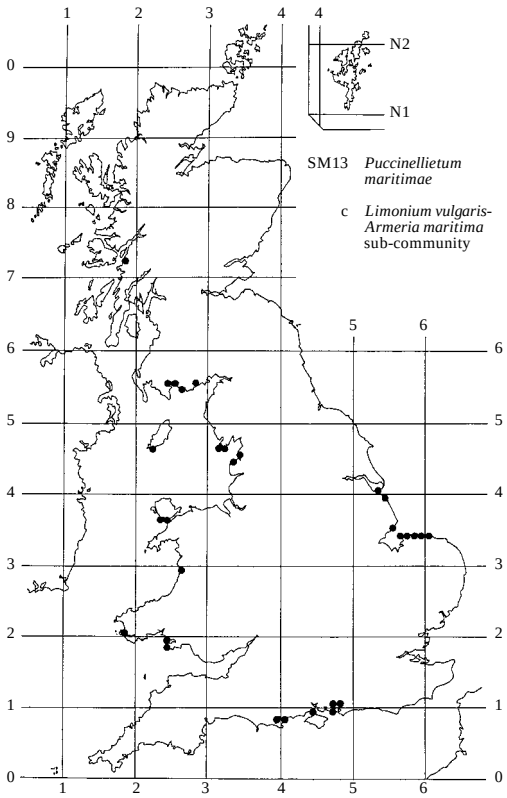
d *Plantago maritima-Armeria maritima* sub-community

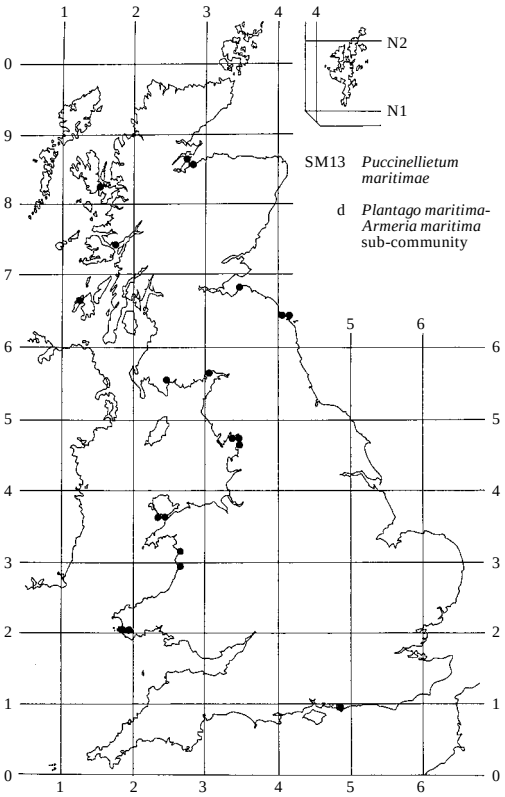
e *Puccinellia maritima*-turf fucoid sub-community

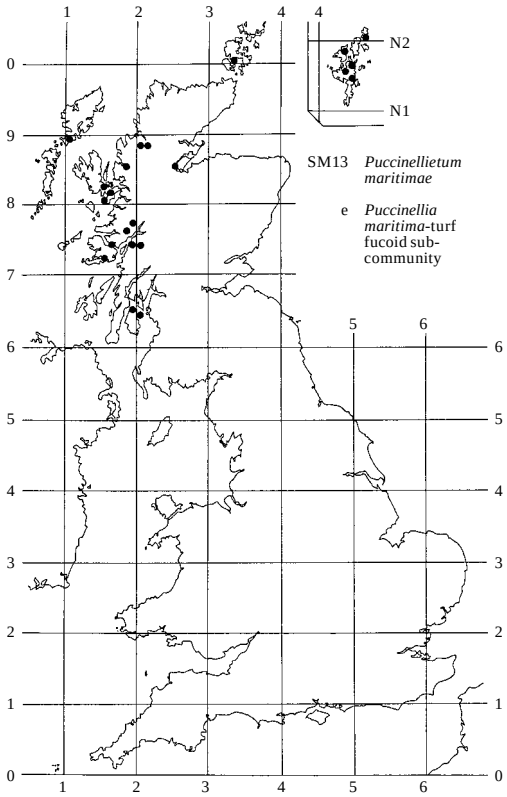
f *Puccinellia maritima-Spartina maritima* sub-community

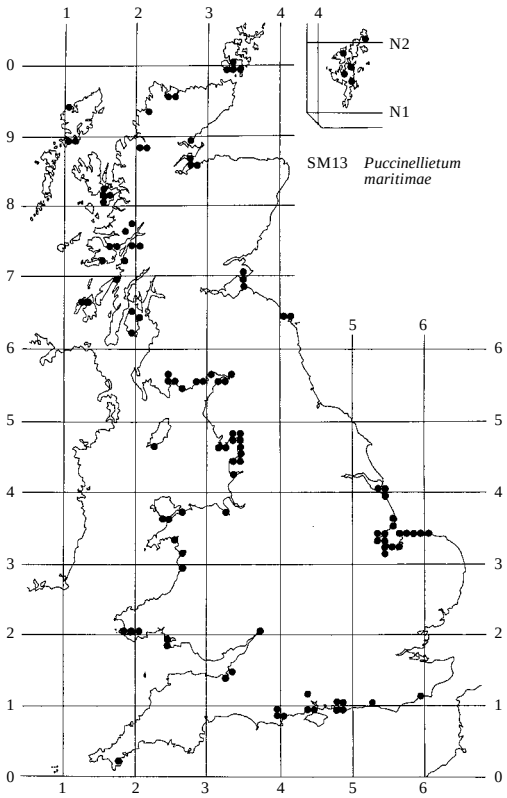
13 *Puccinellietum maritimae* (total)


N2
N1
SM13 *Puccinellietum maritimae*
a *Puccinellia maritima*-dominated sub-community


N2
N1
SM13 *Puccinellietum maritimae*
c *Limonium vulgaris-Armeria maritima* sub-community


N2
N1
SM13 *Puccinellietum maritimae*
d *Plantago maritima-Armeria maritima* sub-community


N2
N1
SM13 *Puccinellietum maritimae*
e *Puccinellia maritima*-turf fucoid sub-community


N2
N1
SM13 *Puccinellietum maritimae*

SM14

Halimione portulacoides salt-marsh community *Halimionetum portulacoidis* (Kuhnholtz-Lordat 1927) Des Abbayes et Corillion 1949

Synonymy
Obionetum and *Halimionetum auct. angl.*

Constant species
Halimione portulacoides, *Puccinellia maritima*.

Rare species
Arthrocnemum perenne, *Frankenia laevis*, *Inula crithmoides*, *Limonium bellidifolium*, *Suaeda vera*.

Physiognomy
This is a closed, species-poor association in which *Halimione portulacoides* is constant and physiognomically conspicuous as a bushy canopy up to 50 cm high or as a virtually prostrate carpet. *Puccinellia maritima* is also constant and there is frequently a little *Suaeda maritima* and sparse records for a variety of species from both low and upper marsh. Epiphytic algae are often abundant on the lower stems of the *H. portulacoides* and at some sites small patches of fucoids are present beneath canopy gaps.

Sub-communities
Géhu & Delzenne (1975) allocated samples of *Halimione portulacoides* vegetation with the red alga *Bostrychia scorpioides* to the separate association *Bostrychio-Halimionetum portulacoidis* (Corillion 1953) R.Tx. 1963. Although *B. scorpioides* was recorded occasionally here, there is no substantial floristic reason for distinguishing samples containing this species as even a sub-community within the *Halimionetum*. The three following sub-communities are, however, quite distinct.

Sub-community with *Halimione portulacoides* dominant. In this most species-poor sub-community, *H. portulacoides* always has high cover values (usually >90%) and there is usually a sparse undercover of *Puccinellia maritima* and some *Suaeda maritima*. The *H. portulacoides* may be present as a low or tall even-topped canopy or as discrete hemispherical bushes 1–2 m diameter and up to 50 cm high. Though this last form is developed on sandy substrates, there is no floristic basis for distinguishing a Sandy *Obionetum* (*sensu* Chapman 1934) within this sub-community.

***Juncus maritimus* sub-community:** *Halimione-Juncus maritimus* nodum Adam 1976. Here *H. portulacoides* is somewhat reduced in cover and varying amounts of *J. maritimus* are present as scattered shoots emerging through the shrubby canopy or as small dense patches, presumably of clonal origin. *Puccinellia maritima* remains constant with low cover but here *Plantago maritima*, *Limonium vulgare* and *Triglochin maritima* are also frequent. *Elymus pycnanthus* is an uncommon but distinctive associate.

***Puccinellia maritima* sub-community:** *Puccinellio-Halimionetum portulacoidis* Sea Meadow Chapman 1934; *Puccinellietum maritimae typicum*, terminal phase with *H. portulacoides* Beeftink 1962. *H. portulacoides* and *P. maritima* are co-dominant in an intimate mixture with the shoots of the former making a diffuse open network (cf. mosaics with discrete patches of *Halimionetum* and *Puccinellietum*). *Suaeda maritima*, *Triglochin maritima*, *Plantago maritima* and *Limonium vulgare* are frequent and sometimes abundant and, at high levels on the marsh, *Festuca rubra* may be common.

Habitat
The association occurs on a variety of substrates including clays, sands, shingle and occasionally soils of high organic content (Chapman 1950, O'Reilly & Pantin 1957, Adam 1976). Most commonly, it is developed on silty clay of low organic content, with some free calcium carbonate and a pH in the range 7.0–8.0. It appears tolerant of a range of submersion regimes: at Scolt Head, Norfolk, the *Halimionetum* extends from about 100 to 400 submergences/year (Chapman 1950, 1960*a*; cf. O'Reilly & Pantin 1957). Proctor (1980) has shown that, in the Exe salt-marshes, Devon, *H. portulacoides*

tolerates chloride levels at 10–24 g l^{-1} (salinity 16–36 g l^{-1}). Within these rather wide limits, the association occurs in two distinct situations, as an extensive belt of variable position in the general zonation or as narrow ribbons on creek levees (the 'Great *Obione* Fringe' of Chapman 1934) and low ridges on the marsh surface (Proctor 1980). The occurrences may reflect a need in *H. portulacoides* for a well-drained aerobic soil environment, at least for seed germination (Chapman 1950). Creek levees offer such conditions and, even in intervening basins where soils may be strongly reduced a few centimetres below the surface, the shallow adventitious roots of *H. portulacoides* may avoid the more severe effects of waterlogging (see Figure 28 in Chapman 1960*b*). Alternatively, levee occurrences may reflect a preference for a good supply of soil nutrients, particularly nitrogen and phosphate.

The *Juncus maritimus* and *Puccinellia maritima* sub-communities occur throughout the habitat range of the association but the bushy form of the *H. portulacoides*-dominated sub-community is confined to sandy substrates where salt-marsh abuts dunes or, less frequently, on the lower marsh.

Halimionetum is generally absent from sheep-grazed marshes (e.g. Yapp & Johns 1917) except for those creek-sides which are inaccessible to the stock. It is, however, found on a number of cattle-grazed marshes, notably around The Wash, and it will tolerate a certain amount of rabbit grazing (Chapman 1950). Brent geese do not graze extensively on *H. portulacoides* when feeding on saltings (Charman & Macey 1978).

Zonation and succession

Where *Halimionetum* occurs within the marsh zonation, its position is variable. It can be either above or below the *Puccinellietum maritimae* and boundaries between the two associations can be marked by mosaics (see Corillion 1953). At some sites, *Halimionetum* may run right from the upper limit of the pioneer zone to the sea wall. Where it does extend far down the marsh there is sometimes an open mosaic of *H. portulacoides* and *Arthrocnemum perenne* at its lower limit.

The association can occur on creek levees whether or not there is a nearby inter-creek zone of *Halimionetum*. Where it occurs in both situations on the same marsh, the creek *Halimionetum* may be above or below the inter-creek zone. Usually the creek *Halimionetum* cuts across the boundaries of a number of marsh communities.

On the high marsh, *Halimionetum* in both situations may give way to a zone of *Atriplici-Elymetum pycnanthi*, sometimes with an intervening but patchy zone of *Artemisietum maritimae*. This zonation may indicate a successional sequence consequent upon sediment accretion.

The origin and successional status of the *Puccinellia maritima* sub-community is obscure. Its distinctive physiognomy may arise by invasion of the *H. portulacoides*-dominated sub-community by *P. maritima* when the canopy opens with ageing of the bushes or as a result of grazing or by invasion of *Puccinellietum* by *H. portulacoides*. Alternatively the co-dominants may simultaneously invade some other salt-marsh community. Only long-term observation can elucidate the process(es) involved here.

Other changes can occur within *Halimionetum* as a result of frost or human disturbance (Beeftink 1977*a*, *b*; Beeftink *et al*. 1978). Killing of *H. portulacoides* on creek levees by frost can result in the temporary replacement of the association by *Artemisietum maritimae* for 4–5 years. Disturbance in inter-creek basins produces a phase characterised by *Suaeda maritima* and *Aster tripolium*.

Distribution

The *Halimionetum* is most widespread and extensive in south-east England: it is estimated that the association covers 30% of the salt-marshes of The Wash (Anon. 1976). It reaches its northern limit in south Scotland and this may be related to the incidence of severe frosts rather than to any effect of low mean summer temperatures (Ranwell 1972, Beeftink 1977*a*, *b*; cf. Chapman 1950). Sensitivity to grazing restricts its occurrences on the west coast. There is evidence of a recent expansion of the community within Europe (Beeftink 1959, 1977*a*).

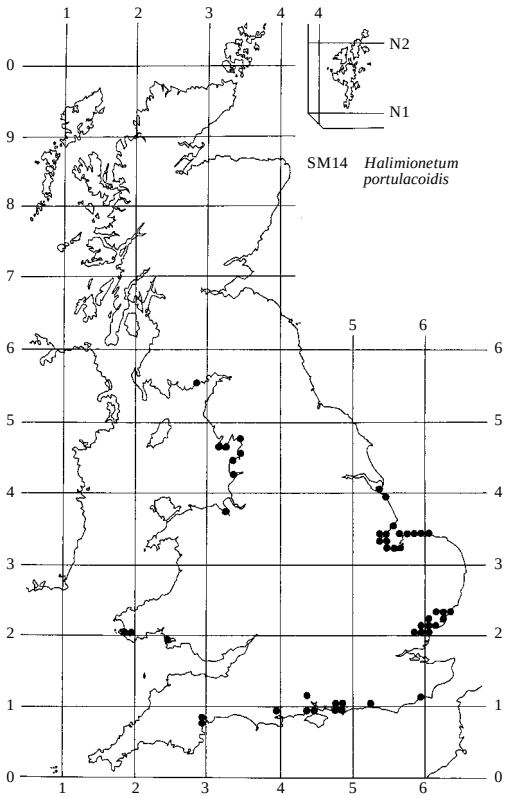
Affinities

Some authorities (e.g. Beeftink 1962) expand the *Halimionetum* to take in the *Artemisia maritima*-dominated vegetation of the high marsh and there may also be a case for considering some *Arthrocnemum perenne* stands as part of the association. Whatever its precise limits, the *Halimionetum* is a distinctive community of widespread occurrence on European coasts. It is usually placed alongside the *Puccinellietum maritimae* in the Asteretea but Géhu (1975) has erected an alliance Halimionion within the Arthrocnemetea to emphasise its affinities with the dwarf chenopod communities best developed around the Mediterranean.

Floristic table SM14

	a	b	c	14
Halimione portulacoides	V (7–10)	V (6–9)	V (5–9)	V (5–10)
Puccinellia maritima	IV (2–5)	IV (3–6)	V (2–8)	V (2–8)
Juncus maritimus		V (4–8)	I (2)	I (2–8)
Plantago maritima	I (1–5)	IV (2–5)	III (1–7)	II (1–7)
Limonium cf. *L. vulgare*	I (1–4)	IV (2–5)	III (1–7)	II (1–7)
Suaeda maritima	III (2–4)	I (2–3)	III (1–6)	III (1–6)
Triglochin maritima	I (1–4)	III (2–6)	III (1–6)	II (1–6)
Algal mat	I (5–8)	II (4–6)	I (3–8)	I (3–8)
Aster tripolium (rayed)	I (2–3)	II (2–3)	II (2–5)	I (2–5)
Salicornia agg.	I (1–5)	I (2–3)	III (2–5)	II (1–5)
Aster tripolium	I (1–3)	I (2–3)	II (1–4)	I (1–4)
Armeria maritima	I (5)	I (3)	I (2–4)	I (2–5)
Artemisia maritima	I (2)	I (2–5)	I (1–5)	I (1–5)
Arthrocnemum perenne	I (1–5)	I (1–2)	I (1–4)	I (1–5)
Spartina anglica	I (1–3)	I (2)	I (1–3)	I (1–3)
Spergularia media	I (1–5)	I (2)	I (1–4)	I (1–5)
Inula crithmoides	I (2–5)			I (2–5)
Elymus pycnanthus		II (1–6)		I (1–6)
Aster tripolium var. *discoideus*	I (1–3)		II (1–6)	I (1–6)
Number of samples	91	19	64	174
Mean number of species/sample	4 (1–10)	7 (4–11)	6 (4–10)	6 (1–10)
Mean vegetation height (cm)	24 (4–40)	46 (35–70)	25 (8–45)	27 (4–70)
Mean total cover (%)	97 (50–100)	95 (80–100)	97 (80–100)	97 (50–100)

a Sub-community with *Halimione portulacoides* dominant
b *Juncus maritimus* sub-community
c *Puccinellia maritima* sub-community
14 *Halimionetum portulacoidis* (total)


N2
N1
SM14 *Halimionetum portulacoidis*

SM15

Juncus maritimus–Triglochin maritima salt-marsh community

Synonymy

Juncetum maritimi auct. angl. p.p.; *Triglochin-Juncus maritimus* nodum Adam 1976.

Constant species

Juncus maritimus, *Plantago maritima*, *Triglochin maritima*.

Physiognomy

Tall tussocks of *Juncus maritimus* are always overwhelmingly dominant in this association and the associates are rather variable. However, *Triglochin maritima* and *Plantago maritima* are constant in usually small amounts in the understorey and various Puccinellion species, such as *Puccinellia maritima*, rayed *Aster tripolium*, *Armeria maritima* and *Glaux maritima*, occur frequently throughout. The association differs from the *Juncus maritimus* salt-marsh in the relative infrequency of *Agrostis stolonifera*, *Festuca rubra* and *Juncus gerardii*. Commonly the bases of the *J. maritimus* shoots support a variety of epiphytic algae, notably *Bostrychia scorpioides* and *Catenella repens*, and there may be an extensive algal mat, locally rich in dwarf free-living fucoids, on the substrate surface. Stands are often based upon discrete and sometimes large clones of *J. maritimus* but may also form a distinct zone within the marsh.

Sub-communities

Adam (1977) suggested that there are three centres of variation within the association around which sub-communities might be erected: stands which are very species-poor, sometimes pure *J. maritimus* in vigorous, tall and dense patches; stands in which *Halimione portulacoides* and *Limonium* cf. *vulgare* are conspicuous and fairly rich stands lacking these two species.

Habitat

J. maritimus is tolerant of a wide range of salinities and soil moisture conditions (Ranwell *et al*. 1964, Gillham 1957*b*) and the association occurs at all levels on salt-marshes and on a variety of substrates. Soil pH is generally around 7.0 but loss-on-ignition varies from 3% to more than 40%.

The most species-poor stands are found on the low marsh, usually on soft anaerobic mud (Gillham 1957*a*, Chater 1973, Adam 1976, 1977, Proctor 1980), though sometimes, as in Scottish sites, on shallow peaty soils over shingle (Gillham 1957*b*, Adam *et al*. 1977). The lowest stand for which accurate data are available experiences 220 submergences/year but many stands seem to occur at lower levels. Richer stands lacking *H. portulacoides* and *Limonium* cf. *vulgare* also occur at low levels, on western salt-marshes frequently along the foot of small erosion cliffs where there is perhaps water-seepage. Stands with these two species are found as a narrow zone in the upper parts of salt-marshes in south-east England (the *Juncetum maritimi* Chapman 1934).

The association occurs on both grazed and ungrazed salt-marshes but, even where there is grazing, stands tend to be avoided by stock.

Zonation and succession

There is a marked difference in the relative position of the association on salt-marshes in south-east England and those elsewhere but lack of submersion data makes it difficult to assess these variations in terms of absolute relationships to tidal levels. On the west and Channel coasts, the association generally occurs at relatively low levels in association with the *Spartinetum townsendii* or more usually within or at the upper limit of the *Puccinellietum maritimae*. In the south-east, a narrow belt of the association occurs normally between the *Puccinellietum maritimae*, *Limonium-Armeria* sub-community, and the *Atriplici-Elymetum pycnanthi* or the tall *Festuca rubra* sub-community of the *Juncetum gerardi*. The association grades smoothly into the *Puccinellietum* which effectively constitutes the understorey of the *Juncus-Triglochin* vegetation. On those few ungrazed western marshes where the *Puccinellietum maritimae*,

Limonium-Armeria sub-community occurs, the association occupies the position typical of south-east salt-marshes.

In at least one site, *Juncus maritimus* has been seen as a coloniser with *Spartina anglica*.

Distribution

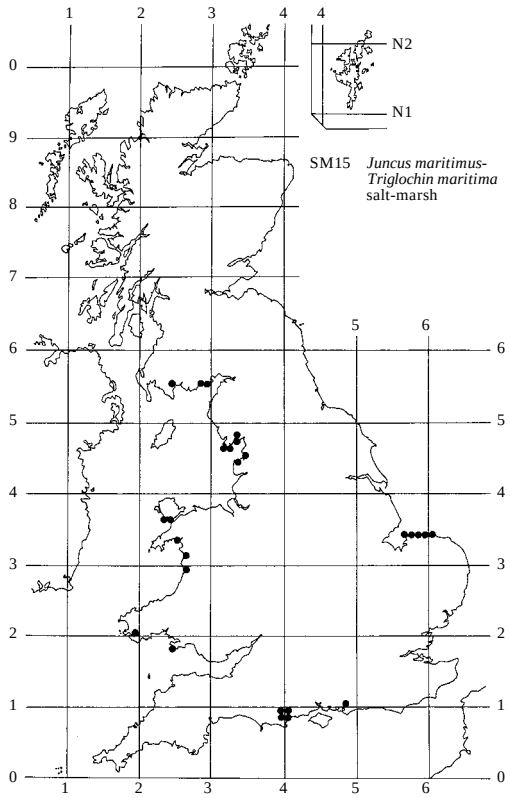
The association is the most widespread community dominated by *J. maritimus* in Great Britain. It is common on the west coast and is the major *J. maritimus* community in south-east England. One of the most extensive stands in the country is at Cefni Marsh, Anglesey where the association forms mosaics with *Scirpetum maritimi* over much of the marsh (Packham & Liddle 1970).

Affinities

The association can be seen as the northern extremity of a continuum of vegetation types in which *J. maritimus*, *Triglochin maritima*, *Limonium vulgare* and *Aster tripolium* are important components and which reaches down to the Mediterranean in the *Junco maritimi-Triglochinetum maritimi* Br.-Bl. 1931 (Braun-Blanquet & de Ramm 1957, Adam 1977). Such a range of vegetation types could be accommodated within the Puccinellion of the Asteretea which would also allow some weight to be given to the interesting low-level occurrences of *J. maritimus* vegetation.

Floristic table SM15

Juncus maritimus	V (5–10)
Triglochin maritima	IV (2–6)
Plantago maritima	IV (2–8)
Aster tripolium (rayed)	III (2–4)
Puccinellia maritima	III (2–7)
Armeria maritima	III (2–5)
Glaux maritima	III (2–5)
Algal mat	III (2–8)
Limonium cf. *L. vulgare*	II (1–6)
Cochlearia anglica	II (1–4)
Juncus gerardii	II (3–7)
Halimione portulacoides	II (1–6)
Festuca rubra	II (2–8)
Agrostis stolonifera	II (2–6)
Aster tripolium	I (1–5)
Cochlearia officinalis	I (2–3)
Salicornia agg.	I (2–5)
Suaeda maritima	I (2–3)
Spartina anglica	I (1–5)
Spergularia media	I (2–4)
Turf fucoids	I (3–6)
Phragmites australis	I (2–6)
Carex extensa	I (1–3)
Atriplex prostrata	I (1–3)
Limonium humile	I (1–3)
Oenanthe lachenalii	I (3–4)
Artemisia maritima	I (1–4)
Number of samples	63
Mean number of species/sample	10 (2–14)
Mean vegetation height (cm)	57 (25–100)
Mean total cover (%)	76 (70–100)


N2
N1
SM15 *Juncus maritimus-Triglochin maritima* salt-marsh

SM16

Festuca rubra salt-marsh community
Juncetum gerardi Warming 1906

Synonymy
Festucetum (*rubrae*) *auct. angl.*

Constant species
Festuca rubra, *Plantago maritima*, *Glaux maritima*.

Physiognomy
The closed grasslands of the *Juncetum gerardi* are normally dominated by mixtures of *Festuca rubra* and *Agrostis stolonifera* with a variety of herbaceous associates among which *Plantago maritima*, *Glaux maritima*, *Armeria maritima* and *Triglochin maritima* are generally the most frequent and abundant. *Juncus gerardii* itself is present in varying amounts: it is usually constant through all but the most anomalous of the *Juncetum* swards and in some cases is dominant or co-dominant. In certain sub-communities, there are frequent records for low-marsh species and an algal mat is often conspicuous over the substrate surface. In other sub-communities, a group of mesotrophic grassland and flush species are well-represented. The *Juncetum gerardi* is the community within which bryophytes reach their lowest limit on salt-marshes.

Sub-communities
As in the other major British salt-marsh association, the *Puccinellietum maritimae*, variation is virtually continuous, largely based on quantitative differences among relatively few species and frequently including a site-specific element reflecting local histories of marsh use. The following sub-communities should therefore be seen as foci of national variation with somewhat hazy boundaries.

***Puccinellia maritima* sub-community:** *Juncus gerardii-Puccinellia maritima* nodum Adam 1976; *Puccinellietum maritimae agrostidetosum* Beeftink 1962. This sub-community comprises generally short swards which are floristically transitional between the *Juncetum gerardi* and the *Puccinellietum maritimae*. *J. gerardi*, *Puccinellia maritima*, *Festuca rubra*, *Plantago maritima*, *Glaux maritima* and *Triglochin maritima* are constant and varying proportions of these species co-dominate. *Agrostis stolonifera*, *Armeria maritima* and rayed *Aster tripolium* are less frequent but each may be abundant in particular stands.

Sub-community with *Juncus gerardii* dominant: *Juncetum gerardi*, *J. gerardii* variant Beeftink 1962; (not *Juncetum gerardi juncetosum* Tyler 1969). *Juncus gerardii* always dominates in the tall swards of this sub-community, the stands of which are rarely extensive, 2–3 m diameter at most, and probably vegetatively expanding clones. Even on heavily-grazed marshes, *J. gerardii* remains largely untouched by stock and clumps remain tall and conspicuous though such clumps are often surrounded by a short cropped turf in which *J. gerardii* is still abundant: this perhaps indicates the existence of genotypes of *J. gerardii* of differing palatability. *Plantago maritima*, *Glaux maritima*, *Triglochin maritima* and rayed *Aster tripolium* are also constant though rarely of great abundance. *Festuca rubra* and *Agrostis stolonifera* are reduced in frequency compared with the association as a whole.

***Festuca rubra-Glaux maritima* sub-community:** *Festucetum rubrae* Yapp & Johns 1917; *Juncus gerardii-Glaux maritima-Agrostis stolonifera* Association Nordhagen 1923; *Festuca-Glaux*, *Festuca-Agrostis* and *Festuca-Armeria* noda Adam 1976; *Juncetum gerardi*, variant with *Festuca rubra* f. *littoralis* Beeftink 1962 *p.p.*; *Juncetum gerardi festucetosum* Tyler 1969 *p.p. Festuca rubra* and *Agrostis stolonifera* are usually co-dominant in the low swards of this sub-community. *Plantago maritima*, *Glaux maritima*, *Triglochin maritima* and *Armeria maritima* are also constant and may each be abundant. *Juncus gerardii* is somewhat variable in amount and even when abundant may be difficult to detect in close-cropped turf. This is the lowest vegetation in which bryophytes are typically encountered on salt-marshes: *Rhytidiadelphus squarrosus*, *Hypnum cupressiforme* and *Eurhynchium praelongum* are the most frequent species. Algae are uncommon.

Within the sub-community stands may be encountered in which either *A. stolonifera* or *F. rubra* are sparsely represented. In other cases, these two species are overwhelmingly co-dominant in short swards in which *J. gerardii* is very poorly represented (the *Agrostis stolonifera* variant). *J. gerardii* is also sparse in some stands where *F. rubra* and *Armeria maritima* are co-dominant in the absence of *A. stolonifera* (the *Armeria maritima* variant). There is good evidence to see these very distinct communities as extreme forms of *Juncetum gerardi* derived as a result of particular marsh management regimes (see below).

***Leontodon autumnalis* sub-community:** *Juncus gerardii-Trifolium repens-Leontodon autumnalis* Association Nordhagen 1923; *Juncetum gerardi leontodetosum* Raabe 1950; *Juncetum gerardi leontodetosum* and *odontitosum* Gillner 1960; *Carex distans-Plantago maritima* Association Ivimey-Cook & Proctor 1966 *p.p.*; *Juncetum gerardi festucetosum* Tyler 1969 *p.p.* This sub-community has much the same physiognomy as the last and here too *Festuca rubra, Agrostis stolonifera* and *Juncus gerardii* can all be well-represented in the short, smooth swards. *Plantago maritima* and *Glaux maritima* remain constant but here there are also frequent records for a variety of species characteristic of non-maritime vegetation. Among these, *Trifolium repens* is constant but *Potentilla anserina*, *Leontodon autumnalis* and *Carex flacca* can each be frequent and abundant. On cattle-grazed marshes, where the vegetation is normally not so shortly cropped as under sheep-grazing, a number of species flower and *L. autumnalis* may be particularly conspicuous. *Carex distans* may also be abundant in this sub-community but this species has different habitat preferences across its British range. It is uncommon on salt-marshes in the south-east but frequent in western England and in Wales; in Scotland, it again becomes rare on salt-marshes though it remains quite common among low coastal rocks (see Jermy & Tutin 1968).

Within the belts occupied by this sub-community there is sometimes a zonation of *T. repens*, *L. autumnalis*, *C. distans* and *P. anserina* in order of lowest occurrence but this is not universal and, indeed, all these species can occur occasionally in the lower marsh *Festuca-Glaux* sub-community. At the highest levels occupied by the *L. autumnalis* sub-community *Lolium perenne*, *Cynosurus cristatus*, *Bromus hordeaceus* ssp. *hordeaceus*, *Elymus repens* and *Poa pratensis* are sometimes found. It is possible that these species seed in from adjacent sea-banks where grassland mixtures have been sown. Another occasional species in the upper-marsh sites is *Trifolium fragiferum* which becomes restricted to coastal communities at the northern limits of its British range. It is rarely extensive, tending to occur in discrete patches often associated with freshwater seepage onto the upper marsh.

As with the *Festuca-Glaux* sub-community there are rather extreme forms of salt-marsh swards which are perhaps best seen in relation to a more central type of *Juncetum gerardi* vegetation. A *Trifolium repens* variant is very similar to the *L. autumnalis* sub-community except for its lower levels of *J. gerardii*.

Low turf very similar in floristics to this sub-community is of common occurrence on some sea cliffs. Here *F. rubra*, *Plantago maritima*, *Armeria maritima* and more rarely *Glaux maritima* are generally co-dominant but *J. gerardii*, *C. distans*, *T. repens* and *L. autumnalis* may all be conspicuous.

***Carex flacca* sub-community.** *Juncetum gerardi festuco-caricetosum nigrae* Tyler 1969; ? *Danthonia decumbens-Agrostis canina* community Tyler 1969; *Agrostis tenuis-Festuca ovina* community Tyler 1969 *p.p.* The floristics and physiognomy of this sub-community are generally similar to the last except that here *C. flacca* is much more frequent and sometimes co-dominant with the grasses and herbaceous halophytes. Bryophytes may also be more conspicuous: *Campylium polygamum*, *Amblystegium serpens*, *Grimmia maritima*, *Cratoneuron filicinum*, *Amblystegium riparium*, *Calliergon cuspidatum*, *Rhytidiadelphus squarrosus*, *Hypnum cupressiforme* and *Eurhynchium praelongum* all occur occasionally and each may be abundant in particular samples.

Sometimes the turf of this sub-community is broken by flushed gravelly patches and here *Blysmus rufus*, *Eleocharis uniglumis*, *E. palustris* and *E. quinqueflora* may be locally abundant.

Sub-community with tall *Festuca rubra* dominant: *Festucetum littoralis* Corillion 1953; Tall *Festuca rubra* nodum Adam 1976; *Juncetum gerardi*, variant with *Festuca rubra* f. *littoralis* Beeftink 1962 *p.p.*; includes *Festuca rubra-Agrostis stolonifera-Hordeum secalinum* associes Ranwell 1961; (not *Festucetum rubrae* Yapp & Johns 1917). The very distinctive springy mattresses of this sub-community are perhaps best seen as a physiognomic variant of the *Juncetum gerardi*. *F. rubra* is consistently dominant. It grows tall and dense and, after tidal inundation, presents a bedraggled appearance. Although all of the species frequent in the association as a whole occur here, most are reduced in frequency and rarely make a major contribution to the sward. *Plantago maritima* and *Agrostis stolonifera* are the most common associates. Some stands are distinctive in the presence of conspicuous amounts of *Halimione portulacoides*; others may have *Elymus pycnanthus* and, in Somerset and the upper Severn estuary, *Hordeum secalinum* occurs in this sub-community (Ranwell 1961, Owen 1972). Flowering appears to be rare in British stands

(cf. Gravesen & Vestegaard 1969 in Denmark). In winter, when the vegetation may remain flattened for long periods, seedlings of *Atriplex* spp. and *Cochlearia* spp. may appear in profusion on top of the matted grass.

Habitat

The *Juncetum gerardi* covers extensive areas of salt-marsh especially in the north and west of Britain where it is the predominant community of the mid- and upper marsh. It occurs on a range of substrates from marsh levels experiencing several hundred submergences/year to the upper tidal limit. It is usually grazed and provides swards that are valuable for commercial turf-cutting.

Regimes of salt-marsh grazing are very variable. The stock involved, the stocking rates, the pattern of use through the year may all vary from marsh to marsh and through time and all these factors might be expected to influence the appearance of the vegetation. Much of the site-specific variation within the *Juncetum gerardi* is probably related to the unique grazing history of every site.

The general effect of grazing is to maintain a fine short sward, preventing the overwhelming dominance of (a) particular species (Dahlbeck 1945, Gillner 1960, Beeftink 1977*a*). It is probably important in controlling the proportions of *Puccinellia maritima*, *Agrostis stolonifera* and *Festuca rubra* in the sward and thus influences the position and the nature of the boundary between the communities of the *Puccinellietum maritimae* and the *Juncetum gerardi* and the extent and composition of the transitional vegetation classified here as the *Puccinellia* sub-community (Ranwell 1968, Gray & Scott 1977*b*). If grazing pressure is generally low or if grazing ceases, *F. rubra* is particularly responsive, growing tall and rank, excluding most potential competitors and eventually producing the sort of tussocky, species-poor grassland that is characteristic of the tall *F. rubra* sub-community. Such vegetation is unpalatable to wildfowl (Cadwalladr *et al*. 1971, Cadwalladr & Morley 1974, Charman & Macey 1978) and to re-introduced sheep.

The preparation and cutting of 'sea-washed' turf is important at a number of salt-marsh sites (e.g. Morecambe Bay; see Gray 1972). The grass-dominated swards of the *Festuca-Glaux* sub-community (the *Agrostis stolonifera* variant) are most favoured and are prepared over a number of years by mowing during the growing season, the application of fertiliser and sometimes of selective herbicides. This produces a virtually pure turf of fine-leaved *F. rubra* and *A. stolonifera*. Cutting is now highly mechanised and involves the removal of shallow (*c*. 3.5 cm deep) turves often over considerable areas. Recolonisation of cuttings produces a diverse and irregular succession (see below) and may involve the development of the transitional *Puccinellia* sub-community.

There is a broad correlation between variation in the sub-communities of the *Juncetum gerardi* and the incidence of tidal submersion. The transitional *Puccinellia* sub-community usually extends furthest down-marsh and it may be subject to more than 250 submergences/year, though it can also occur in very slight hollows in the upper marsh. Where it extends down into the *Puccinellietum* it is found on knolls and creek levees. The *Festuca-Glaux* sub-community is also found in such situations though the lower limit of continuous swards experiences between 150 and 200 submergences/year. The *Leontodon* sub-community occurs at higher levels which are subject to up to 100–120 submergences/year. Where vegetation virtually identical to this sub-community occurs on sea cliffs, it is found in situations which receive very considerable amounts of sea-spray and its soils show some of the highest values of Na/organic matter encountered in that habitat. The *Carex flacca* sub-community is best developed at the the storm-tide level where there are usually only one or two flooding tides per annum and perhaps at extremes up to 25 submergences/year. Despite the frequent seepage of freshwater into sites occupied by this sub-community, the soil salinity during droughts may reach quite high values (Gillham 1957*b*).

Substrates on which the *Juncetum gerardi* occurs include clays, silts, sands, shingle and soils of high organic content. The *Puccinellia* sub-community spans the entire range of substrate variation. Other sub-communities are more restricted: the tall *Festuca rubra* sub-community tends to occur on clays, silts and sands while the *Festuca-Glaux* and *Leontodon* sub-communities are generally confined to sandier material with some occurrences on more organic soils. Although the *Juncus gerardii* sub-community occurs on various substrates, its occurrences in south-east England frequently indicate the presence of shingle below the top soil horizon and, in some cases, this vegetation can develop directly on shingle banks. The *Carex flacca* sub-community is most frequently found on soils with high organic content, at least in the upper part of the profile. The pH of the substrates on which the *Juncetum* occurs varies between 5.0 and 7.0, with finer material without organic enrichment being more basic.

A combined effect of tidal inundation and substrate type is mediated through soil permeability. The degree of waterlogging probably has some effect on the proportions of *F. rubra*, *A. stolonifera* and *Puccinellia maritima* in the vegetation. *F. rubra* may suffer competitively against *P. maritima* under waterlogged and more saline conditions and against *A. stolonifera* in waterlogged and less saline situations (Gray & Scott 1977*a*). On cliffs, the factor which favours the development of the *Leontodon* sub-community of the *Juncetum gerardi* rather than some form of *Festuca-Armeria* sward is probably the

retention of water in the heavy gleyed soils: both vegetation types receive similar amounts of salt-spray and both are grazed.

Among the grasses of the *Juncetum gerardi*, *A. stolonifera* seems more resistant to oil and refinery effluent spillage than either *F. rubra* or *P. maritima* and it may gain a competitive advantage in vegetation recovering from such pollution. *Armeria maritima*, *Plantago maritima* and *Triglochin maritima* are able to resist considerable amounts of spillage by virtue of their underground storage organs (Baker 1979).

Zonation and succession

In general, the *Juncetum gerardi* occupies a position above the *Puccinellietum maritimae* in the salt-marsh zonation but the extent of the *Juncetum* in the south-east differs strikingly from its contribution to salt-marshes elsewhere. In the south-east, the association is of very limited extent and occurs only at high levels in the marsh, most often forming a discontinuous zone in contact with the *Limonium-Armeria* sub-community of the *Puccinellietum*. In the north and west, the *Juncetum* is usually very extensive in both the mid- and upper-marsh. The exact reasons for this difference, and for the more seaward extension of particular species in the west, are unknown (Beeftink 1977*a*, *b*, Adam 1978) but the major factor controlling the relative positions of the two associations is the degee of submersion. In upper estuaries, where there is freshwater dilution, the positions of the *Juncetum* and *Puccinellietum* are reversed. The location and nature of the junction between the associations is also affected markedly by the extent and nature of the grazing.

Within the *Juncetum*, there is usually a zonation of the different sub-communities in relation to their tolerance of submersion. The detailed pattern varies from site to site and, though the *Festuca-Glaux* sub-community usually gives way to the *Leontodon* sub-community upmarsh, the relative depth of the zones is very variable (Figure 9). In some cases, there is a complex mosaic of the two communities over the mid-marsh. The *Leontodon* sub-community may, in turn, pass into the *Carex flacca* sub-community. Provided that the upper limit of the salt-marsh is not an artificial boundary, the topmost zone grades into non-maritime grassland or mire (e.g. Gillham 1957*b*). The tall *Festuca rubra* sub-community often forms part of zonations with the *Halimionetum*, sometimes occupying a position between this association and fragmentary stands of the *Artemisietum*.

The zonation of the sub-communities may represent a successional sequence in response to substrate accretion and the gradual raising of salt-marsh surfaces. Grazing too, can, be responsible for considerable temporal changes within the *Juncetum gerardi* (see above) and may shift the succession towards the development of other associations. Very heavy grazing, particularly by cattle and horses on clay and silt substrates, can lead to poaching and the appearance of *Puccinellietum maritimae* or to communities characteristic of disturbed saline sites such as the *Puccinellietum distantis* and the *Agrostis stolonifera-Alopecurus geniculatus* community.

Turf-cutting opens up areas for colonisation by a variety of species. In the early stages a variety of annuals and short-lived perennials predominate: *Spergularia marina*, *Juncus bufonius*, *Plantago coronopus* and *Sagina maritima*, for example, often with *Pottia heimii*. Diverse assemblages of such species have sometimes been classified within the Saginetea. *Puccinellia maritima* is frequently an early colonist and a closed *Puccinellietum maritimae* may develop. *P. maritima* may persist within a *Festuca rubra* sward to produce a patchwork of the transitional vegetation of the *Puccinellia* sub-community of the *Juncetum gerardi*. It is this pattern of recolonisation which helps make grazing and turf-cutting compatible activities on the same salt-marsh.

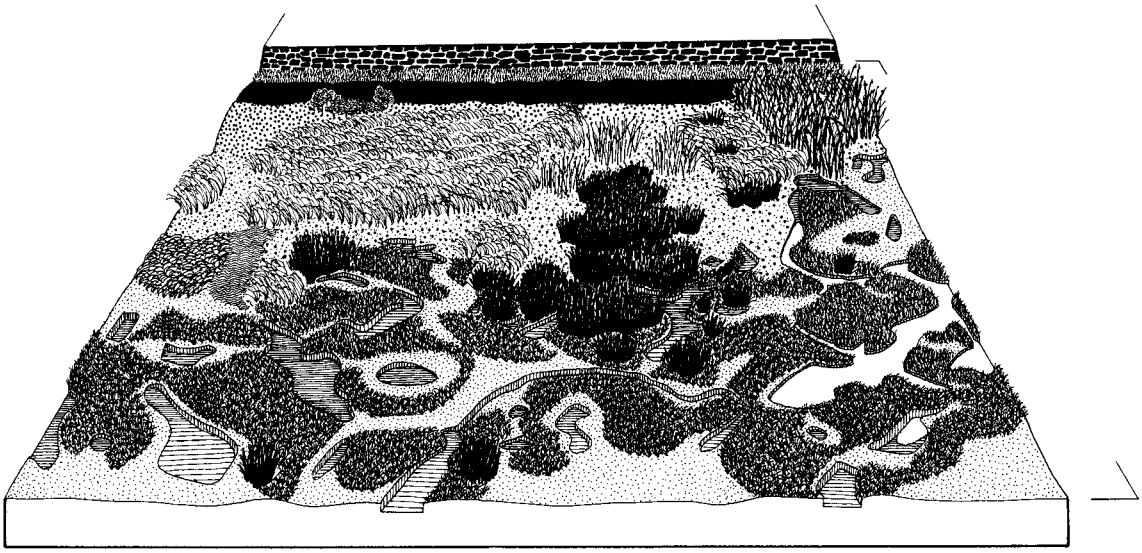
Distribution

The *Juncetum gerardi* is widespread except in the south-east where it is local and where the *J. gerardii*-dominated sub-community is the most frequent representative of the association. The *Festuca-Glaux* and *Leontodon* sub-communities are virtually ubiquitous in western Britain but very sparsely distributed in the south-east. In north Norfolk, for example, their only extensive occurrence is at Brancaster which, interestingly, is the only marsh in the area still subject to regular grazing. Both sub-communities have been reported from brackish reclaimed pastures and they may be more widespread in this habitat. Where the *Leontodon* sub-community occurs on sea cliffs it is chiefly northern with some isolated occurrences in Wales and Cornwall where its distribution may be related to localised flushing rather than a generally high precipitation. It is commonest in west Scotland, the Outer Isles, Orkney and Shetland. The grass-dominated swards of the *Festuca-Glaux* and *Leontodon* sub-communities have been encountered chiefly in those areas where sheep-grazing and turf-cutting are most intensive. The *Carex flacca* sub-community is widespread in the west but most frequent in west Scotland.

Affinities

The *Juncetum gerardi* is one of the most important communities on British salt-marshes but its internal diversity and its affinities have been little discussed. The view of the *Juncetum* adopted here is a broad one, roughly comparable to that of Tyler (1969*b*). A similar range of vegetation types to that included here occurs widely in northern Europe and numerical studies (Adam 1977) have emphasised the close relationship between the British and European communities.

Figure 9. Complex of upper marsh communities at Bolton-le-Sands, Morecambe Bay.
The bulk of the marsh vegetation comprises various kinds of SM16 *Juncetum gerardi*. In the foreground, as a mosaic around the largely dried-up pans, are the *Festuca-Glaux* and *Juncus gerardii* sub-communities, with a small patch of the tall *Festuca rubra* sub-community to the left. Above, these give way to the *Leontodon* sub-community. Scattered through the *Juncetum gerardi* are dense clumps of the SM18 *Juncus maritimus* salt-marsh. On the slope below the road, the *Juncetum* gives way to a narrow zone of the MG11 *Festuca-Agrostis-Potentilla* grassland with small stands of OV25 *Urtica-Cirsium* vegetation on rotting horse faeces. On the flushed ground below are small stands of the SM20 *Eleocharitetum uniglumis* and some larger areas of S21 *Scirpetum maritimi* and S20 *Scirpetum tabernaemontani*; from one of these, a small stand of MG13 *Agrostis-Alopecurus* grassland runs down the marsh towards a large pan. The flooded pans to the right have thick festoons of the SM2 *Ruppietum maritimae*.



Salt-marsh communities

SM16 *Juncetum gerardi* *Leontodon* sub-community *Trifolium* variant

SM16 *Juncetum gerardi* *Festuca-Glaux* sub-community *Armeria* variant

SM16 *Juncetum gerardi* *Juncus gerardii*-dominated sub-community

SM16 *Juncetum gerardi* Sub-community with tall *Festuca rubra* dominant

SM18 *Juncus maritimus* salt-marsh *Oenanthe* sub-community

SM20 *Eleocharitetum uniglumis*

Swamps

S21 *Scirpetum maritimi*

S20 *Scirpetum tabernaemontani*

Mesotrophic grasslands

MG13 *Agrostis-Alopecurus* community

MG11 *Festuca-Agrostis-Potentilla* community (with *Urtica* patches)

MG6 *Lolio-Cynosuretum*

The *Festuca-Glaux* sub-community can be regarded as the core of the British *Juncetum gerardi*. Floristic transitions from this sub-community to the *Puccinellietum maritimae* are obvious and the major difficulty is deciding where exactly to draw the line between the two associations. In other directions, floristic affinities are more diverse and contentious. Certain authorities would see some of the samples included here within the *Leontodon* sub-community as part of the Elymo-Rumicion crispi, emphasising the transitional nature of the vegetation (see the *Agrostidetum stoloniferae* sub-association of var. *salina* and *Trifolium fragiferum* Westhoff 1947 and *Ononis spinosa-Carex distans* Association Runge 1966 in Westhoff & den Held 1969; Géhu 1973*b*). An alternative treatment of the high level stands of the *Leontodon* sub-community with pasture grasses would be to place such vegetation in a maritime sub-community of the *Lolio-Cynosuretum cristati* (e.g. Raabe 1953; see also Gillner 1960).

Carex-rich upper marsh grasslands similar to those included here within the *Carex flacca* sub-community have been described from Scandinavia (Nordhagen 1923, Du Rietz & Du Rietz 1925, Almquist 1929, Gillner 1960, Tyler 1969*b*), Germany (Tüxen 1937) and The Netherlands (Westhoff 1947). Some would place these again within the Elymo-Rumicion crispi, while others see them as variants of inland mire types occasionally encountered in maritime or paramaritime situations (cf. the *Isolepsis setacea* variant of the *Schoeno-Juncetum serratuletosum* in Wheeler 1980*b* and the Caricion davallianae dune-slack communities of Westhoff & den Held 1969).

The *J. gerardii*-dominated sub-community bears some resemblance to communities of the Eleocharion. It should, however, be distinguished from the *Juncetum gerardi juncetosum* (Tyler 1969*b*) which possesses a distinctive suite of bryophytes not represented here.

The tall *Festuca rubra* sub-community is a somewhat diverse assemblage united by the overwhelming dominance of *F. rubra*. It could be divided on a strict floristic basis between the *Juncetum gerardi*, the *Halimionetum* and the *Atriplici-Elymetum pycnanthi*. Alternatively, the entire sub-community could be separated entirely from the *Juncetum* as part of the *Festucetum littoralis* Corillion 1953 (e.g. Géhu 1975, Géhu & Delzenne 1975).

Floristic table SM16

	a	b	c	d	e	f	16
Festuca rubra	IV (2–7)	III (2–7)	V (2–10)	V (5–10)	V (2–9)	V (4–8)	V (2–10)
Juncus gerardii	V (3–7)	V (6–10)	V (2–7)	I (2–3)	V (2–7)	V (3–6)	V (2–10)
Glaux maritima	V (2–8)	IV (2–7)	V (2–8)	II (2–6)	V (2–7)	IV (2–6)	IV (2–8)
Plantago maritima	V (3–8)	IV (2–6)	V (2–8)	IV (1–5)	IV (2–7)	V (2–6)	IV (2–8)
Agrostis stolonifera	III (2–9)	II (3–7)	IV (2–8)	III (2–8)	V (2–8)	V (3–8)	IV (2–9)
Triglochin maritima	V (1–7)	IV (2–5)	IV (1–6)	II (1–5)	III (1–6)	III (1–5)	III (1–7)
Armeria maritima	III (2–6)	III (2–5)	IV (2–8)	I (2–3)	III (2–5)	III (2–6)	III (2–8)
Aster tripolium (rayed)	III (1–5)	IV (1–4)	III (1–5)	II (2–6)	I (1–4)	I (3)	II (1–6)
Puccinellia maritima	V (2–9)	I (3–6)	I (2–6)	II (2–5)			I (2–9)
Algal mat	II (3–8)	II (3–8)	I (4–8)	I (3)	I (4–5)		I (3–8)
Spergularia media	II (1–4)	I (2)	I (2–3)	II (1–4)	I (2–3)		I (1–4)
Aster tripolium	II (2–4)	I (3)	I (1–3)	I (1–4)			I (1–4)
Salicornia agg.	II (2–5)	I (2)	I (1–3)		I (2)		I (1–5)
Atriplex prostrata	I (3)	II (2–3)	I (1–3)	II (1–4)	I (2–3)	I (2)	I (1–4)
Cochlearia anglica	I (2–4)	II (2–3)	I (2–3)		I (2)		I (2–4)
Halimione portulacoides	I (2–4)	II (2–3)	I (1–2)	II (1–8)			I (1–8)
Limonium cf. *L. vulgare*	I (2–6)	II (2–4)	I (1–8)	II (1–5)	I (2)		I (1–8)
Trifolium repens		I (2–4)	I (2–5)	I (2–4)	IV (2–7)	V (1–7)	II (1–7)
Leontodon autumnalis		I (2)	I (2–5)	I (2–4)	III (1–6)	V (2–5)	II (1–6)
Carex flacca	I (3)				I (2–6)	IV (1–7)	I (1–7)
Carex distans		I (2)	I (1–3)	I (2–3)	III (1–7)	II (1–5)	I (1–7)
Potentilla anserina			I (2)	I (3–6)	II (2–8)	III (3–7)	I (2–8)
Holcus lanatus				I (3–6)	I (2–5)	I (2–6)	I (2–6)
Lotus corniculatus			I (4)	I (2–4)	I (2–5)	I (2–6)	I (2–6)
Cerastium fontanum			I (2)	I (2)	I (2–3)	II (2–3)	I (2–3)
Sagina procumbens			I (2–4)		I (2–5)	II (2–5)	I (2–5)
Eurhynchium praelongum			I (3–4)		I (2–7)	I (3–6)	I (2–7)
Rhytidiadelphus squarrosus			I (3)		I (3–5)	I (3–8)	I (3–8)
Hypnum cupressiforme			I (2)		I (2–3)	I (4–6)	I (2–6)
Anthoxanthum odoratum				I (3)	I (3)	I (2–5)	I (2–5)
Plantago lanceolata				I (2)	I (2–3)	I (1–3)	I (1–3)

Floristic table SM16 (*cont*.)

	a	b	c	d	e	f	16
Cynosurus cristatus					I (2–3)	I (5–6)	I (2–6)
Ranunculus acris					I (2)	I (1–4)	I (1–4)
Number of samples	34	49	150	85	149	46	513
Mean number of species/sample	9 (6–13)	8 (3–12)	9 (5–16)	7 (3–12)	11 (7–18)	16 (9–31)	10 (3–31)
Mean vegetation height (cm)	7 (2–25)	26 (2–40)	11 (2–75)	26 (10–60)	10 (2–50)	10 (2–60)	14 (2–75)
Mean total cover (%)	95 (70–100)	96 (50–100)	96 (50–100)	99 (80–100)	100 (90–100)	100 (90–100)	98 (50–100)

a *Puccinellia maritima* sub-community
b Sub-community with *Juncus gerardii* dominant
c *Festuca rubra-Glaux maritima* sub-community
d Sub-community with tall *Festuca rubra* dominant
e *Leontodon autumnalis* sub-community
f *Carex flacca* sub-community
16 *Juncetum gerardi* (total)

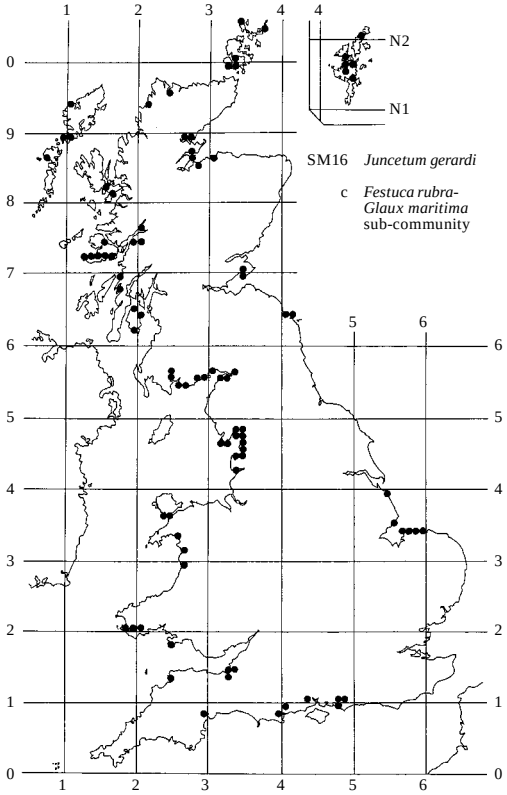
SM16 sub-communities

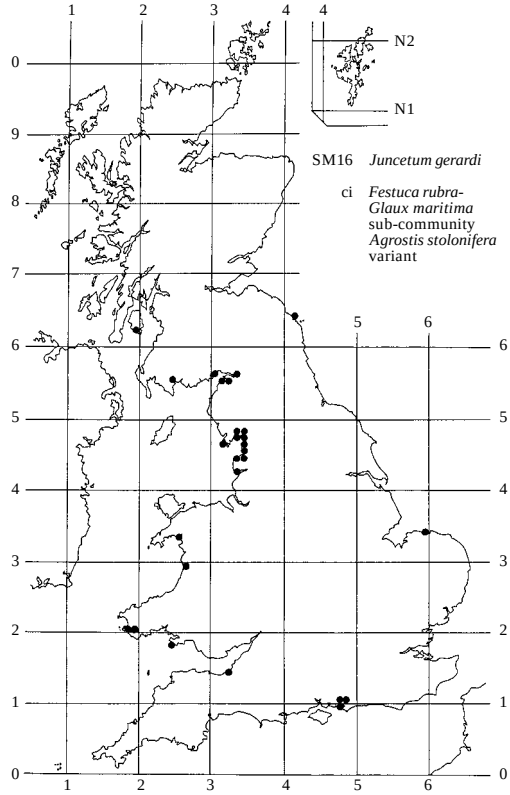
	c	ci	cii	e	ei
Festuca rubra	V (2–10)	V (5–10)	V (5–10)	V (2–9)	V (4–9)
Juncus gerardii	V (2–7)	I (2)	I (1)	V (2–7)	I (3–4)
Glaux maritima	V (2–8)	IV (2–7)	V (3–7)	V (2–7)	IV (2–7)
Plantago maritima	V (2–8)	IV (1–8)	V (2–7)	IV (2–7)	IV (2–5)
Agrostis stolonifera	IV (2–8)	V (3–8)		V (2–8)	V (4–8)
Triglochin maritima	IV (1–6)	III (2–5)	IV (1–7)	III (1–6)	II (2–4)
Armeria maritima	IV (2–8)	IV (2–8)	V (2–8)	III (2–5)	III (2–5)
Aster tripolium (rayed)	III (1–5)	II (1–4)	III (2–7)	I (1–4)	I (2)
Puccinellia maritima	I (2–6)	I (2–6)	I (2–5)		
Algal mat	I (4–8)	I (3–6)	II (3–7)	I (4–5)	
Spergularia media	I (2–3)	II (1–3)	II (2–3)	I (2–3)	I (1)
Aster tripolium	I (1–3)	I (3)	I (2–5)		
Salicornia agg.	I (1–3)	I (2–3)	II (2–3)	I (2)	
Atriplex prostrata	I (1–3)	I (1–2)	I (1–2)	I (2–3)	I (2–3)
Cochlearia anglica	I (2–3)	I (2)	I (2–3)	I (2)	I (2)
Halimione portulacoides	I (1–2)	I (4)	I (1–2)		
Limonium cf. *L. vulgare*	I (1–8)	I (1–2)	I (1–2)	I (2)	
Suaeda maritima	I (1–3)	I (2)	II (1–4)	I (2)	I (1)
Trifolium repens	I (2–5)			IV (2–7)	V (2–8)
Leontodon autumnalis	I (2–5)	I (2–5)		III (1–6)	II (2–5)
Carex flacca				I (2–6)	I (5)
Carex distans	I (1–3)			III (1–7)	I (2–4)
Potentilla anserina	I (2)	I (5)		II (2–8)	I (2–6)
Holcus lanatus				I (2–5)	I (2–3)
Lotus corniculatus	I (4)			I (2–5)	I (3–4)
Cerastium fontanum	I (2)			I (2–3)	I (2–3)
Sagina procumbens	I (2–4)	I (4)		I (2–5)	I (2)
Eurhynchium praelongum	I (3–4)	I (4)		I (2–7)	I (3)
Rhytidiadelphus squarrosus	I (3)			I (3–5)	I (3–4)
Hypnum cupressiforme	I (2)			I (2–3)	
Anthoxanthum odoratum				I (3)	

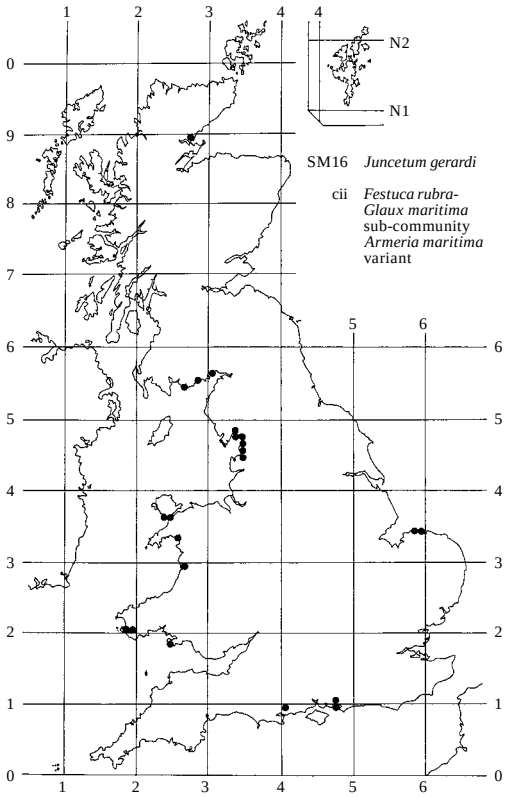
SM16 sub-communities (*cont.*)

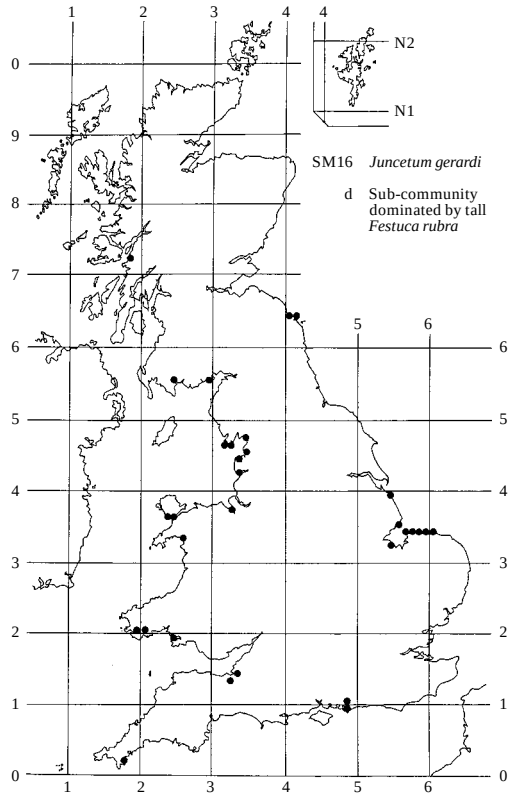
	c	ci	cii	e	ei
Plantago lanceolata				I (2–3)	
Cynosurus cristatus				I (2–3)	
Ranunculus acris				I (2)	
Number of samples	150	68	51	149	30
Mean number of species/sample	9 (5–16)	6 (2–12)	7 (4–12)	11 (7–18)	9 (5–13)
Mean vegetation height (cm)	11 (2–75)	5 (2–20)	5 (2–15)	10 (2–50)	7 (2–25)
Mean total cover (%)	96 (50–100)	98 (80–100)	96 (80–100)	100 (90–100)	99 (85–100)

c *Festuca rubra-Glaux maritima* sub-community
ci *Agrostis stolonifera* variant
cii *Armeria maritima* variant
e *Leontodon autumnalis* sub-community
ei *Trifolium repens* variant


N2
N1
SM16 *Juncetum gerardi*
c *Festuca rubra-Glaux maritima* sub-community


N2
N1
SM16 *Juncetum gerardi*
ci *Festuca rubra-Glaux maritima* sub-community *Agrostis stolonifera* variant


N2
N1
SM16 *Juncetum gerardi*
cii *Festuca rubra-Glaux maritima* sub-community *Armeria maritima* variant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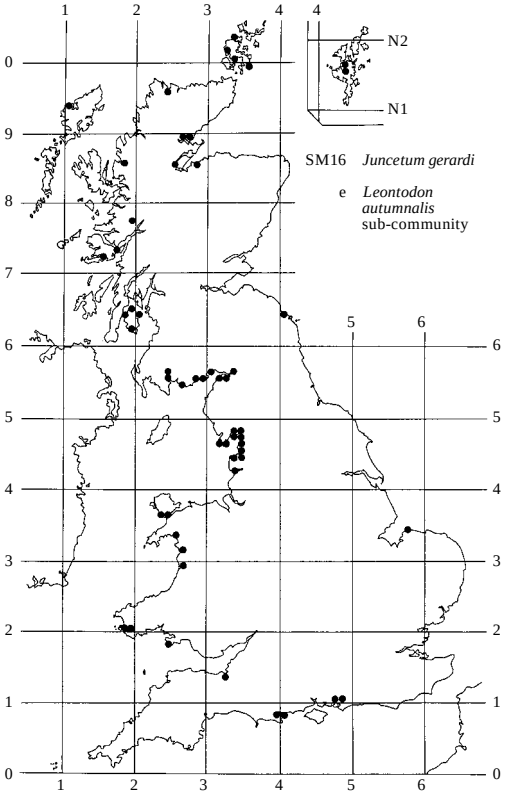
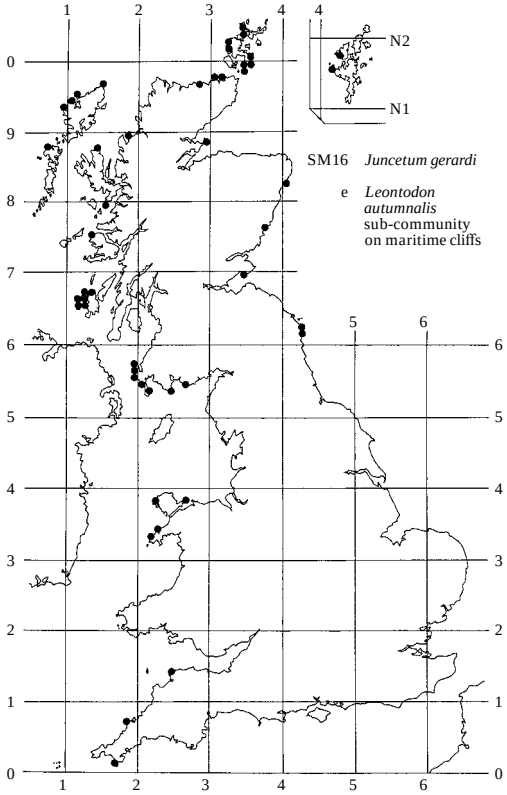
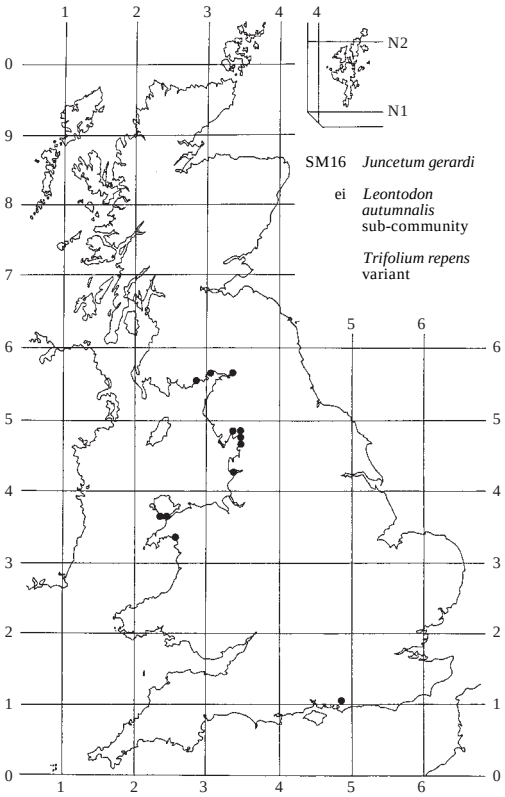
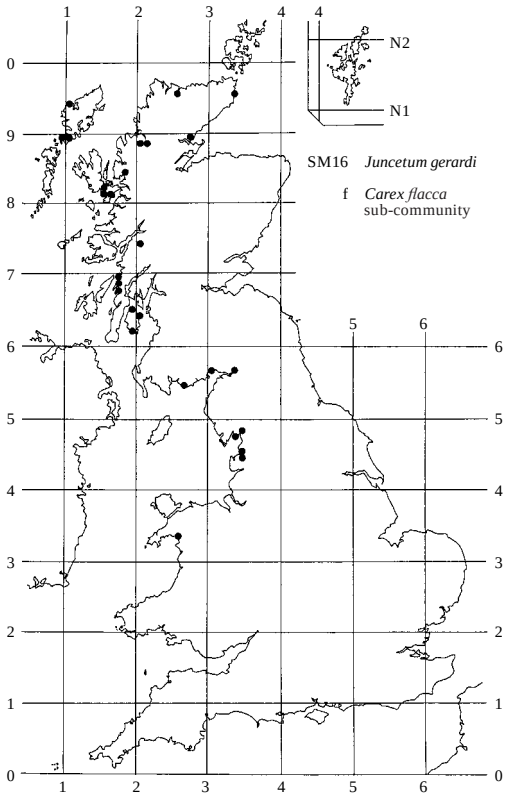
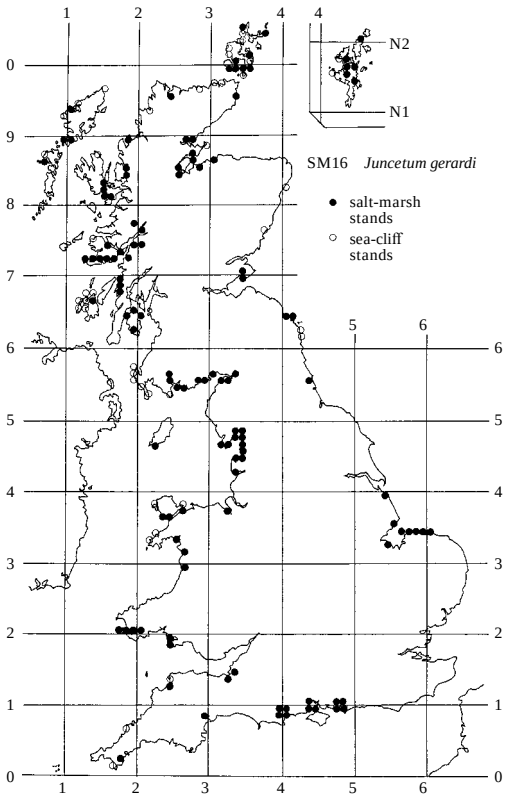
N1
SM16 *Juncetum gerardi*
d Sub-community dominated by tall *Festuca rubra*


N2
N1
SM16 *Juncetum gerardi*
e *Leontodon autumnalis* sub-community


N2
N1
SM16 *Juncetum gerardi*
e *Leontodon autumnalis* sub-community on maritime cliffs


N2
N1
SM16 *Juncetum gerardi*
ei *Leontodon autumnalis* sub-community
Trifolium repens variant


N2
N1
SM16 *Juncetum gerardi*
f *Carex flacca* sub-community


N2
N1
SM16 *Juncetum gerardi*
salt-marsh stands
sea-cliff stands

SM17

Artemisia maritima salt-marsh community

Artemisietum maritimae Hocquette 1927

Synonymy

Festucetum littoralis artemisietosum Ghestem 1972; includes *Halimionetum portulacoidis*, terminal phase with *Artemisia maritima* Beeftink 1962.

Constant species

Artemisia maritima, *Festuca rubra*, *Halimione portulacoides*, *Plantago maritima*.

Rare species

Limonium binervosum, *L. humile*, *Suaeda vera*.

Physiognomy

This is a species-poor community of somewhat variable physiognomy. Stands are generally small and fragmentary but they range from rank grassy patches dominated by *Festuca rubra* with prominent *Artemisia maritima* to open bushy vegetation with *A. maritima* over low *Halimione portulacoides*. There is usually a little *Plantago maritima*; *Limonium* cf. *vulgare* and *Puccinellia maritima* are also frequent.

Habitat

The *Artemisietum maritimae* is an upper-marsh community occurring on a variety of substrates, though often in association with tidal litter and inwashed shell fragments. Its most usual habitat is on creek levees where it forms small patches on the usually heavy clay soils which frequently show organic enrichment in the upper part of the profile. It is also found on ridges and mounds on the upper marsh and sometimes forms a fringe along the foot of sea walls or around stands of *Atriplici-Elymetum pycnanthi*. Where such zones occur at the marsh/dune interface the substrate is often a coarse sand.

Most occurrences are on ungrazed marshes but this may be a reflection of the predominantly south-eastern distribution of the association.

Zonation and succession

The association is normally found as a patchy zone between the *Halimionetum* and *Atriplici-Elymetum pycnanthi*. Junctions with the former may be marked by an intermediate zone with abundant *Festuca rubra*. This zonation may reflect a succession related to increase in marsh height with sediment accretion.

Distribution

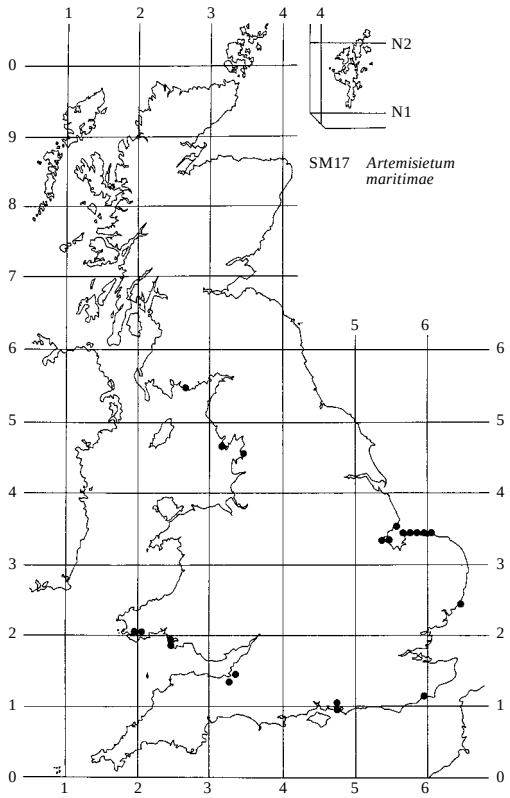
The *Artemisietum* is widespread in East Anglia and along the south coast and it extends north into Scotland. West coast occurrences are scattered and restricted mainly to ungrazed marshes.

Affinities

Traditionally, an *Artemisia maritima* community has not been distinguished in British accounts of salt-marsh vegetation (e.g. Chapman 1934, Tansley 1939) and some Continental authorities regard the community as a subdivision of the *Halimionetum* or *Festucetum littoralis*. Nonetheless, though British stands are generally fragmentary and united mainly by the prominence of *Artemisia maritima*, the major associates represent a distinctive assemblage of species. Furthermore, Continental stands of this vegetation are frequently far more extensive and floristically distinct than those in Britain. A British *Artemisietum* could thus be sensibly seen as a somewhat impoverished extension of an association which occupies a noteworthy floristic transition between a number of Puccinellion and Armerion communities.

Floristic table SM17

Artemisia maritima	V (3–9)
Festuca rubra	V (2–9)
Halimione portulacoides	IV (1–8)
Plantago maritima	IV (1–5)
Limonium cf. *L. vulgare*	III (2–6)
Puccinellia maritima	III (2–7)
Armeria maritima	II (2–4)
Glaux maritima	II (1–4)
Triglochin maritima	II (2–5)
Aster tripolium (rayed)	II (2–4)
Aster tripolium	I (1–3)
Cochlearia anglica	I (1–3)
Juncus gerardii	I (3–5)
Agrostis stolonifera	I (2–5)
Atriplex prostrata	I (2–3)
Elymus pycnanthus	I (2–4)
Suaeda vera	I (1–3)
Spergularia media	I (1–4)
Plantago coronopus	I (2–5)
Cochlearia officinalis	I (2)
Elymus repens	I (2–3)
Juncus maritimus	I (3–5)
Suaeda maritima	I (2–4)
Salicornia agg.	I (2)
Parapholis strigosa	I (2–4)
Hordeum marinum	I (3–4)
Number of samples	42
Mean number of species/sample	7 (2–12)
Mean vegetation height (cm)	19 (7–35)
Mean total cover (%)	98 (50–100)



SM18
Juncus maritimus salt-marsh community

Synonymy
Juncetum maritimi auct. angl. p.p., includes *Juncus maritimus-Oenanthe lachenalii* ass. R.Tx. 1937

Constant species
Agrostis stolonifera, *Festuca rubra*, *Glaux maritima*, *Juncus gerardii*, *J. maritimus*.

Physiognomy
The association is dominated by tall dense clumps of *Juncus maritimus* with an understorey of *Agrostis stolonifera*, *Festuca rubra*, *Glaux maritima* and *Juncus gerardii*. There is a rich subsidiary flora in which mesotrophic grassland species (notably *Leontodon autumnalis* and *Trifolium repens*) and weed species (for example, *Atriplex hastata*, *Elymus repens* and *Rumex crispus*) are conspicuous. Bryophytes may be locally abundant with patches of *Calliergon cuspidatum*, *Amblystegium riparium*, *A. serpens* and *Eurhynchium praelongum*. Stands of the association may be based on individual clones of *J. maritimus*, in some cases up to 15 m in diameter, or occur as an extensive zone.

Sub-communities

***Plantago maritima* sub-community:** *Juncetum maritimi* Yapp & Johns 1917; *Festuca rubra-Juncus maritimus* nodum Adam 1976. *Plantago maritima* and *Triglochin maritima* attain constancy in the often luxuriant vegetation of this sub-community and there are frequent records for *Leontodon autumnalis*, rayed *Aster tripolium* and *Armeria maritima*. It sometimes occupies extensive areas, notably at Ynys Hir in the Dovey estuary, Dyfed.

***Oenanthe lachenalii* sub-community:** *Juncus maritimus-Oenanthe lachenalii* ass. R.Tx. 1937; *Oenanthe lachenalii-Juncus maritimus* nodum Adam 1976. *Triglochin maritima*, *Leontodon autumnalis* and *Oenanthe lachenalii* are constant here, the last giving a particularly distinctive appearance to the vegetation in the flowering season, though it is rarely present in abundance. Individual stands, even those in close proximity, may have singular characteristics and different weed species, germinating in trapped drift litter, are especially variable. Some stands have abundant *Cirsium arvense*, others *Atriplex hastata*, *Sonchus arvensis* or *Urtica dioica*.

***Festuca arundinacea* sub-community:** *Festuca arundinacea-Juncus maritimus* nodum Adam 1976. *Oenanthe lachenalii*, remains constant in this sub-community but salt-marsh species like *Glaux maritima*, *Juncus gerardii*, *Plantago maritima* and *Triglochin maritima* are less frequent. However, the most obvious feature here is the constancy of *Festuca arundinacea*, the large tussocks of which may be co-dominant with the *Juncus maritimus*, and of *Leontodon autumnalis*, *Potentilla anserina* and *Trifolium repens* in the understorey. Other mesotrophic grassland species such as *Holcus lanatus*, *Lotus corniculatus*, *Ranunculus acris* and *Vicia cracca* are also frequent.

Habitat
The association is predominantly an upper-marsh community but the sub-communities differ in their tolerance of tidal submersion. The lowest recorded site for the *Festuca arundinacea* sub-community experienced 25 submergences/year while the *Oenanthe* sub-community seems to be able to tolerate at least 150 submergences/year. As the *Plantago* sub-community is normally found seaward of the *Oenanthe* sub-community, its tolerance is presumably even greater.

The association occurs on a variety of substrates but the pH is generally around 7.0 (cf. Bridges 1977 who recorded values down to 5.1). There is normally an appreciable accumulation of organic matter in the top 10–20 cm of the soil and superficial litter trapping may be considerable. This material provides a suitable substrate for colonisation by weed species.

Although the association is common on grazed marshes, *Juncus maritimus* is itself unpalatable and its dense tall growth confers protection on the associated

species. Yapp & Johns (1917) and Tansley (1939) suggested that the luxuriance of vegetation within *J. maritimus* stands may also be due to the higher and more constant humidity levels attained there. Extensive spread of the association on grazed marshes reduces their agricultural value but eradication has been attempted on only a small local scale. Mowing, draining, the use of herbicides and physical removal of *J. maritimus* have all been attempted. Packham & Liddle (1970) have reported some success in control on Cefni Marsh, Anglesey, by cutting close to the ground in early summer.

Oenanthe lachenalii is remarkably resistant to oil and refinery effluent spillage (Baker 1979). Even after repeated oiling, plants respond simply by producing new shoots.

Zonation and succession

At a few sites, there is a zonation within single extensive stands of the association from the *Plantago* sub-community through the *Oenanthe* sub-community to the *Festuca* sub-community. More generally, isolated stands of each of the sub-communities occur within other communities, the *Oenanthe* and *Plantago* sub-communities usually within the *Juncetum gerardi*, though the *Plantago* sub-community may also extend down-marsh into the upper part of the *Puccinellietum maritimae*. Unlike these two sub-communities where stands are sharply defined the *Festuca* sub-community often has rather diffuse boundaries with its neighbouring communities on the upper marsh.

Juncus maritimus can be an aggressive invader. Packham & Liddle (1970) reported the transformation of an area of *Puccinellietum maritimae* within the space of 20 years. It has been conventional in British accounts to regard *Juncus maritimus* salt-marsh, if not as the true climax of succession, then at least as a very stable stage in upper marsh development which can be considered for most purposes as the climax. The association is clearly important on those marshes where it occurs but it is probably better to see it as part of a seral sequence parallel to that involving the *Juncetum gerardi*.

Distribution

The association is widespread on the west coast as far north as Arran but very local in south-east England, though it may occur there on derelict reclaimed land. In Norfolk, the association is replaced by the *Juncus maritimus-Triglochin maritima* salt-marsh.

Affinities

The classification of *Juncus maritimus* vegetation poses a number of problems (Adam 1977). *J. maritimus* occurs widely in British salt-marshes but those vegetation types in which it is dominant or co-dominant are nonetheless distinct. Two of these are best considered as sub-communities of other well-defined associations: the *Halimionetum portulacoidis* and the *Atriplici-Elymetum pycnanthi*. A further community forms the distinctive, partly low-marsh, *Juncus maritimus-Triglochin maritima* association.

The three remaining types are those grouped here as the *Juncus maritimus* salt-marsh. The *Juncetum maritimi* of British authors has not been taken up in Continental studies but, although this partly reflects a different approach to classification, it is probably also an indication of the less important role which *J. maritimus* plays outside Great Britain. An alternative approach to these three types of *J. maritimus* salt-marsh would be to consider them as variants of the *Juncetum gerardi* (see Braun-Blanquet & Tüxen 1952, Ivimey-Cook & Proctor 1966, Moore *et al*. 1970 and Moore & O'Reilly 1977 in Ireland). However, although the two associations share a considerable number of species, the *Juncus maritimus* salt-marsh is distinct in containing conspicuous weed species and also in its striking physiognomy. The representation of ruderals has led some workers to place *J. maritimus* vegetation in various taxa of the Elymo-Rumicion crispi (e.g. Westhoff & den Held 1969).

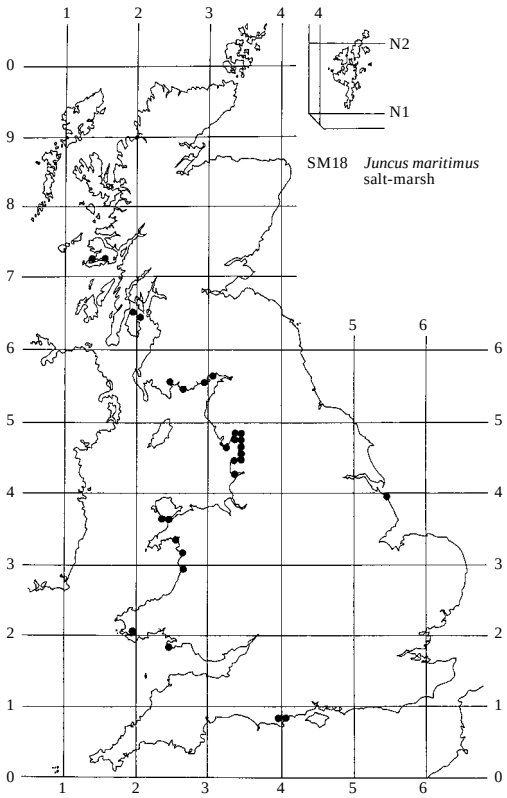
There is no single well-described phytosociological equivalent of the association diagnosed here. Tüxen (1937) reported a *Juncus maritimus-Oenanthe lachenalii* association from north Germany and similar communities have been encountered from other sites in that region (Libbert 1940, Voderberg 1955, Passarge 1964), from The Netherlands (Westhoff & den Held 1969) and from north Spain (Tüxen & Oberdorfer 1958, Bellot 1966). These have not been fully described or related to British *J. maritimus* vegetation but it may eventually be sensible to incorporate them into a single association.

The general floristic similarities to the *Juncetum gerardi* suggest that the *Juncus maritimus* salt-marsh is best placed within the Armerion maritimae of the Asteretea.

Floristic table SM18

	a	b	c	18
Juncus maritimus	V (7–9)	V (2–9)	V (5–8)	V (2–9)
Agrostis stolonifera	V (3–8)	V (3–8)	V (4–7)	V (3–8)
Festuca rubra	V (1–8)	V (3–8)	V (5–7)	V (1–8)
Glaux maritima	IV (2–7)	IV (2–6)	III (2–4)	IV (2–7)
Juncus gerardii	IV (3–5)	IV (2–6)	III (3–5)	IV (2–6)
Triglochin maritima	IV (2–5)	IV (2–5)	II (2–3)	III (2–5)
Plantago maritima	V (2–6)	III (2–4)	II (2–3)	III (2–6)
Oenanthe lachenalii	I (1–3)	V (2–5)	V (2–5)	III (1–5)
Leontodon autumnalis	III (2–4)	IV (2–5)	IV (1–4)	II (1–5)
Festuca arundinacea	I (2)	I (2–3)	V (3–7)	II (2–7)
Potentilla anserina	I (3–5)	II (2–7)	IV (2–7)	II (2–7)
Trifolium repens	II (2–6)	III (3–8)	IV (3–5)	III (2–8)
Aster tripolium (rayed)	III (2–4)	II (2–3)	I (2)	II (2–4)
Armeria maritima	III (2–5)	I (2–4)	I (2–3)	II (2–5)
Algal mat	II (4–8)	I (4–5)		I (4–8)
Atriplex prostrata	II (1–5)	III (2–5)	II (2–3)	II (1–5)
Elymus repens	I (4)	II (2–6)	III (3–6)	II (2–6)
Carex distans	I (2–3)	II (2–5)	III (1–4)	II (1–5)
Lotus corniculatus	I (4)	I (2–4)	III (3–5)	I (2–5)
Eurhynchium praelongum	I (3–5)	II (3–6)	III (3–7)	II (3–7)
Carex extensa	II (3–4)	I (1–4)	I (3)	I (1–4)
Poa pratensis	I (3–5)	II (2–5)	I (2–4)	I (2–5)
Rumex crispus	I (1–3)	II (2–3)	I (1–3)	I (1–3)
Samolus valerandi	I (3)	I (2–4)	II (2–4)	I (2–4)
Cirsium arvense		I (2–7)	II (2–3)	I (2–7)
Holcus lanatus		I (2–7)	II (2–7)	I (2–7)
Ranunculus acris		I (2–3)	II (2–4)	I (2–4)
Vicia cracca		I (2–4)	II (1–6)	I (1–6)
Carex otrubae		I (2–4)	I (2–4)	I (2–4)
Cochlearia officinalis	II (2–4)	II (2–3)	II (1–3)	II (1–4)
Amblystegium serpens	I (3–5)	I (3)	I (3–5)	I (3–5)
Galium palustre	I (3)	I (2–4)	I (3)	I (2–4)
Lychnis flos-cuculi	I (3)	I (2–3)	I (3)	I (2–3)
Sonchus arvensis	I (3)	I (2–3)	I (2–5)	I (2–5)
Number of samples	51	71	33	155
Mean number of species/sample	11 (5–20)	13 (7–25)	15 (8–32)	13 (5–32)
Mean vegetation height (cm)	51 (5–100)	49 (30–100)	53 (30–100)	50 (5–100)
Mean total cover (%)	98 (85–100)	99 (70–100)	99 (95–100)	98 (70–100)

a *Plantago maritima* sub-community
b *Oenanthe lachenalii* sub-community
c *Festuca arundinacea* sub-community
18 *Juncus maritimus* salt-marsh (total)


1
2
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SM18 *Juncus maritimus* salt-marsh
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9
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SM19

Blysmus rufus salt-marsh community

Blysmetum rufi (G. E. & G. Du Rietz 1925) Gillner 1960

Synonymy

Juncus gerardii-Carex extensa Association Birks 1973 *p.p.*

Constant species

Blysmus rufus, Agrostis stolonifera, Glaux maritima, Juncus gerardii, Triglochin maritima.

Rare species

Blysmus rufus.

Physiognomy

The *Blysmetum rufi* is a species-poor association, generally dominated by *Blysmus rufus* but often with abundant *Agrostis stolonifera, Glaux maritima* and *Juncus gerardii. Triglochin maritima, Festuca rubra, Plantago maritima* and *Carex extensa* are all frequent but rarely present in quantity. Some stands may have an extensive algal mat and certain bryophytes may be abundant: *Amblystegium riparium, A. serpens, Calliergon cuspidatum, Campylium stellatum, C. polygamum, Drepanocladus aduncus* and *Cratoneuron filicinum*. Cover may be somewhat open, especially on gravelly or rocky substrates, and stands are usually small (10–20 m^2), though at a number of Scottish sites the association covers hundreds of square metres.

Habitat

The association occurs on a variety of substrates but sites are often either poorly-drained or subject to flushing by brackish or fresh-water. The characteristic situation is in small depressions in the upper marsh. In some cases, the *Blysmetum* may develop in old upper-marsh pans, especially where these have a shingle base, and it is sometimes present along path edges (Gillner 1960, Tyler 1969*b*, Beeftink 1977*a*). In west Scotland, small stands are widespread within rocky flushes in the salt-marsh/mire transition on raised beaches and also among coastal rocks (Gillham 1957*b*, Birks 1973, Adam *et al.* 1977). The majority of occurrences are on grazed salt-marshes, although *B. rufus* itself does not appear to be much eaten.

Zonation and succession

Although *B. rufus* sometimes occurs as scattered shoots within the *Juncetum gerardi* (notably at Caerlaverock NNR, Dumfries & Galloway; Martin 1977), stands of the *Blysmetum* are usually rather sharply defined from the *Juncetum gerardi* which is the usual surrounding vegetation. Freshwater flushing over gravel sometimes allows the association to develop at fairly low levels in the marsh but it is unlikely that the *Blysmetum* plays any role in succession.

Distribution

B. rufus is one of the very few species constituting a northern element in the British salt-marsh flora (Ratcliffe 1977) and the association is locally distributed along the west coast from mid-Wales northwards, being commonest in west Scotland. Its generally small stands render it vulnerable to local extinction following habitat disturbance but, though there is some evidence for the loss of *B. rufus* in the southern part of its range (Perring & Walters 1962, Martin 1977, Ratcliffe 1977), there is nothing to suggest a large-scale contraction in distribution.

Affinities

The *Blysmetum rufi* is not discussed in the early descriptions of British salt-marshes which were mainly concerned with communities in south-east England. It has, however, been referred to in more recent accounts from northern and western Britain (Gillham 1957*b*, Greenwood 1972, Birks 1973, Adam *et al.* 1977) and the association is widely described on the Continent, where it is especially widespread in southern Scandinavia.

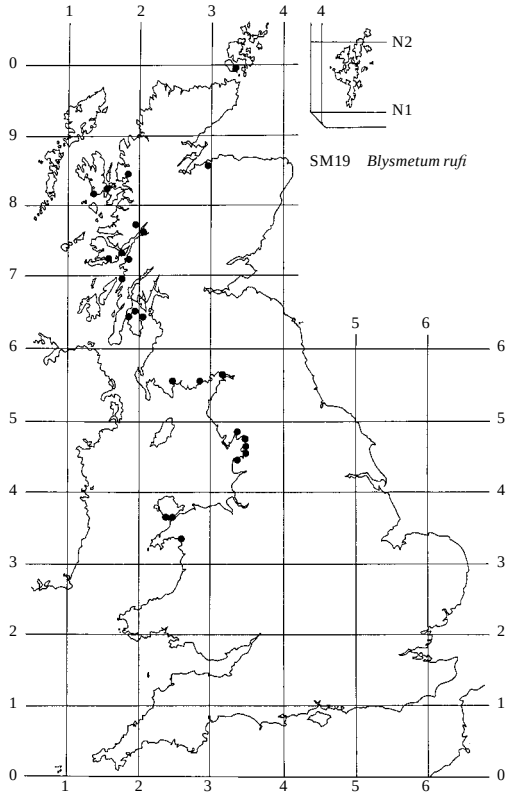
The *Blysmetum* shows clear affinities with the *Juncetum gerardi* and some accounts of the community

regard it as part of that association (e.g. Birks 1973) or as a closely-related association within the Armerion maritimae (e.g. Beeftink 1965, 1977*a*). An alternative treatment is to place the association alongside the *Eleocharitetum uniglumis*, which is similar in its physiognomy and its habitat to the *Blysmetum*, and which is itself the centre of a separate alliance, the Eleocharion uniglumis (Siira 1970, Tyler *et al*. 1971).

There are some ecological similarities between the *Blysmetum* of the Scottish raised-beach flushes and certain of the Caricion davallianae communities *sensu* Wheeler (1980*b*).

Floristic table SM19

Blysmus rufus	V (3–9)
Agrostis stolonifera	V (2–7)
Glaux maritima	V (2–7)
Juncus gerardii	V (2–6)
Triglochin maritima	IV (1–5)
Festuca rubra	III (2–6)
Plantago maritima	III (2–5)
Carex extensa	III (2–5)
Aster tripolium (rayed)	II (2–3)
Armeria maritima	II (2–5)
Algal mat	II (3–7)
Trifolium repens	II (2–5)
Juncus articulatus	II (1–6)
Eleocharis uniglumis	II (4–9)
Alopecurus geniculatus	I (3–5)
Potentilla anserina	I (2–3)
Leontodon autumnalis	I (2–3)
Eleocharis quinqueflora	I (5)
Triglochin palustris	I (2–3)
Amblystegium riparium	I (3–4)
Amblystegium serpens	I (2–4)
Carex nigra	I (3–4)
Calliergon cuspidatum	I (3–7)
Cochlearia anglica	I (2)
Campylium polygamum	I (2–5)
Oenanthe lachenalii	I (3)
Puccinellia maritima	I (1–4)
Carex lepidocarpa	I (2–3)
Campylium stellatum	I (3–5)
Number of samples	23
Mean number of species/sample	10 (5–17)
Mean vegetation height (cm)	17 (6–25)
Mean total cover (%)	90 (50–100)



SM20

Eleocharis uniglumis salt-marsh community

Eleocharitetum uniglumis Nordhagen 1923

Constant species
Eleocharis uniglumis, *Agrostis stolonifera*.

Physiognomy
Although *Eleocharis uniglumis* is a widespread minor constituent of a variety of damp transitional communities along the upper marsh fringes (Birks 1973, Adam 1976), it is here dominant in a species-poor association, similar in floristics and appearance to the *Blysmetum rufi*. There is often an extensive undercarpet of *Agrostis stolonifera* and *Juncus gerardii*, *Glaux maritima*, *Festuca rubra*, *Triglochin maritima*, *Potentilla anserina* and *Alopecurus geniculatus* all occur frequently and may be abundant in particular stands. As in the *Blysmetum*, cover is variable and algae and bryophytes may form a patchy carpet over the substrate surface.

Habitat
In Britain, the *Eleocharitetum* occurs most frequently in depressions in the upper marsh. Some of the most extensive stands occur in brackish marshes by the River Gilpin, Cumbria. Rarely, it occurs in what is a widespread habitat in Scandinavia, as a fringe of emergent vegetation, as around the brackish and atidal Loch an Amadain in Skye.

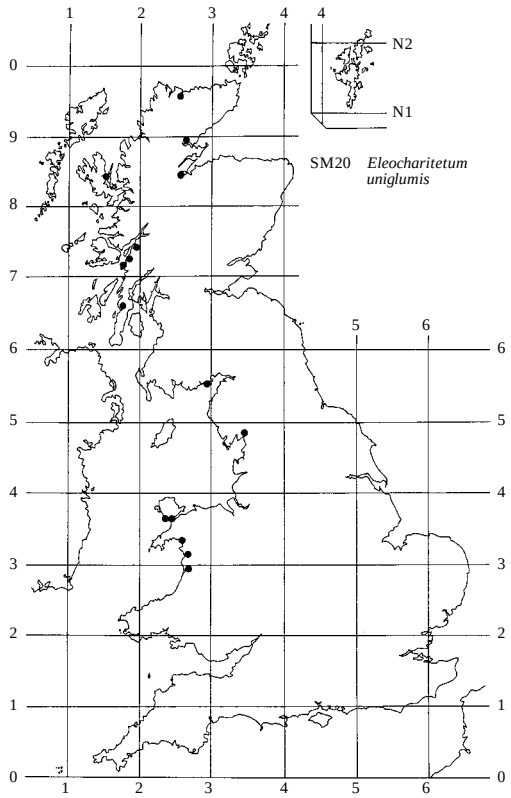
Zonation and succession
The *Eleocharitetum* occurs patchily within other upper-marsh associations such as the *Juncetum gerardi* and it does not play a major role in salt-marsh succession.

Distribution
The association is a rare community on British salt-marshes occurring locally along the west coast from the Dovey estuary northwards.

Affinities
British vegetation dominated by *E. uniglumis* is clearly closely related to that described from Scandinavia (Gillner 1960, Tyler 1969*b*, Siira 1970) although the emergent stands in Britain lack the aquatic species characteristic of the *Eleocharetum* of, for example, the Baltic. Siira (1970) and Tyler *et al*. (1971) assign the association to the alliance Eleocharion uniglumis, and a sensible treatment of both the *Eleocharitetum* and the *Blysmetum rufi* would be to regard them as constituting, in this alliance, the brackish end of variation within the Asteretea.

Floristic table SM20

Eleocharis uniglumis	V (5–10)
Agrostis stolonifera	V (3–7)
Glaux maritima	III (2–5)
Juncus gerardii	III (3–6)
Festuca rubra	II (2–7)
Triglochin maritima	II (2–5)
Alopecurus geniculatus	II (2–6)
Potentilla anserina	II (2–7)
Aster tripolium (rayed)	I (2–3)
Plantago maritima	I (4)
Armeria maritima	I (2–3)
Algal mat	I (8)
Carex extensa	I (3)
Trifolium repens	I (3–6)
Leontodon autumnalis	I (2–3)
Juncus articulatus	I (3–6)
Eleocharis quinqueflora	I (2–3)
Triglochin palustris	I (2)
Amblystegium riparium	I (3)
Carex nigra	I (2–4)
Hydrocotyle vulgaris	I (3–8)
Atriplex prostrata	I (2–3)
Samolus valerandi	I (3–4)
Carex distans	I (3–4)
Galium palustre	I (3–4)
Oenanthe lachenalii	I (1–4)
Scirpus maritimus	I (2–3)
Number of samples	17
Mean number of species/sample	8 (4–22)
Mean vegetation height (cm)	22 (10–45)
Mean total cover (%)	90 (60–100)



SM21
Suaeda vera–Limonium binervosum salt-marsh community

Synonymy
Suaedeto-Limonietum Chapman 1934 *p.p.*; *Halimioneto-Limonietum* Chapman 1934 *p.p.*; ? *Suaedetum fruticosae* Tansley 1939 *p.p.*; *Suaedeto-Limonietum binervosi* Adam 1976; *Halimiono-Frankenietum laevis* Adam 1976 *emend.*; Norfolk *Frankenia laevis* stands Brightmore 1979.

Constant species
Armeria maritima, *Halimione portulacoides*, *Limonium binervosum*, *Puccinellia maritima*, *Suaeda vera*.

Rare species
Frankenia laevis, *Limonium bellidifolium*, *L. binervosum*, *Suaeda vera*.

Physiognomy
The rather open vegetation of this community is generally dominated by scattered bushes of *Suaeda vera* and *Halimione portulacoides* up to 40 cm high with a patchy cover of herbaceous halophytes between. Among the constants, *Puccinellia maritima* and *Limonium binervosum* are usually most abundant with smaller amounts of *Armeria maritima*. *Suaeda maritima* is fairly frequent throughout.

Sub-communities

Typical sub-community: *Suaedeto-Limonietum binervosi* Adam 1976. *Festuca rubra*, *Plantago maritima* and *Artemisia maritima* are frequent in this sub-community, the first sometimes in abundance. There are occasional records for a variety of species characteristic of disturbed places on the upper marsh and of strandlines.

***Frankenia laevis* sub-community:** *Halimiono-Frankenietum laevis* Adam 1976 *emend*. *Frankenia laevis* and *Limonium bellidifolium* are constant in this sub-community which is more species-poor than the above.

Habitat
The community is characteristic of salt-marsh/dune interfaces, spit laterals, eroded dunes and some sand-dune lows where there is a base of shingle covered with varying amounts of blown sand and inwashed silt (Chapman 1934, 1960*b*, Tansley 1939).

The sub-communities differ in their tolerance of tidal inundation. The Typical sub-community is most frequently encountered at or above the tidal limit where there is inundation only during severe storms. The *Frankenia* sub-community extends further down-marsh and at its lower limit there may be a thick layer of heavy clay over the shingle base. During the summer, high soil salinities may be experienced with a salt crust forming on the soil surface (see also Brightmore 1979).

Grazing, especially by rabbits, is, or has been, of considerable importance in the maintenance of this community. Heavy grazing of low *Suaeda vera* and *Halimione portulacoides* helps to maintain an open cover but reduction of grazing or resumed grazing of taller bushes of these species (Brightmore 1979) may allow the development of a closed or more erect canopy which can shade out *Frankenia laevis* from the *Frankenia* sub-community.

Zonation and succession
In general the community occupies a stable position at the uppermost end of the salt-marsh zonation but reduction of grazing may lead eventually to the development of the *Elymo-Suaedetum verae*, especially at lower levels.

Distribution
The community is endemic to Great Britain and is restricted to the north Norfolk coast. *Frankenia laevis*, *Limonium bellidifolium*, *L. binervosum* and *Suaeda vera* are all members of the Mediterranean element in the British flora (Matthews 1955) but, though of restricted

occurrence, they are not, apart from *L. bellidifolium*, confined to north Norfolk and their distributions overlap elsewhere. Neither is the distinctive salt-marsh/sand-dune interface habitat restricted to that area. Yet there is no evidence to suggest that this particular species assemblage has ever had a more widespread distribution (Adam 1978). Both *Frankenia laevis* and *Suaeda vera* are conspicuous members of other communities in a similar habitat.

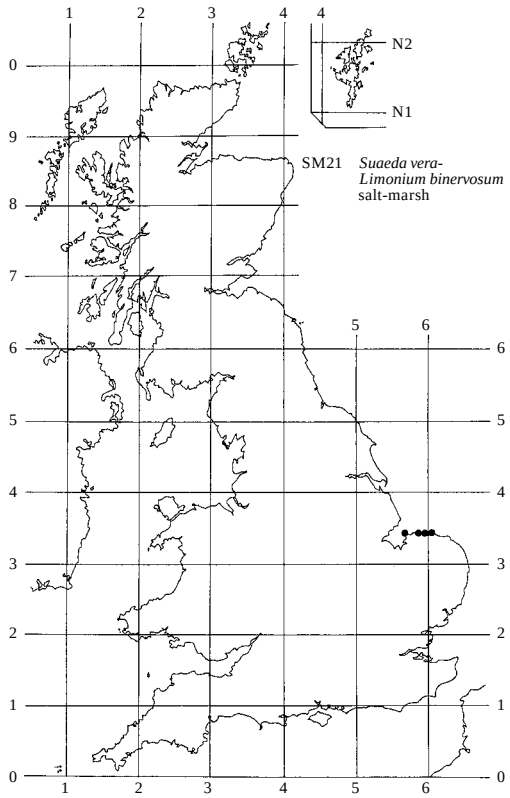
Affinities

Together with the *Limonio vulgaris-Frankenietum laevis*, this community represents vegetation which has floristic affinities with the Puccinellion communities yet which stands alongside the Armerion communities in its high position on the salt-marsh. Géhu & Géhu-Franck (1975) erected a new taxon, the Frankenio-Armerion, for similar vegetation described from France and suggested that this might be regarded as a sub-alliance within the Armerion.

Floristic table SM21

	a	b	21
Suaeda vera	V (1–4)	V (1–7)	V (1–7)
Puccinellia maritima	V (3–7)	V (2–6)	V (2–7)
Armeria maritima	V (2–7)	IV (2–5)	IV (1–7)
Halimione portulacoides	V (1–6)	IV (2–7)	IV (1–7)
Limonium binervosum	V (2–7)	IV (1–5)	IV (1–7)
Suaeda maritima	II (3)	III (2–6)	II (2–6)
Artemisia maritima	III (1–4)		I (1–4)
Festuca rubra	III (5–6)	I (3)	II (3–6)
Plantago maritima	III (2–4)	I (2–3)	II (2–4)
Elymus pycnanthus	II (1–2)		I (1–2)
Limonium cf. *L. vulgare*	II (2–5)		I (2–5)
Sagina maritima	II (2–3)	I (2)	I (2–3)
Spergularia marina	II (2–3)	I (2)	I (2–3)
Glaux maritima	I (3)		I (3)
Spergularia media	I (2)	I (1)	I (1–2)
Frankenia laevis		V (2–5)	III (2–5)
Limonium bellidifolium	II (1–4)	IV (1–6)	III (1–6)
Cochlearia anglica	I (2–3)	II (2)	I (2–3)
Cochlearia danica	I (2–3)	II (3)	I (2–3)
Salicornia agg.	I (3)	II (2–3)	I (2–3)
Cochlearia officinalis		I (1–2)	I (1–2)
Number of samples	11	14	25
Mean number of species/sample	10 (5–13)	8 (5–12)	8 (5–13)
Mean vegetation height (cm)	15 (4–40)	18 (3–40)	17 (3–40)
Mean total cover (%)	63 (20–90)	53 (20–80)	57 (20–90)

a Typical sub-community
b *Frankenia laevis* sub-community
21 *Suaeda vera-Limonium binervosum* salt-marsh (total)


N2
N1
SM21 *Suaeda vera-Limonium binervosum* salt-marsh

SM22

Halimione portulacoides-Frankenia laevis salt-marsh community

Limonio vulgaris-Frankenietum laevis Géhu & Géhu-Franck 1975

Synonymy

Halimiono-Frankenietum laevis Adam 1976 *p.p*; Sussex *Frankenia laevis* stands Brightmore 1979.

Constant species

Armeria maritima, Frankenia laevis, Halimione portulacoides.

Rare species

Frankenia laevis, Inula crithmoides, Arthrocnemum perenne.

Physiognomy

This community has a short uneven open sward dominated by *Halimione portulacoides* and *Frankenia laevis* with scattered plants of *Armeria maritima* and *Puccinellia maritima*. *Festuca rubra, Limonium vulgare*, annual *Salicornia* spp. and *Spergularia media* are frequent at low cover values and at some sites *Inula crithmoides* is conspicuous.

Habitat

The community generally occurs on mixtures of silt, sand and shingle at salt-marsh/sand-dune interfaces. Similar vegetation but lacking *H. portulacoides* has been recorded from Chalk undercliffs and rubble (Brightmore 1979).

Distribution

The community is confined to the south coast of Sussex where the best stands are developed at East Head, Chichester Harbour. *Frankenia laevis* has recently been reported from Anglesey (Roberts 1975) where it has become well established (after original planting?) among *Festuca rubra, Armeria maritima* and *Puccinellia maritima* to produce vegetation rather similar to this community.

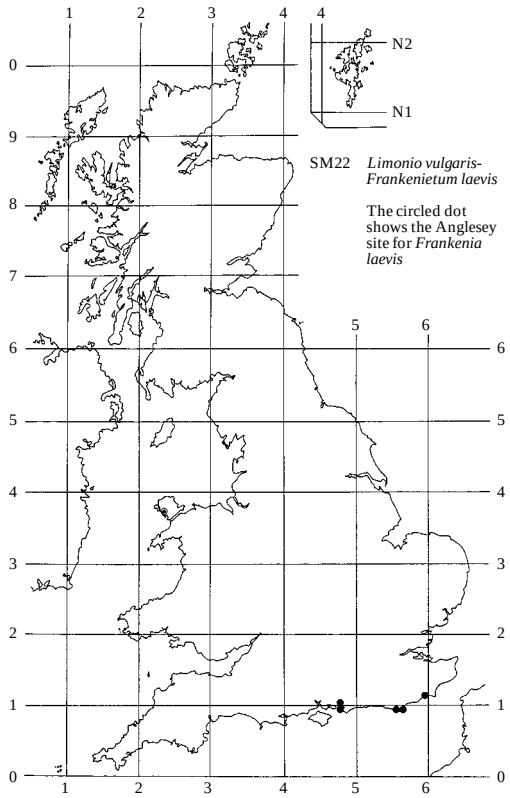
Affinities

The community is distinguished from the *Suaeda vera-Limonium binervosum* salt-marsh by the absence here of *S. vera* and the replacement of *Limonium bellidifolium* and *L. binervosum* by *L. vulgare*. Géhu & Géhu-Franck (1975) and Géhu & Delzenne (1975) regard the Sussex stands as representing a species-poor parallel to the *Frankenio-Limonietum lychnidifolii* of north-west France and have provisionally assigned them (and the Anglesey vegetation) to the *Limonio vulgaris-Frankenietum laevis*. This association and the *Suaeda vera-Limonium binervosum* community could be placed together in the Frankenio-Armerion.

Floristic table SM22

Frankenia laevis	V (3–8)
Halimione portulacoides	IV (3–9)
Puccinellia maritima	IV (2–5)
Armeria maritima	III (2–4)
Spergularia media	III (1–2)
Festuca rubra	II (3–5)
Salicornia agg.	II (1–3)
Elymus farctus	II (3–4)
Limonium vulgare	II (1–5)
Parapholis strigosa	II (1–4)
Suaeda maritima	I (1–2)
Arthrocnemum perenne	I (1–2)
Plantago maritima	I (1–2)
Plantago coronopus	I (1–5)
Number of samples	18
Mean number of species/sample	8 (6–13)
Mean vegetation height (cm)*	3 (2–5)
Mean total cover (%)	86 (80–100)

* Data of four samples only.


N2
N1
SM22 *Limonio vulgaris-Frankenietum laevis*
The circled dot shows the Anglesey site for *Frankenia laevis*

SM23

Spergularia marina-Puccinellia distans salt-marsh community

Puccinellietum distantis Feekes (1934) 1945

Synonymy
Sperguletum marinae Tyler 1969.

Constant species
Spergularia marina, *Puccinellia distans*, *P. maritima*.

Physiognomy
The *Puccinellietum distantis* is a generally open association of scattered but often abundant individuals of *Spergularia marina*, *Puccinellia distans* and *P. maritima* with rather variable amounts of *Agrostis stolonifera* and sparse records for a variety of salt-marsh species (especially in coastal sites) and ruderal glycophytes. An algal mat is sometimes conspicuous in coastal stands but bryophytes are always rare.

Sub-communities
Sampling of coastal stands of the association has been insufficient to detect the existence of well-defined sub-communities but individual stands bear some resemblance to the *Puccinellietum distantis polygonetosum* R.Tx. 1956 *emend*. Beeftink 1962 (with *Polygonum aviculare*) and the *Puccinellietum distantis pholiuretosum* (with *Parapholis strigosa*) described from The Netherlands (Beeftink 1962, 1965, 1977*a*). Lee (1977) encountered inland stands similar to the 'initial' (with *Atriplex hastata*) and 'degraded' (without *A. hastata* and *Spergularia marina*) sub-associations recognised on Polish coastal marshes (Piotrowski 1974) and to the *Puccinellietum distantis juncetosum* Westhoff 1947 (with *Juncus ambiguus* Guss.) described from the Netherlands (Beeftink 1962). Lee's (1977) *asteretosum* is probably best considered in relation to the *Aster tripolium* communities of salt-marshes and brackish habitats. Further sampling is necessary to establish the validity of these sub-divisions in Britain.

Habitat
The association is characteristic of disturbed situations with soils of variable but generally high salinity. On coastal marshes, it is found in dried-up pans in the upper marsh, in old turf-cuttings, along paths and (particularly in The Wash) in cattle-poached areas. It also occurs on and behind sea walls.

Inland, *Puccinellietum distantis* has been described (Lee 1977) from both natural brine springs and marshes, where it is best developed on the most saline, cattle-poached soils, and from the artificial habitats associated with the salt and alkali industries. Disturbance helps maintain and extend the association, especially through the establishment of the prolifically-seeding annual *Spergularia marina*. Lee found this species best able to tolerate the most saline conditions, though it appeared to suffer from competition with *Puccinellia distans* on soils of lower salinity. Differential response of these two species formed the basis of small-scale mosaics over uneven spoil and soil surfaces.

In these inland sites, the so-called 'initial' sub-association (after Piotrowski 1974) persisted provided soil salinity remained high. The 'degraded' sub-association, dominated by *P. distans*, was characteristic of drier soils and the *juncetosum* of wetter soils, both of lower salinity.

Zonation and succession
Mosaics of the various sub-communities appear to develop in relation to differences in soil salinity levels and the height of the water-table. In coastal sites, the association is usually rather sharply marked off from the surrounding vegetation, often *Juncetum gerardi* or *Puccinellietum maritimae*, though in some cases there may be a more gradual transition to a *Puccinellietum maritimae* with large amounts of *Puccinellia distans* (e.g. the upper reaches of the tidal Nene; Adam & Akeroyd 1978).

The association is maintained by continued disturbance. If this ceases, then a closed sward of the surrounding vegetation is likely to extend into the *Puccinellietum distantis*.

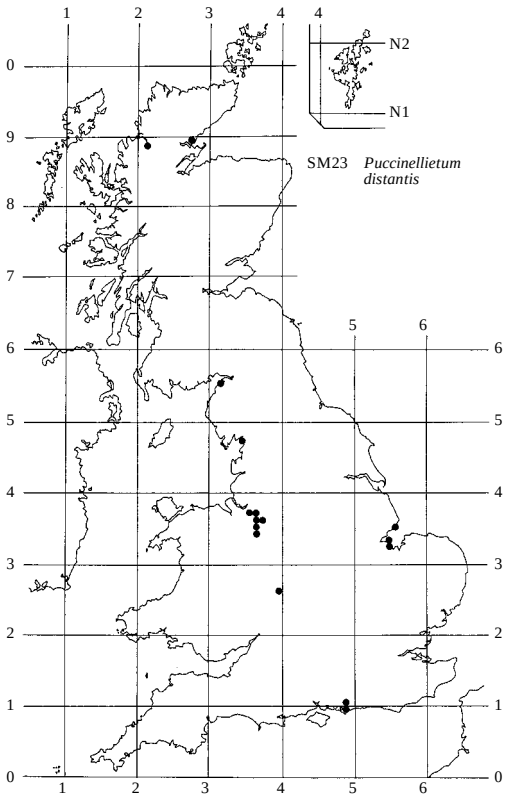
Distribution
Fragmentary stands occur on coastal marshes throughout the country. Inland, the association is confined to areas with percolation of saline waters or accumulation of salt and alkali waste. The most extensive sites are in Cheshire, though some of these have been lost by reclamation (Lee 1975, 1977).

Affinities
The British stands are typical of the *Puccinellietum distantis* widely described from Europe. The association is most closely related to the *Puccinellietum maritimae* but its distinctive ephemeral nature has led some authorities to place it in a separate alliance, the Puccinellion distantis, within the Asteretea.

Floristic table SM23

	a	b
Spergularia marina	V (4–8)	V (2–9)
Puccinellia maritima	V (1–7)	IV (4–5)
Puccinellia distans	II (1–6)	IV (2–8)
Agrostis stolonifera	II (4–6)	IV (2–7)
Salicornia agg.	III (2–7)	
Suaeda maritima	III (2–5)	
Glaux maritima	II (2–5)	I (1)
Algal mat	II (5–8)	
Parapholis strigosa	II (4–8)	
Halimione portulacoides	II (1–3)	
Atriplex prostrata	II (1–5)	I (2–3)
Triglochin maritima	II (2–3)	I (1)
Plantago maritima	II (2–4)	
Elymus pycnanthus	II (1–4)	
Aster tripolium (rayed)	I (3–4)	I (1–9)
Alopecurus geniculatus	I (2–5)	I (2–3)
Juncus bufonius	I (3–4)	I (2–9)
Polygonum aviculare	I (3–4)	
Festuca rubra	I (3–4)	
Spergularia media	I (3–8)	
Number of samples	13	180
Mean number of species/sample	7 (2–11)	6 (3–8)*
Mean vegetation height (cm)	6 (3–15)	no data
Mean total cover (%)	70 (50–90)	71 (30–100)*

* Means of 25 samples only.
a Coastal stands
b Inland stands (Lee 1977)


N2
N1
SM23 *Puccinellietum distantis*

SM24

Elymus pycnanthus salt-marsh community

Atriplici-Elymetum pycnanthi Beeftink & Westhoff 1962

Synonymy

Agropyretum pungentis Perraton 1953; includes *Agropyron pungens-Juncus maritimus* nodum Adam 1976.

Constant species

Elymus pycnanthus.

Physiognomy

The association is invariably dominated by the stiff clumps of *Elymus pycnanthus* and this may be the sole species. Usually, however, there are a few associates though these are somewhat varied and individual stands may be rendered distinctive by the abundance of (a) particular species. Sometimes there is a patchy or extensive understorey of *Halimione portulacoides*, *Artemisia maritima* and/or *Puccinellia maritima*. In other cases, *Atriplex prostrata* and/or *Festuca rubra* may be conspicuous. *Juncus maritimus* is sometimes abundant though stands with this species are not worthy of distinction as a subcommunity (cf. Adam 1976, 1977). Other stands have a prominent umbelliferous element with *Conium maculatum*, *Foeniculum vulgare* and *Smyrnium olusatrum* and, more locally, *Petroselinum segetum* and *Sison amomum*.

Habitat

The *Atriplici-Elymetum* is an upper-marsh community occurring on a variety of substrates including organically-enriched clay, sand (where *Festuca rubra* is often abundant) and shingle. Substrates are generally well-drained and there is often considerable free calcium carbonate derived from inwashed shell fragments. The pH is generally above 7.0. The association also occurs on older, partly decayed drift litter, where *Atriplex prostrata* flourishes, but in many stands there is little litter except at the seaward edge.

The association may be confined to a narrow strip around the tidal limit or form extensive stands in the upper marsh; occasionally it forms mosaics with other communities. It may extend down the marsh on creek levees and reach above the tidal limit, sometimes covering unmown sea walls where unbellifer-rich stands are characteristic.

Most stands occur on ungrazed or cattle-grazed marshes. Where sheep are admitted to sites with established stands, these are avoided by stock (Cadwalladr & Morley 1973) but the rarity of the association on marshes with a long tradition of sheep-grazing suggests that establishment may not be possible under such a management regime.

Zonation and succession

The association often terminates the zonation at the upper limit of British salt-marshes. A common pattern, seen on many Essex salt-marshes and around the Exe in Devon (Proctor 1980), runs from *Spartinetum townsendii* or *Asteretum tripolii* through *Halimionetum portulacoidis* to the *Atriplici-Elymetum*. The largest stands of the association appear to have developed from the *Halimionetum*.

On creek levees, the association may develop from the *Artemisietum maritimae* or, more locally, the *Spartinetum townsendii*. On high-level drift, there is sometimes a succession from the *Atriplex* strand-lines to the association. In sites inundated by only very exceptional storms, the association may be invaded by shrubs and trees but succession to woodland is likely to be prevented by the occasional subjection to saline waters.

Distribution

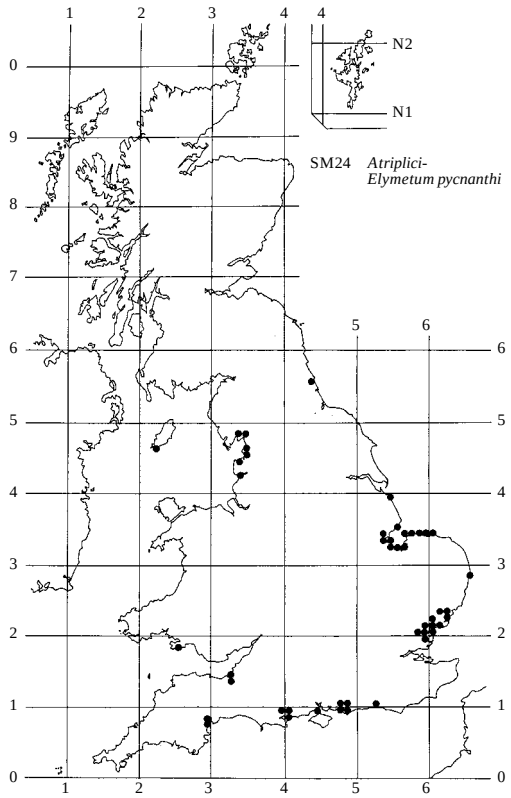
The association is most abundant in south-east England and stands on the west coast are local and small. *Elymus pycnanthus* reaches its northern limit in Britain at the Solway.

Affinities

Westhoff & den Held (1969) emphasise the nitrophilous character of the *Atriplici-Elymetum* by assigning it to the Angelicion litoralis in the Artemisietea but the similarities here are weaker than those between the association and other clearly maritime communities of the upper marsh and strand-line. A better solution is to place the association with the *Elymo pycnanthi-Suaedetum verae* in the Elymion pycnanthi of the Elymetea (Géhu & Géhu 1969).

Floristic table SM24

Elymus pycnanthus	V (2–10)
Halimione portulacoides	III (1–8)
Festuca rubra	III (1–9)
Atriplex prostrata	II (1–5)
Glaux maritima	II (1–5)
Puccinellia maritima	I (2–7)
Juncus maritimus	I (2–8)
Agrostis stolonifera	I (3–8)
Artemisia maritima	I (2–7)
Suaeda vera	I (1–7)
Juncus gerardii	I (2–5)
Limonium cf. *L. vulgare*	I (1–5)
Plantago maritima	I (1–5)
Armeria maritima	I (1–4)
Beta maritima	I (1–3)
Atriplex littoralis	I (1–3)
Sonchus arvensis	I (2–3)
Parapholis strigosa	I (2–4)
Potentilla anserina	I (2–3)
Aster tripolium var. *discoideus*	I (1–3)
Aster tripolium (rayed)	I (1–3)
Galium aparine	I (2–3)
Phragmites australis	I (2–6)
Ammophila arenaria	I (1–6)
Hypnum cupressiforme var. *lacunosum*	I (4–6)
Number of samples	110
Mean number of species/sample	6 (1–16)
Mean vegetation height (cm)	61 (30–100)
Mean total cover (%)	98 (75–100)



SM25

Suaeda vera drift-line community

Elymo pycnanthi-Suaedetum verae (Arènes 1933) Géhu 1975

Synonymy
Suaedetum fruticosae Tansley 1939 *p.p.*; *Agropyro-Suaedetum fruticosae* Adam 1976; *Halimiono-Suaedetum fruticosae* Adam 1976.

Constant species
Halimione portulacoides, *Suaeda vera*.

Rare species
Arthrocnemum perenne, *Suaeda vera*.

Physiognomy
The *Elymo pycnanthi-Suaedetum verae* is of variable appearance. The two association constants are sometimes co-dominant as a more or less closed shrubby cover; in other cases they occur as scattered bushes in a grassy ground. The *S. vera* shoots provide a niche for a varied flora of epiphytic lichens (Ellis 1960).

Sub-communities

***Elymus pycnanthus* sub-community:** *Elymo pycnanthi-Suaedetum verae typicum* Géhu & Delzenne 1975; *Agropyro-Suaedetum fruticosae* Adam 1976. Here the cover of *H. portulacoides* is low and the vegetation is dominated by complementary proportions of *S. vera* bushes and stiff clumps of *Elymus pycnanthus* with usually a little *Festuca rubra*. The upper edge of stands may be marked in spring by a narrow band of winter annuals such as *Cochlearia danica*, *Myosotis ramosissima*, *Sagina maritima* and *Valerianella locusta* germinating on drift debris.

***Halimione portulacoides* sub-community:** *Elymo pycnanthi-Suaedetum verae halimionetosum* Géhu & Delzenne 1975; *Halimiono-Suaedetum fruticosae* Adam 1976. *S. vera* and *H. portulacoides* are co-dominant as a shrubby canopy of variable height over a ground of scattered *Puccinellia maritima* and *Limonium* cf. *vulgare*, often with a little *Aster tripolium*, annual *Salicornia* spp., *Spergularia media* and *Suaeda maritima*. The sub-community provides an occasional high-level context for *Bostrychia scorpioides* and *Pelvetia canaliculata*.

Habitat
The association is most characteristic of drift-lines at salt-marsh/shingle interfaces with a tendency for the *Halimione* sub-community to be associated with superficial smears of sticky yellow-brown clay. The *Elymus* sub-community often runs down-marsh on ridges of drier silt and shorter-growing stands of the *Halimione* sub-community can tolerate up to about 120 submergences/year.

Zonation and succession
The association marks a particular type of transition from the upper marsh to other maritime communities and the driftline stands are probably stable in time.

The low-level stands of the *Halimione* sub-community overlap the habitat of the *Frankenia laevis* sub-community of the *Suaeda vera-Limonium binervosum* salt-marsh and at some sites in north Norfolk there is a mosaic of the two communities. The balance between them could be controlled by rabbit-grazing. Chapman (1960*b*) suggested that *Limonium bellidifolium* declined on Hut Marsh, Scolt Head Island, Norfolk because of the increased vigour of *H. portulacoides* following the reduction there of rabbit-grazing.

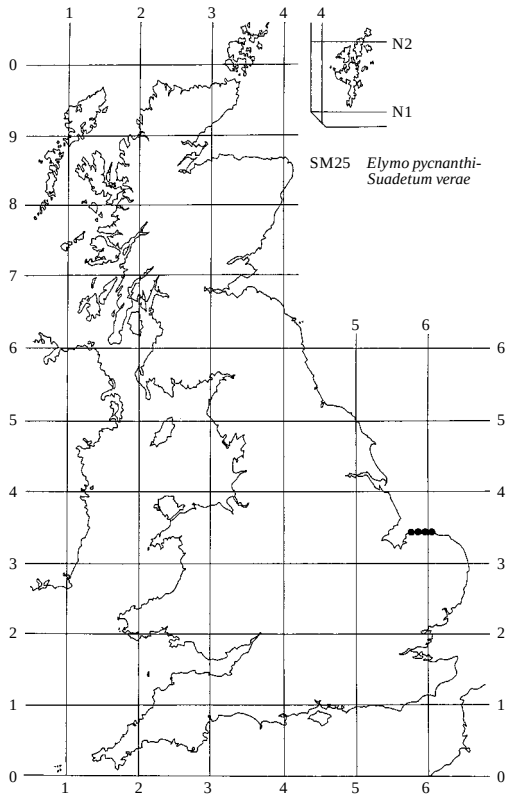
Distribution
The association occurs in north Norfolk and Essex.

Affinities
Vegetation similar to the British stands of the *Elymo-Suaedetum* has been described from western France (Corillion 1953, Vanden Berghen 1965*a*, Géhu & Géhu 1969, Géhu 1972, 1975). Géhu (1975) and Géhu & Delzenne (1975) have emphasised the Mediterranean affinities of *Suaeda vera* by assigning the association to the Halimionion in the Arthrocnemetea fruticosae. An alternative view would be to stress the drift-line character of the vegetation and place the association with the *Atriplici-Elymetum pycnanthi* in the Elymion pycnanthi.

Floristic table SM25

	a	b	25
Suaeda vera	V (1–8)	V (3–8)	V (1–8)
Halimione portulacoides	V (2–4)	V (6–9)	V (2–9)
Elymus pycnanthus	V (4–10)		IV (4–10)
Festuca rubra	III (2–5)		II (2–5)
Artemisia maritima	II (1–2)		I (1–2)
Cochlearia anglica	II (1–3)	I (1)	I (1–3)
Cochlearia danica	II (1–3)		I (1–3)
Glaux maritima	II (2–3)		I (2–3)
Plantago maritima	II (1–5)		I (1–5)
Atriplex littoralis	I (2)		I (2)
Puccinellia maritima	I (2)	V (1–7)	III (1–7)
Limonium cf. *L. vulgare*	I (1–4)	V (2–3)	II (1–4)
Suaeda maritima	I (2–3)	III (2–3)	II (2–3)
Aster tripolium	I (2)	III (1–2)	I (1–2)
Bostrychia scorpioides		III (2–5)	I (2–5)
Salicornia agg.		III (3)	I (3)
Spergularia media		III (3–4)	I (3–4)
Arthrocnemum perenne		II (1–2)	I (1–2)
Cochlearia officinalis		II (2–3)	I (2–3)
Pelvetia canaliculata		II (4)	I (4)
Triglochin maritima		II (2–3)	I (2–3)
Algal mat		I (5)	I (5)
Number of samples	13	7	20
Mean number of species/sample	6 (4–8)	8 (5–11)	7 (4–11)
Mean vegetation height (cm)	70 (50–100)	43 (20–73)	61 (20–100)
Mean total cover (%)	95 (70–100)	84 (50–100)	91 (50–100)

a *Elymus pycnanthus* sub-community
b *Halimione portulacoides* sub-community
25 *Elymo pycnanthi-Suaedetum verae* salt-marsh (total)


N2
N1
SM25 Elymo pycnanthi-Suadetum verae

SM26
Inula crithmoides on salt-marshes

Inula crithmoides is a maritime perennial largely confined to southern England and Wales: it is recorded from Essex round to Anglesey with an isolated station in south-west Scotland (Perring & Walters 1962). Although it occurs in maritime cliff communities throughout its range, occurrences in salt-marsh vegetation are restricted to south-east England from Essex to Hampshire.

Here it is an occasional in various associations but it is sometimes encountered in abundance, usually with *Halimione portulacoides* as a co-dominant. In the few available samples there is a distinction between stands where *Puccinellia maritima*, annual *Salicornia* spp. and *Limonium* cf. *vulgare* are constant in generally small amounts and those which have abundant *Elymus pycnanthus*. The former occur on low-marsh sites with coarse sand; the latter on moderately organic soils with much drift litter on the upper marsh.

Ranwell (1972; Ranwell & Boorman 1977) has correlated the distribution of *I. crithmoides* on salt-marshes with the occurrence of lime-rich freshwater influence and the presence of Chalk bedrock near the surface. Though this may be true, it is difficult to see the ecological significance of the observation: most salt-marshes are alkaline to some degree and *I. crithmoides* may be climatically restricted to salt-marshes which are coincidentally particularly base-rich.

Within its limited range on salt-marshes, *I. crithmoides* tends to be more confined to high-marsh occurrences with *Elymus pycnanthus* in Essex (see Rose 1964, Rose & Géhu 1964).

The most obvious affinities of the *I. crithmoides* salt-marsh vegetation are with the *Halimionetum portulacoidis*. Vanden Berghen (1965*a*) has suggested that, along the Biscay coast of France, *I. crithmoides* and *Arthrocnemum perenne* characterise a southern variant of the *Halimionetum*. Stands with abundant *Elymus pycnanthus* will perhaps find a place within the *Atriplici-Elymetum pycnanthi* but could also be seen as the northern limit of the Mediterranean association *Elymo pycnanthi-Inuletum crithmoidis* Br.-Bl. 1952 (Molinier & Tallon 1974).

The rather striking difference in distribution between salt-marsh and maritime cliff communities with *I. crithmoides* points to the possibility of there being distinct ecotypes of the species in Great Britain.

Floristic table SM26

	a	b	26
Inula crithmoides	V (4–7)	IV (5–9)	V (4–9)
Halimione portulacoides	V (5–9)	IV (3–8)	V (3–9)
Puccinellia maritima	V (2–4)		III (2–4)
Salicornia agg.	V (3–5)		III (3–5)
Limonium cf. *L. vulgare*	V (2–5)		III (2–5)
Plantago maritima	III (3)		II (3)
Armeria maritima	III (3–7)		II (3–7)
Suaeda maritima	III (2–4)	I (3)	III (2–4)
Arthrocnemum perenne	II (3–5)		II (3–5)
Algal mat	II (5)		II (5)
Spergularia media	II (2)		II (2)
Spartina anglica	I (2)		I (2)
Festuca rubra	I (2)		I (2)
Aster tripolium (rayed)	I (4)		I (4)
Elymus pycnanthus		IV (5–9)	III (5–9)
Bostrychia scorpioides		II (4)	I (4)
Number of samples	6	4	10
Mean number of species/sample	8 (3–10)	4 (3–5)	6 (3–10)
Mean vegetation height (cm)	26 (8–50)	50 (35–60)	36 (8–60)
Mean total cover (%)	93 (80–100)	100	96 (80–100)

a Stands with *Puccinellia maritima*, *Salicornia* agg. and *Limonium* cf. *L. vulgare*
b Stands with *Elymus pycnanthus*
26 *Inula crithmoides* stands

SM27

Ephemeral salt-marsh vegetation with *Sagina maritima*

Saginion maritimae Westhoff, van Leeuwen & Adriani 1962

Small stands of ephemeral vegetation with an often open cover of annuals and short-lived perennials occur patchily on British salt-marshes. Recurrent assemblages are rare and there seems to be a large element of chance in the floristic composition, early arrivals frequently pre-empting the niche. Such vegetation may include *Sagina maritima*, *S. nodosa* and *Plantago coronopus*, more rarely *Bupleurum tenuissimum* (to the south-east) and *Centaurium littorale* (to the north) and provide a salt-marsh context for ephemerals such as *Cochlearia danica* and *Desmazeria marina* which also occur in other maritime habitats.

Breaks in the turf of mid- and upper-marsh communities provide the most usual habitat for such species and they are especially characteristic of old turf-cuttings where they form part of the sequence of recolonising vegetation giving way to mixtures of *Festuca rubra*, *Agrostis stolonifera*, *Puccinellia maritima* and *Potentilla anserina*, which come to approximate to the *Puccinellietum maritimae*, the *Juncetum gerardi* or the *Festuca-Agrostis-Potentilla* mesotrophic grassland. Such ephemerals also occur in disturbed situations around reclamation banks (e.g. Gray 1977, 1979, Adam & Akeroyd 1978).

This kind of vegetation is the nearest equivalent in Britain to similarly diverse assemblages on Continental salt-marshes which have been assigned to the Saginion alliance in the Saginetea maritimae Westhoff, van Leeuwen & Adriani 1962 (e.g. Beeftink 1962, 1965, 1975, 1977*a*; Tüxen & Westhoff 1963; Westhodd & den Held 1969). There, too, the vegetation is characteristic of upper-marsh situations, being especially associated with salt-marsh/sand-dune transitions where there is a contact between more and less maritime sediments of low soil moisture content but fluctuating salinity.

SM28

Elymus repens salt-marsh community

Elymetum repentis maritimum Nordhagen 1940

Synonymy

Elymetum repentis maritimum, *Elymus repens*, *Potentilla anserina-Elymus repens-Vicia* and *Elymus repens-Potentilla anserina* soziations ? Nordhagen 1940.

Constant species

Agrostis stolonifera, *Atriplex prostrata*, *Elymus repens*, *Festuca rubra*.

Rare species

Allium scorodoprasum, *Hordeum marinum*.

Physiognomy

The *Elymetum repentis* has a closed grassy sward up to about 1 m tall, generally dominated by *Elymus repens* with usually smaller amounts of *Festuca rubra* and *Agrostis stolonifera* and, beneath, scattered plants of *Atriplex prostrata* and an open ground cover of *Potentilla anserina*. *Oenanthe lachenalii*, *Sonchus arvensis*, *Rumex crispus* and *Cirsium arvense* are occasional and often give a scruffy appearance to the vegetation and tussocks of *Juncus gerardii* or *Festuca arundinacea* may be locally prominent. The community is generally richer and more varied than the *Atriplici-Elymetum* with a wide range of occasionals of low frequency, some characteristic of other disturbed upper-marsh vegetation of strand-lines and reclamation banks, others more typical of rank inland grasslands. *Allium scorodoprasum* has been recorded in vegetation of this kind on the north Solway coast and *Hordeum marinum* from Somerset. Bryophytes occur occasionally with *Eurhynchium praelongum*, *Amblystegium riparium*, *Funaria hygrometrica*, *Pottia heimii* and *Bryum* spp.

Habitat

The community is characteristic of similar situations to those occupied by the *Atriplici-Elymetum*: upper-marsh areas where there is often a combination of disturbance, drift-litter deposition and some freshwater influence. It is, however, less consistently confined to well-drained sites, occasionally growing on heavy waterlogged clays. At Cefni salt-marsh in Anglesey, it occupies the areas marked as 'drift' on the map of Packham & Liddle (1970). The community also occurs on the recently-excavated material thrown on to the banks of drainage channels while, on some brackish marshes, such as those at the tidal limit in estuaries (as in the Lune in Lancashire), it may form extensive stands.

Zonation and succession

Like the *Atriplici-Elymetum*, this community is often part of the vegetation which terminates the salt-marsh vegetation at its upper limit and in such situations it may occur in clear zonations or confused mosaics with such communities as the *Juncetum gerardi*, the *Juncus maritimus* salt-marsh, the *Potentillo-Festucetum arundinaceae*, the *Festuca rubra-Agrostis stolonifera-Potentilla anserina* grassland and various of the vegetation types in which Cyperaceae or tall swamp helophytes predominate in brackish pools and ditches.

Distribution

The community can be seen as the north-western equivalent of the *Atriplici-Elymetum*, being especially frequent around the Irish Sea coast. It is probably more widespread in eastern Scotland than the map suggests.

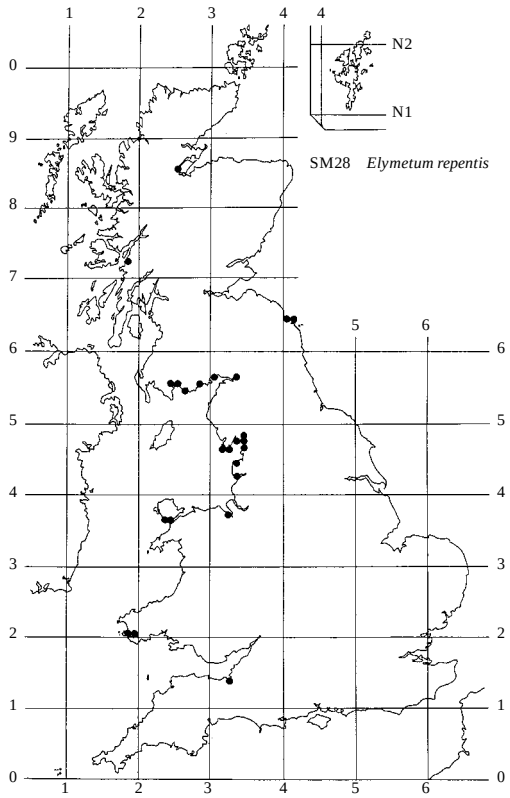
Affinities

Although there are clear floristic similarities between this community and *Elymus repens* vegetation of foredunes and shingle strand-lines, salt-marsh *Elymetum repentis* is sufficiently distinct to be considered as a separate vegetation type. *Elymus repens* growing on salt-marshes is morphologically distinct and may represent a separate ecotype.

As defined here, the community is synonymous with the vegetation described by Nordhagen (1940) which is frequent in Scandinavia and northern Germany (see also Störmer 1938, Tüxen 1950, Gillner 1960, Tyler 1969*b*). Authors differ as to whether the community is best placed in a narrowly-defined Elymo-Rumicion crispi (Nordhagen 1940), in that alliance as expanded by Tüxen (1950) or alongside the *Atriplici-Elymetum* in the Elymion pungentis (Géhu & Géhu 1969).

Floristic table SM28

Elymus repens	V (4–10)
Festuca rubra	V (3–8)
Agrostis stolonifera	IV (3–8)
Atriplex prostrata	IV (2–6)
Potentilla anserina	III (2–8)
Oenanthe lachenalii	II (1–4)
Sonchus arvensis	II (2–6)
Rumex crispus	II (1–5)
Festuca arundinacea	II (1–9)
Cirsium arvense	II (1–4)
Juncus gerardii	II (2–6)
Vicia cracca	I (2–5)
Matricaria maritima	I (1–4)
Carex otrubae	I (1–6)
Cochlearia officinalis	I (2–4)
Glaux maritima	I (2–4)
Atriplex littoralis	I (2–5)
Galium aparine	I (1–4)
Aster tripolium (rayed)	I (2–4)
Oenanthe crocata	I (1–5)
Triglochin maritima	I (2)
Cochlearia anglica	I (2–4)
Eurhynchium praelongum	I (2–5)
Lotus corniculatus	I (3–4)
Poa pratensis	I (3–4)
Melilotus altissima	I (2–5)
Deschampsia cespitosa	I (3–5)
Leontodon autumnalis	I (1–2)
Urtica dioica	I (3–5)
Lolium perenne	I (2–3)
Plantago maritima	I (2)
Arrhenatherum elatius	I (2–7)
Stellaria media	I (2–6)
Cirsium vulgare	I (1–2)
Scirpus maritimus	I (4)
Puccinellia maritima	I (3)
Beta vulgaris ssp. *maritima*	I (2–5)
Holcus lanatus	I (2–4)
Taraxacum sp.	I (2–3)
Trifolium repens	I (2–4)
Plantago lanceolata	I (1–2)
Algal mat	I (4–6)
Anthriscus sylvestris	I (1–4)
Aster tripolium	I (2–3)
Torilis japonica	I (2)
Odontites verna	I (2–3)
Alopecurus geniculatus	I (2–6)
Eleocharis uniglumis	I (4)
Rumex conglomeratus	I (2–3)
Dactylis glomerata	I (3)
Medicago lupulina	I (2–3)
Silene vulgaris ssp. *maritima*	I (1–4)
Centaurea nigra	I (2–3)
Heracleum sphondylium	I (1–2)
Apium graveolens	I (2)
Calystegia sepium	I (4–6)
Number of samples	62
Number of species/sample	9 (2–27)
Vegetation height (cm)	66 (30–120)
Total cover (%)	99 (70–100)


N2
N1
SM28 *Elymetum repentis*