

A2. Saltmarsh Ecology

A2.1 Introduction

Ecology is that branch of biology which deals with the interactions between plants and animals and their environment; saltmarshes have proved to be excellent places to study such interactions. This is partly because saltmarsh ecosystems are relatively simple, characterised by a limited number of different species and an environment that is largely dominated by abiotic, largely physical, forces. These processes control the numbers and distribution of plants and animals and can be studied on saltmarshes. Understanding these processes is the first step towards being able to manage saltmarshes to ensure that their function is maintained (see Appendix A1). A flow model describing the structure and function of the saltmarsh ecosystem is shown as Figure A2.1.

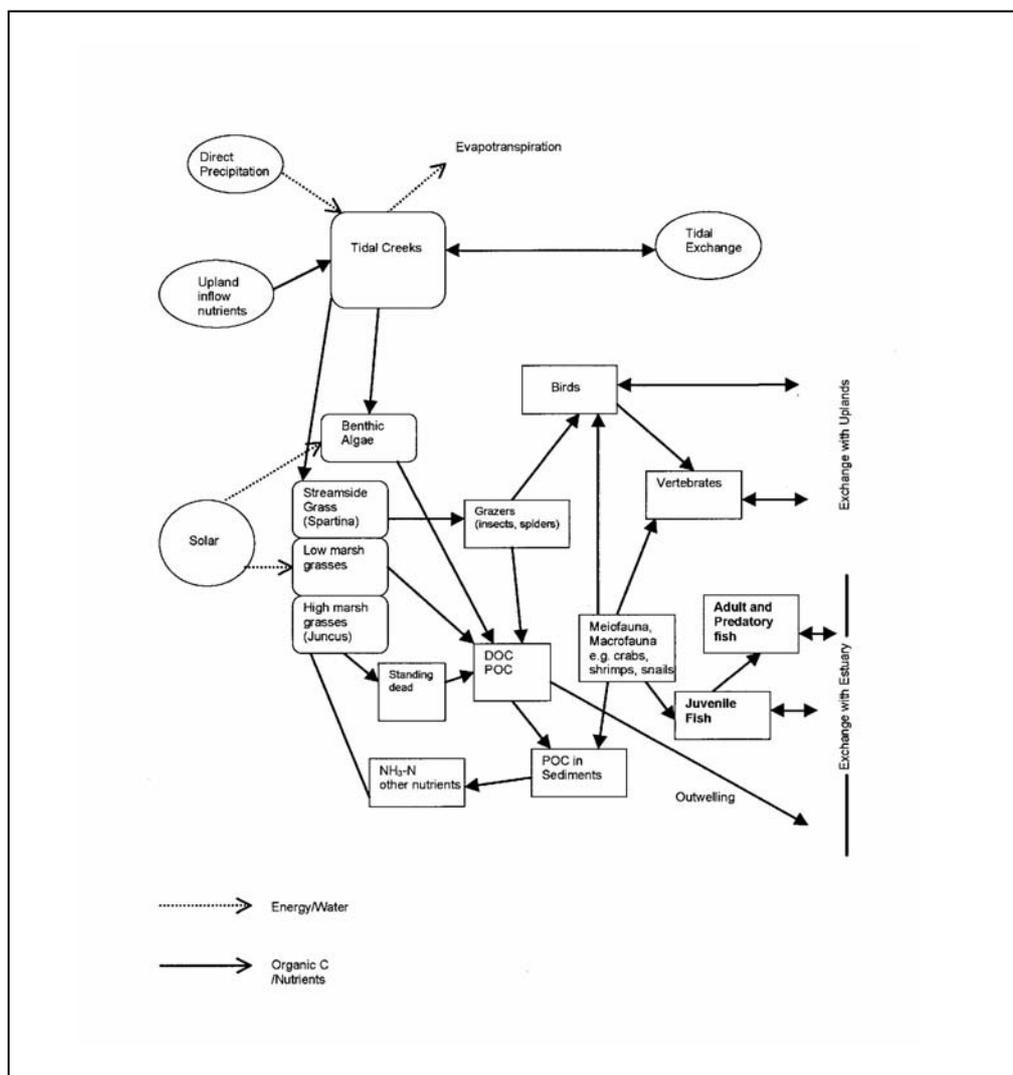


Figure A2.1 A conceptual model of a tidal salt marsh (from Mitsch & Gosselink, 2000)

Saltmarshes provide a good illustration of the process of primary succession. This can be defined as a sequential change in plant species (and the animals associated with them) on a land surface which has not been vegetated before (or at least not in the recent past) and which initially contains no plant propagules. Saltmarshes can be observed forming from initial bare intertidal mud and, in the course of time, developing an increasingly complex community of plants and associated animals. Mature saltmarshes also respond to the ongoing physical processes within estuaries. For this reason Section A2.2 (below) and Section 2.3.1 consider the processes that control the development of saltmarsh and the distribution of different species within the marsh.

Section A2.3 describes the different types of saltmarsh found in Great Britain and some of the key species and communities. This includes discussion of the relationship between intertidal habitats and *Spartina anglica* or common cord-grass (this plant is generally referred to by its scientific generic name to distinguish it from the other main *Spartina* species in the UK, the native *S. maritima*, naturalised *S. alterniflora* and the hybrid *S. x townsendii*). *Spartina anglica* is widespread within saltmarsh in Great Britain, often dominating in a number of English and Welsh saltmarshes. Expansion and planting of this species in the last 100 years has had a significant impact on saltmarsh and mudflat habitats (see Section 2.3.2).

Section A2.4 provides a broader context and considers the ecosystems function of saltmarshes (i.e. as more-or-less self-contained systems with various interdependent trophic (i.e. feeding) levels). This section briefly reviews the major floral and faunal interests of saltmarsh ecosystems.

A2.2 Saltmarsh development

A2.2.1 Pre-marsh processes

The development of saltmarshes depends fundamentally on a range of physical and chemical conditions becoming sufficiently benign to allow flowering plants to colonise intertidal mudflats. The seaward limit of the colonists is conventionally regarded as the lower edge of the saltmarsh. However, the processes leading to saltmarsh development, including biological processes, are likely to have started on the mudflats seaward of the vegetation.

Significantly, it has been demonstrated in parts of The Wash that populations of benthic microalgae, particularly epipellic diatoms, are vital precursors to saltmarsh growth (Coles, 1979). These minute organisms secrete large amounts of mucus, binding fine sediments and increasing surface stability. Indeed, sediment accretion rates during the summer proved to be higher on the mudflats immediately in front of the saltmarsh than in the saltmarshes themselves and the experimental small-scale removal of microalgae resulted in local erosion of the mudflat (Coles, 1979).

In contrast, the role of the more visible algal species as precursors to saltmarsh is less clear. Being essentially marine species, algae are able to tolerate frequent tidal submergences and high salinity, but there is evidence that green macro algae, such as the green seaweed (*Enteromorpha* species) and sea lettuce (*Ulva lactuca*), and brown

algae such as various wrack (*Fucus*) species are sensitive to substrate stability, for example tolerating only very low sediment accretion rates. The green macro algae in particular may be regarded as opportunistic species, able to respond to short-term fluxes of nutrients in seawater. They have, for example, become associated in many areas, particularly in semi-enclosed estuaries and harbours of the south and east coasts of England, not with saltmarsh growth but with saltmarsh decay. Here extensive mats of *Enteromorpha* and sea lettuce blanketing the mudflats display seasonal growth patterns linked in one study to raised phosphate levels, possibly from domestic sewage discharge.

Similarly, marine seagrass communities in the UK, consisting mainly of species of eelgrass (*Zostera* species), are regarded by most investigators as largely functionally and biologically independent from saltmarshes. Being either permanently submerged or exposed only at low water on spring tides, seagrass beds tend to occur over a relatively narrow range of sedimentary and substrate conditions and are not necessary precursors to saltmarshes. In fact, their landward limits are probably controlled by increasing drying out. This is suggested by the fact that eelgrass (*Zostera marina*) in Britain has been found to occur at lower levels in places where low water spring tides occur in the middle of the day. Nevertheless, seagrass communities, particularly where the density of plants is high, may strongly modify their habitat. Studies mainly in North America have shown seagrass to affect current flow, sediment particle size and stability, and the local abundance and composition of animal communities. The landward limits of the most intertidal (as opposed to subtidal) species in Britain, dwarf eelgrass (*Zostera noltii*) overlaps in a few places with the seaward limit of the terrestrial grass, *Spartina* (most famously at Lindisfarne in Northumberland) and eelgrasses are linked with saltmarsh plants as part of the diet of several herbivores, notably Brent geese and Wigeon. However, a functional and causal connection between eelgrass communities and saltmarshes remains largely tenuous.

A2.2.2 Abiotic factors

The effect of strong tidal currents was demonstrated in a classic study in the Dovey estuary almost 60 years ago, in which it was shown that seedling establishment of annual glasswort (*Salicornia europaea*) was influenced by the current strength and frequency of tidal coverage. No more than 25% of seedlings survived to adult plants on mudflats that were submerged daily, whereas 65% survived in areas which remained tide-free for periods of three or more days. The adult plants in the lower zones showed clear signs of exposure to tidal currents, their stems bent and twisted from being dragged by the tide (see Figure A2.2). The uprooting of seedlings and the tidal transport of seed has also been shown to affect *Spartina* plants. Transplant experiments in the Dutch Oosterschelde and in southern England indicate that well-established adult plants can withstand the increased amounts of submergence at lower elevations but that wave action on seedlings and small plants prevents the natural seaward spread of the grass. As the velocity of tidal currents is roughly a function of tidal range, the fact that saltmarshes do not extend so far seaward in estuaries with a large tidal range (see below) must, to a large measure, be because of the effects of physical forces on plants.

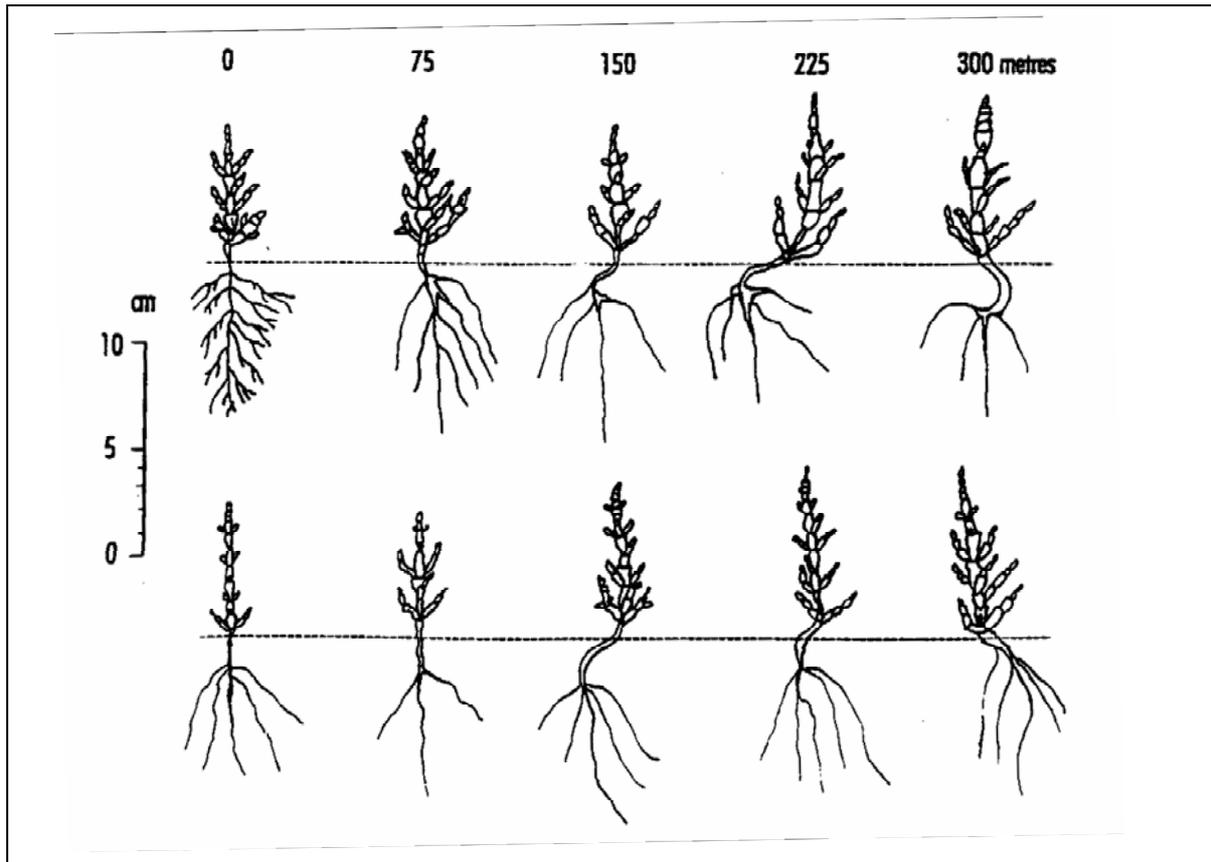


Figure A2.2 Drawings of glasswort plants from five positions along a transect from landward (0m) to seaward in the Dovey estuary in July. Plants seaward of mean high water neap tides (150m) show the effects of exposure to tidal currents (after Adam, 1990)

The rates of vertical accretion of sediments on saltmarshes depend on a range of factors (discussed in Appendix A1.4) but can, at least locally and in the short-term, be very high. Whilst published average rates vary between zero and around 10mm per year, accretion of 30mm, 100mm and, in one study in Bridgwater Bay, up to 150mm of silt has been recorded in a single year. These measurements were all made in seaward marshes, among glasswort or *Spartina* grass, and in all cases the plants appeared to survive, growing upward through the sediments. Burial by a sudden influx of sediment (often sand), particularly during the growing season, can kill plants in the landward parts of marshes where the species are more sensitive to burial. On the whole, however, high accretion rates *per se* are unlikely to be a limiting factor in the seaward growth of saltmarshes.

Although tidal submergence cuts down the amount of time available for photosynthesis and both reduces and alters the quality of the light reaching submerged plants, it is difficult to disentangle the effects of these factors from other aspects of flooding. We know from one experiment that *Spartina* can survive continuously and fully submerged in clear seawater for 4.5 months and that at its lowest limits in Poole Harbour, and in some New Zealand estuaries, it is exposed to daylight in some months for only two or three hours a day (Hubbard & Partridge, 1981).

Saltmarsh soils are more or less permanently waterlogged, at least at the lower elevations. Two major inter-related effects of this are the production of anoxic conditions and the presence of substances normally toxic to plant growth. Saltmarsh plants display adaptations to such conditions ranging from the development of air-filled spaces and pathways (aerenchyma) in the roots and rhizomes, which are aerated via the shoots, to the (at least partial) tolerance of phytotoxins such as ferric ions and sulphide compounds. However, most species are likely to require some periods of soil aeration for successful growth. Measurements of redox potential on a Humber saltmarsh have shown that, even in the lowest zones, the mainly reducing conditions are alleviated temporarily during neap tides, albeit only near the surface. Increasing periods of aeration were found with increasing elevation, and better drainage, of the marsh. In the mid to low zones redox potentials were lowered each month by the spring tides and in the higher areas the mainly oxidizing conditions were affected only by the highest spring tides, producing a general gradient in the degree of soil aeration across the marsh.

In contrast, gradients of soil salinity directly related to the amount of tidal submergence may not always be present and may even be exceptional. The interaction of tidal submergence with rainfall and evapotranspiration from the marsh surface can produce extensive and local fluctuations in soil salinity. Salinities more than three times that of seawater have been recorded during mid-summer on high saltmarshes in north Norfolk. On such marshes the salinity gradient may, therefore, be reversed during much of the growing season, the lower zones being frequently bathed in (relatively less saline) seawater.

Perhaps not surprisingly, therefore, all saltmarsh plants, whatever their distribution, exhibit salt tolerance; indeed it is their ability to tolerate saline conditions that separates them from most other vascular plants. The mechanisms they have evolved to cope with salinity are manifold and are not described in detail here.

A2.2.3 Zonation and succession

The overriding influence of tidal submergence on plant distributions means that broad categories of zonation can be related to tide levels. One distinction which has been made is between saltmarshes below and above mean high water (MHW) level. These have been called 'submergence' marshes and 'emergence' marshes to reflect the dominant factors. Submergence marshes receive more than 360 annual tides, are never exposed continuously for more than nine days and are submerged daily in daylight for more than 1-2 hours; whereas emergence marshes are covered by less than 360 tides a year, have a minimum of 10-days continuous exposure and less than an hours daily daylight submergence.

It is also possible to recognise three main zones, which have been given various names but will be called here 'pioneer', 'low' and 'upper' marsh. Although their boundaries are relative rather than absolute, that between the upper and low marsh is often drawn around MHW (as described above). Pioneer marshes typically extend down to around mean high water neap tide (MHWN) level, but the position of the most seaward vegetation, and that of different communities, varies from place to place depending on a

number of factors. It is usually possible to add a fourth category of saltmarsh types at the upper level, which can be called 'driftline' or 'transitional' marshes. Centred around extreme high water spring tide (EHWS) level, these marshes are not always present, particularly where seawalls have been constructed, although several of their typical species (such as sea couch-grass (*Elytrigia atherica*), sea beet (*Beta maritima*) and common reed (*Phragmites australis*)) can be found on the seawalls or in adjacent land claimed for agriculture. In some parts of southern England, communities of shrubby sea-blite (*Sueda vera*) occur. This community is most frequently found at the upper limit of tidal inundation and is found in association with transitions to sand dunes or shingle structures. In a few localities on the south and east coast of England a similar community develops, but with dense stands of perennial glasswort (*Sarcocornia perennis*) with a small number of herbaceous species.

The effects of tidal range may be modified by a number of other, largely local, factors to determine how far seaward the saltmarsh may develop. These include the fetch of water in front of the marsh and the position of the marsh within the estuary; saltmarshes extend relatively further seaward in areas of shorter fetch and on mudflats nearer the estuary mouth. Latitude is also an important factor. For example, allowing for the effect of tidal range, *Spartina* marshes extend further landward in the south of England than in the north. All these factors can be used to predict the likely lower and upper limits (i.e. range) of each species. Indeed, such limits can probably be predicted with reasonable accuracy from their linear relationship with MHWN level, particularly for plants which occur in the mid and upper marshes. Research has shown that more than 70% and up to 96% of the total variation in the upper and lower limits of some dominant species could be explained by a simple linear regression equation.

As an example, the upper and lower vertical limits of the common saltmarsh grass (*Puccinellia maritima*) were described by:

$$\text{Upper limit, m} = 0.12 + 1.80 \text{ MHWN}$$

$$\text{Lower limit, m} = 0.23 + 1.39 \text{ MHWN}$$

Such equations accounted for more than 95% of the between-estuary variation in limits and more than 86% of the total variation in limits. Again, some of the residual variation in limits not accounted for by the relationship with tide level can be explained from partial correlations with variables such as fetch and spring tidal range.

The value of such equations is in their application to novel situations. For example, with refinement, they offer the hope of predicting in detail what areas of mudflat might be invaded by *Spartina* grass in an estuary (either an estuary it has not yet invaded or one altered by structures such as tidal barrages), or what vegetation types will develop on newly-created mudflats as part of a managed re-alignment scheme.

Figure A2.3 is derived from a development of this work, in which the vertical limits of six common species are shown along a gradient of standardised marsh heights. The different, but overlapping, vertical distributions of the species are clearly displayed. In particular, it can be seen that, described in this way, the broad vertical ranges of common saltmarsh grass and sea purslane (*Atriplex portulacoides*) are more or less the same; these two species occupy an identical sector of the tidal range. What then determines their local distribution? Similarly, if all species are capable of growing in ordinary soils, why are some replaced by others at higher elevations?

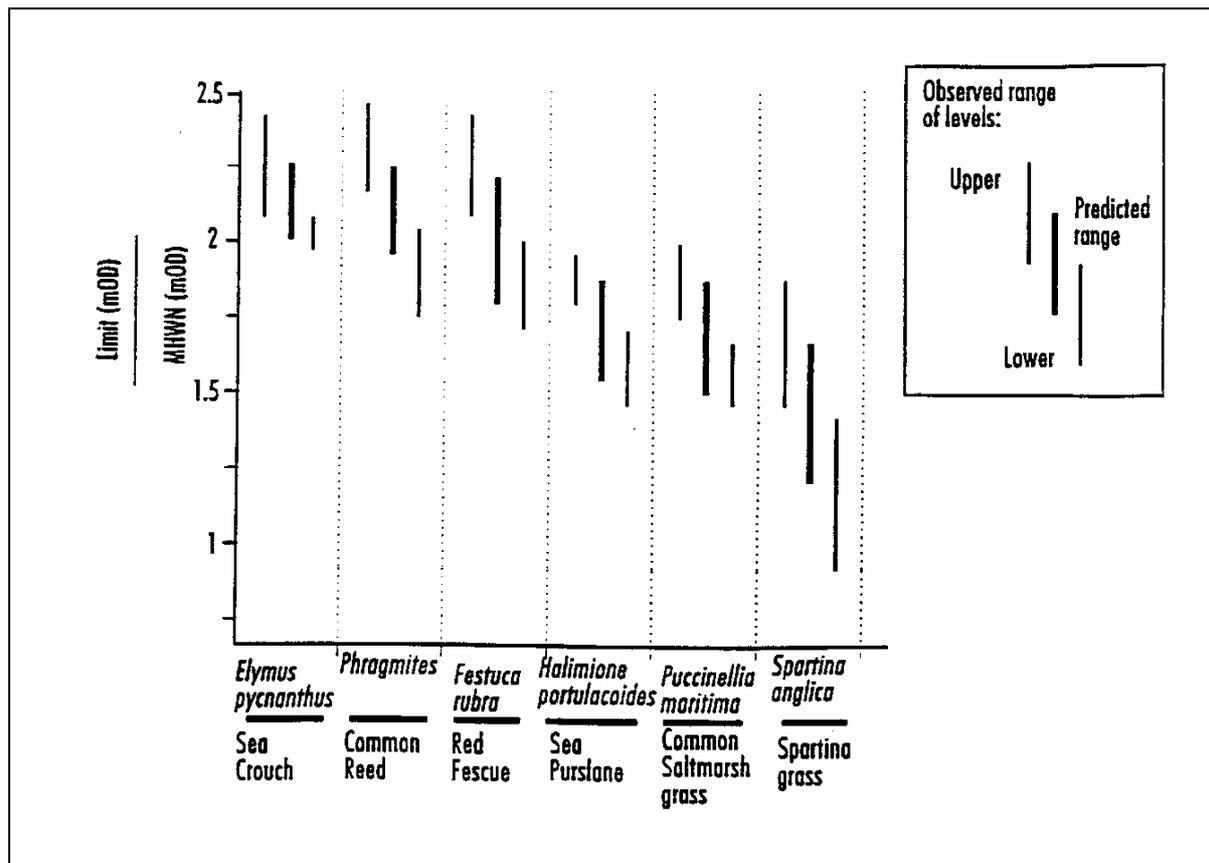


Figure A2.3 The vertical ranges and variations in the upper and lower limits of six common species along a gradient of standard heights; the predicted range is derived from a single linear regression with MHWNs

The traditional answer is that the prime force in determining local species distributions is interspecific competition. Although the absolute lower vertical limit may be fixed by the species' tolerance of abiotic factors related to tidal submergence, the upper limit is determined by its ability to compete with other, perhaps less tolerant but more vigorous, species. Competition, or more precisely competitive ability, is not an absolute quality of a species, or indeed an individual plant, it changes under changing environmental conditions. Thus, the outcome of competitive interactions between two species will change as the external conditions change.

The view that it is mainly the changing factors related to tidal submergence that determines the outcome of interspecific competition has been supported by several

experimental studies. For example, the salt and flooding tolerance in glasshouse experiments of 16 species taken from a Dutch saltmarsh could be ranked in a very similar order to that in which they occurred in the zonation. In competition experiments in which three grass species from Morecambe Bay saltmarshes (common saltmarsh grass, red fescue (*Festuca rubra*) and creeping bent-grass (*Agrostis stolonifera*) were grown under different salinities, water-levels and soil types, the outcome of two-species interactions matched, and helped to explain, the distributions of the three species in the field (Gray & Scott, 1977).

Competition between species can also be demonstrated by experiments in the field. In one particularly revealing experiment, either *Spartina* grass or common saltmarsh grass (whose vertical niches commonly overlap; see Figure A2.3) were systematically removed from two plots at slightly different elevations in their zone of overlap on a Dutch saltmarsh. The results, depicted in Figure A2.4, indicated that the removal of all *Spartina* grass shoots in early August on the lower plot led to a significant increase in yield of common saltmarsh grass (compared to its yield in areas from which *Spartina* grass had not been removed). This did not happen on the higher plot. Conversely, removal of common saltmarsh grass in the higher plot enabled a significant increase in *Spartina* growth, but had no effect in the lower plot. This pattern of interaction points to asymmetric competition, *Spartina* grass being depressed by common saltmarsh grass in the higher plot with the reverse occurring in the lower plot.

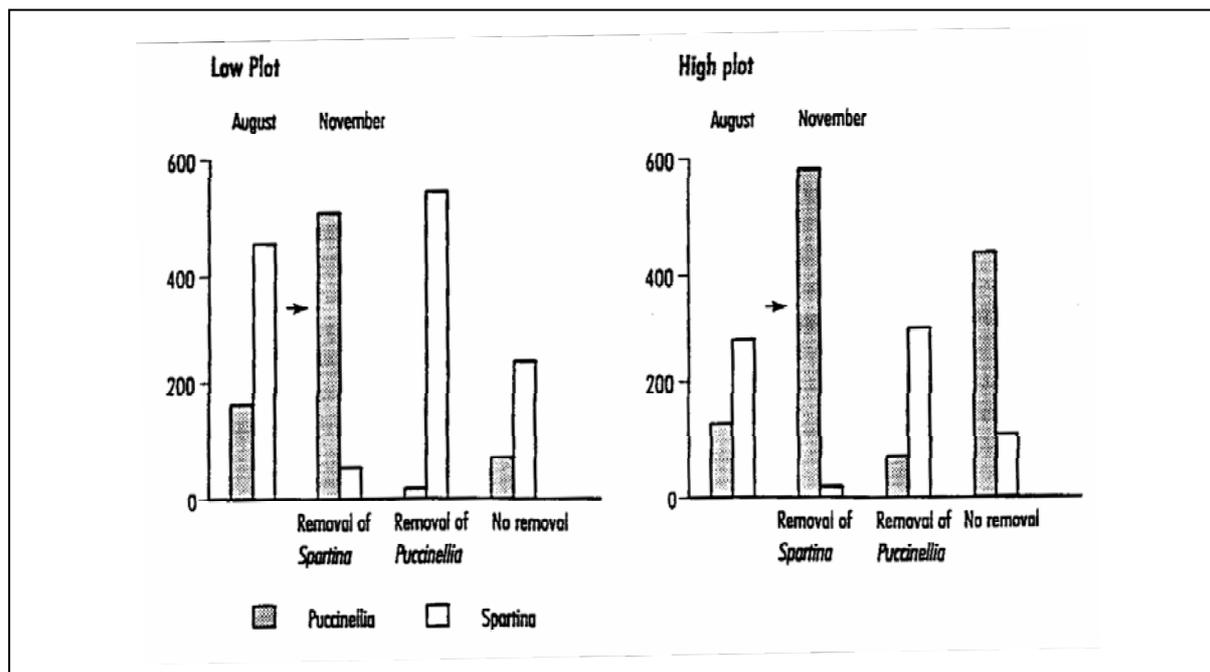


Figure A2.4 Shoot biomass of common saltmarsh grass and *Spartina* at the start of the deletion experiment (August) and at the end of the experiment (November) in both high and low plots

Interestingly, this shift in competitive advantage appears to have occurred over a very short distance along the edge of a shallow creek and over a rise in elevation of only 40 mm, corresponding to a 15-20 minute difference on average in the period of tidal submergence. As with the three grass species mentioned above, local, relatively small-scale differences in elevation resulting from microtopographic variation in the marsh

surface, and hence drainage, can shift the balance of competition in favour of one species over another. The local distribution of sea purslane on creek edges and on slightly raised areas within the marsh suggests that, although they occupy similar sectors of the tidal range, sea purslane has the competitive edge over common saltmarsh grass in locally elevated and well-drained soils.

A different type of biotic interaction, facilitation, may be important in structuring some saltmarsh plant communities. Facilitative interactions are those in which the presence of one species enhances the performance of another or modifies the habitat so as to make it more suitable for another species. In an experiment with saltmarsh rush, the colonisation of bare patches within the saltmarsh rush zone in New England, USA, was facilitated by prior invasion of saltmeadow cord-grass. This was presumably because the bare patches became too saline as a result of evapotranspiration for saltmarsh rush to grow, but not for the cord-grass, which invaded, ameliorating the conditions so that the rush could grow. A similar facilitation process has been described from southern Spain where, on newly-accreting saltmarsh, colonization by the perennial glasswort (*Salicornia perennis*) was shown to be dependent on prior invasion by *Spartina* grass.

A2.2.4 Dynamics and decline

It is also important to realise that successional changes may have vastly different rates in different places and that the observed zonation may not have resulted from the orderly replacement of one species, or group of species, by another with changing elevation. For example, some of the saltmarshes behind barrier islands along the north Norfolk coast may have changed very little in hundreds of years. Indeed the positions of the marshes and of major features such as channels appear to have been stable for at least 4000 years (Pye, 1992). Whilst these ancient marshes change extremely slowly, those to seaward of the shingle barriers are often highly dynamic. They are known from one study of permanent plots near Wells-on-Sea to have developed rapidly from pioneer marsh through to mid marsh in less than a decade, before being buried, at first by sandy sediments and later by mudflats with pioneer glasswort species (Pye, 1992). Clearly the high marshes above the barrier are, in successional terms, disconnected from the lower ones; the one zone is not evolving into the other.

A similar conclusion was drawn from long-term studies of permanently marked plots on a newly accreting mudflat in a part of the Wadden Sea. Changes in these plots between 1953 and 1980 showed little evidence, except locally, of zonation being generated by successional changes. Several separate sets of changes occurred depending on elevation and sediment type, so that the final zonation did not represent a complete sequence of changes from pioneer to upper marsh.

The best example in which zonation does not reflect succession is the presence of a pioneer *Spartina* grass marsh around much of the English and Welsh coastline. In most areas this species invaded mudflats below pre-existing saltmarsh and, because it is able to tolerate greater tidal submergence, actually added a zone on to the marsh. Although, particularly in the north west, *Spartina* is being replaced in a successional sequence to low marsh vegetation, over much of its distribution in the south east it

arrived, spread and is now dying back without successional change to a different type of vegetation.

A2.3 Saltmarsh types

A2.3.1 Key species and communities

Several attempts have been made to classify the different combinations of plant species into distinct communities. This is a difficult task in view of the overlap of vertical niches and the rich mosaics of species produced by topographic variation such as creeks and pans. Nevertheless, three important recent surveys have each produced a useful framework for such classification. One, by the (then) Nature Conservancy Council (NCC; Burd, 1989) is based on a traditional British approach to saltmarsh vegetation classification in which broad communities are distinguished by, and usually named after, the most common or dominant plant (see Table A2.1). Another has been produced as part of a scheme to classify all the plant communities of the British Isles, called the National Vegetation Classification (NVC), and is more in the classificatory traditions of continental Europe (and is based largely on the detailed work of Adam, 1981). The correspondence between these two types of classification for the four major saltmarsh types recognised earlier (Section A2.2.3) is given in Table A2.2.

Although there is not space to describe them here, the detailed communities of the NVC provide a common frame of reference for saltmarsh classification and are widely adopted in primary surveys. Some of the plant species found on saltmarshes in England and Wales are illustrated and described in *A Guide to Saltmarsh Vegetation* (Burd, 1994). Following on from these classification systems, a further classification was developed in order to form a basis for the selection of Special Areas of Conservation (SAC) under the Habitats Regulations 1994. The system developed is shown below in Table A2.2 and shows the *Natura* 2000 codes and equivalent NVC categories.

Other saltmarsh NVC types are also found with these main communities, often in restricted situations. SM22 *Halimione portulacoides-Frankenia laevis* saltmarsh is restricted to the Sussex coast; SM23 *Spergularia marina-Puccinellia distans* saltmarsh is typical of inland sites with saline conditions, also known as 'Annex I habitat 1340 – Inland saltmeadows' and is not considered further here. SM24 *Elymus pycnanthus* saltmarsh community is widespread and typical of the tideline vegetation. SM26 *Inula crithmoides* on saltmarshes is restricted to the south and east coast of England. SM28 *Elymus repens* saltmarsh is also found only at the limit of tidal influence in the northwest.

Table A2.1 Simplified classification of major saltmarsh plant communities (partly after Burd, 1989)

MAIN ZONE	NCC (Burd, 1989)	NVC COMMUNITIES	KEY SPECIES
PIONEER MARSH (down to MHW)	1. <i>Spartina</i>	SM4, SM5, SM6	Spartina grass
	2a. <i>Salicornia/Suaeda</i>	SM7, SM8, SM9	Annual glasswort
	2b. <i>Aster</i>	SM11, SM12	Rayless sea aster
LOW MARSH (up to MHW)	3a. <i>Puccinellia</i>	SM10, SM13	Common saltmarsh grass
	3b. <i>Atriplex (Atriplex)</i>	SM14	Sea Purslane
UPPER MARSH (from MHW up to EHWS)	4a. <i>Limonium/Armeria</i>	SM13	Sea lavender or Sea thrift
	4b. <i>Puccinellia/Festuca</i>	SM13, SM16, SM17	Red thrift
	4c. <i>Juncus gerardii</i>	SM16	Saltmarsh rush
	4d. <i>Juncus maritimus</i>	SM15, SM18	Sea rush
DRIFTLINE (around EHWS)	5a. <i>Agropyron (Elytrigia)</i>	SM24, SM28	Sea couchgrass
	5b. <i>Suaeda vera</i>	SM25	Shrubby sea-blite
TRANSITIONAL (around and above HAT)	6. Upper marsh swamps	S4, S19, S20, S21	Common reed & various rushes
	7i. Shingle/dune transition	SM21, SM22	Shrubby sea-blite Sea heath
	7ii. Freshwater transition	MG11	Various including Creeping bent-grass
	7iii. Grassland transition	MG12	Various including Tall fescue

Table A2.2 Coastal habitats of Community interest (saltmarshes) forming the basis for the selection of SACs (from the Interpretation Manual of European Union Habitats, European Commission, October 1999)

Codes	Directive Name	National Vegetation Classification corresponding communities, relevant pages (Rodwell, 2000), applicable to the UK only
Atlantic and continental saltmarshes and salt meadows		
1310	<i>Salicornia</i> and other annuals colonising mud and sand	SM7 <i>Arthrocnemum perenne</i> stands SM8 Annual <i>Salicornia</i> saltmarsh SM9 <i>Suaeda maritima</i> saltmarsh SM27 Ephemeral saltmarsh vegetation with <i>Sagina maritima</i>
1320	<i>Spartina</i> swards (<i>Spartinion maritimae</i>)	SM4 <i>Spartina maritima</i> saltmarsh SM5 <i>Spartina alterniflora</i> saltmarsh [SM6 <i>Spartina anglica</i> saltmarsh]
1330	Atlantic salt meadows (<i>Glaucopuccinellietalia maritimae</i>)	SM10 Transitional low-marsh vegetation SM11 <i>Aster tripolium</i> var. <i>discoideus</i> saltmarsh SM12 Rayed <i>Aster tripolium</i> saltmarsh SM13 <i>Puccinellia maritima</i> saltmarsh SM14 <i>Halimione portulacoides</i> saltmarsh SM15 <i>Juncus maritimus</i> - <i>Triglochin maritima</i> saltmarsh SM16 <i>Festuca rubra</i> saltmarsh SM17 <i>Artemisia maritima</i> saltmarsh SM18 <i>Juncus maritimus</i> saltmarsh SM19 <i>Blysmus rufus</i> saltmarsh SM20 <i>Eleocharis uniglumis</i> community SM27 Ephemeral saltmarsh vegetation with <i>Sagina maritima</i>
Mediterranean and thermo-Atlantic saltmarshes and salt meadows (NB – note that 1410 Mediterranean saltmeadows is not considered to occur in the UK)		
1420	Mediterranean and thermo-Atlantic halophilous scrubs (<i>Sarcocornitia fruticosi</i>)	SM7 <i>Arthrocnemum perenne</i> stands SM21 <i>Suaeda vera</i> - <i>Limonium binervosum</i> saltmarsh SM25 <i>Suaeda vera</i> saltmarsh

A2.3.2 British saltmarsh types

Much of the work undertaken on saltmarsh classification has drawn a contrast between saltmarshes in the south and east and those in the north and west. Attempts to provide a broad geographical classification of British saltmarshes have also noted this distinction. Adam (1990) recognises three main groups of communities which he calls Type A, B and C.

Type A marshes are relatively low in diversity with *Spartina* grass or rayless sea aster commonly occurring as pioneers, sea purslane common in the mid marsh and sea couch a frequent component of the upper marsh. Type A marshes mostly occur in southeast England. Type B marshes may also have *Spartina* present but the pioneer and lower marsh is usually dominated by common saltmarsh grass and the mid and upper marsh by red fescue and saltmarsh rush. Type B marshes are common in northwest England and Wales. Type C marshes are characteristically species-rich, especially in the upper marsh and include many non-halophytes. Although they occur elsewhere (as do marshes of Type A and B), Type C marshes are most abundant on the west coast of Scotland.

There are other important general differences between marshes in the west and those in the south and east. The most important may be the recent history of grazing, most west coast marshes having been extensively grazed for many decades, but variation in substrate is also a confounding factor. West coast saltmarshes occur mainly on sandy substrates whereas those on the east and south coasts are predominantly on fine silts and clays. There are climatic differences too, with higher rainfall and less extreme temperatures in the west.

It is also possible to recognise geographical variation in the British saltmarsh flora, variation which reinforces the contrast between Scottish, west coast and south east saltmarsh types. One group of species does not occur further north than a line between the Solway and the Firth of Forth. It includes sea purslane, sea couchgrass, sea hard-grass and both common and lax-flowered sea lavender (*Limonium humile*). A second group, restricted to saltmarshes below a line from The Wash to South Wales, includes species from the upper marsh such as sea heath and shrubby sea blight whose main centre of distribution is the Mediterranean, as well as low and mid marsh species such as cord-grass, perennial glasswort and golden samphire (*Inula crithmoides*).

The combination of all of these factors, floristic elements, substrate, climate and history of management, especially stock grazing, makes it difficult to be dogmatic about a 'natural' classification of British saltmarshes. Whilst bearing in mind the broad northwest/southeast distinction, it is important to note that there is a good deal of local variation and that, perhaps contrary to popular belief, saltmarshes are far from uniform in nature.

A2.3.3 Spartina marsh

Originating in Southampton Water, this grass evolved by a process known as allopolyploidy, which involves two separate events. The first is the creation of a hybrid, in this case between the native European cord-grass *Spartina maritima* and a species from North America, smooth cord-grass *Spartina alterniflora*, which must have been accidentally introduced into Southampton Water, probably in ships' ballast water, in the early part of the nineteenth century. The hybrid, which is sterile, was first discovered near Hythe in 1879 (and was given the name *Spartina x townsendii*). (Hubbard & Stebbings, 1967). The second event necessary to create an allopolyploid is the doubling of the chromosome number (which restores fertility) and this must have happened sometime before 1892, when the first plant with fertile seed was found near Lymington. (In fact, the main detective work on the species' origins was not done until the 1950s and 1960s and was initiated by Charles Hubbard, then curator of the grass herbarium at Kew, who later gave the fertile plant the name *Spartina anglica*).

The spread of the grass, at first naturally and then by deliberate planting has been well documented. It may also have spread naturally to the French coast in the early part of this century and deliberate introductions further enhanced its spread in Europe. The first record of deliberate planting is from the Beaulieu estuary in 1898, but most of the planting was done in the 1920s (much of it by, or at the instigation of, James Bryce of the Essex Institute of Agriculture). By the 1930s nearly all of the south and east coast

estuaries south of the Humber had been planted with *Spartina* or were colonised as a result of natural spread from introduced material. Successful introductions were made to the west coast but the major spread of the species here appears to have been since the late 1960s.

It is clear from studies of the vertical range of *Spartina* that the grass added a new lower zone of perennial vegetation to pioneer marsh. In some areas this had an enormous impact on the local hydrography and sedimentary dynamics. In Poole Harbour, Dorset, for example, depths of up to 1.8m of accreted sediment have been recorded below *Spartina* marshes. Changes in the bed levels of the major navigation channels within the harbour (Figure A2.5) during the period in which *Spartina* invaded and subsequently died back, reflect the capture and eventual resuspension and release of extremely large volumes of sediment. From about 770ha of *Spartina* marsh in 1925, the harbour today has less than 350ha, and the marshes continue to recede. Attempts to halt or slow down the erosion of *Spartina* saltmarshes are currently being made in several areas in the south and east, where seawalls or harbour facilities appear to be under threat (e.g. at Lyminster where the use of protective matting is being tried).

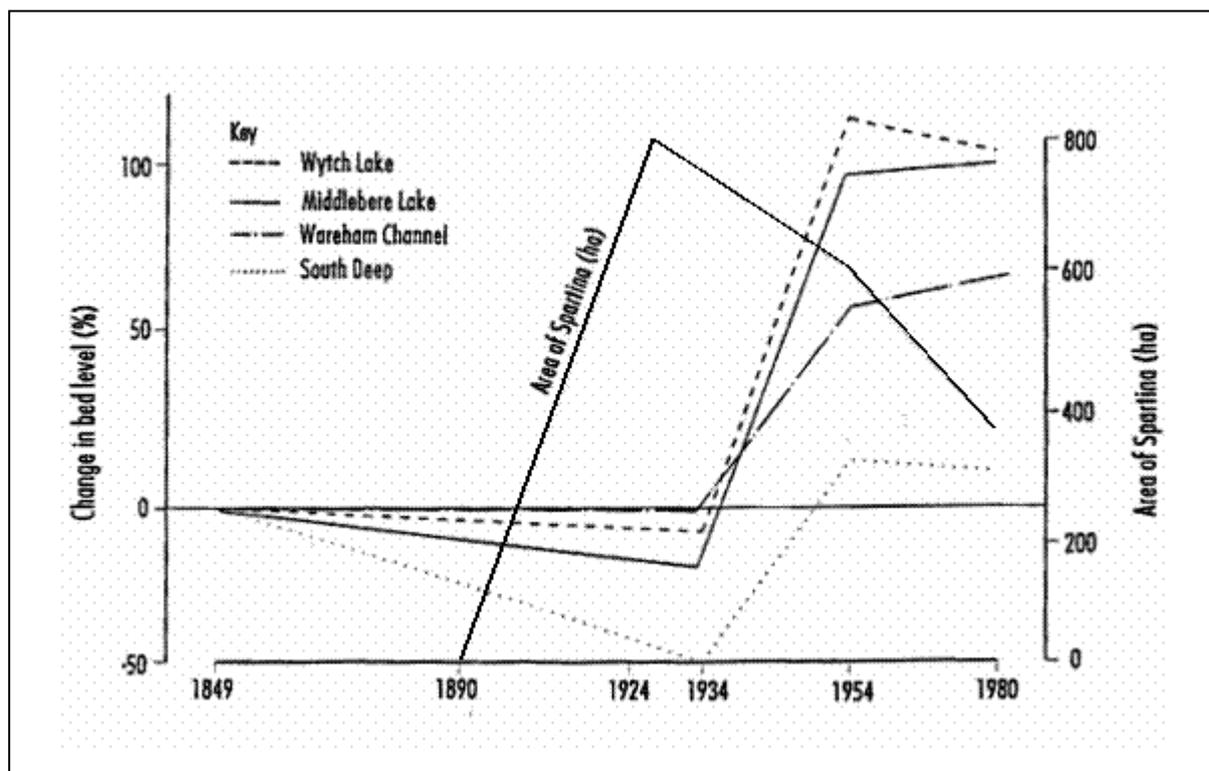


Figure A2.5 The percentage change in bed levels of four major channels in Poole Harbour, Dorset, between the Admiralty Surveys of 1849 and those of 1934, 1954 and 1980 (modified from Gray et al., 1990)

In contrast, the invasion of *Spartina* on the northern and western coasts of England, where it has encroached onto amenity beaches, colonised mudflats that are bird-feeding areas or threatened the floristic diversity of nearby saltmarsh has prompted attempts to control further spread. Physical methods for the removal of *Spartina*, at least on a local short term scale, tend to be the cheapest and have been used in most of the places where management has been implemented. However, as well as being very labour intensive, the direct removal of shoots and rhizomes appears to be only

effective for single plants and small clones. Remaining rhizomes have the potential to regenerate later on in the season and thus the process of removal will need to be repeated. More efficient mechanical methods of control include techniques such as Rotoburying, that work by smothering *Spartina* by ploughing it several centimetres into the ground. This method has met with success at a National Nature Reserve in Lindisfarne, Northumberland, where six years following rotoburying, *Spartina* had not regenerated. Although rotoburying has met with some success, its use is limited as it cannot be used in soft sediments where *Spartina* is usually more extensive (Denny & Anderson, 1998 in Lacambra *et al.*, 2004).

Chemical control using herbicides is an effective but expensive technique for managing *Spartina* and there are a number of restrictions on the use of herbicides. The use of any herbicide should always be preceded by a risk assessment. It is an offence to use non-approved products or to use approved products in a manner that does not comply with the statutory conditions of use. General guidance on the use of herbicides on areas of nature conservation importance is available in 'The Herbicide Handbook' produced in 2003 by English Nature/FACT (Britt *et al.*, 2003). The most widely used herbicide in experimental trials in the UK has been glyphosate (Roundup Pro Biactive®) sprayed either from a backpack, a tractor-mounted boom or aurally. Dalapon®, a sodium salt of dichloropropionic acid, has also been used. Control programmes in areas where the grass is well-established can be very costly and involve a long-term commitment to repeated spraying. An interesting current case-study involving the evaluation of control took place at Lindisfarne where, in conjunction with Monsanto PLC, the manufacturers of Roundup Pro®, English Nature attempted to control *Spartina* by spraying over the intertidal flats between Holy Island and the mainland. Spraying during neap tides in July and August using a boom sprayer mounted on an all-terrain tracking met with initial success and in some areas led to the recovery of benthic invertebrate populations to pre-*Spartina* levels.

There is a clear need to continue to monitor the ability of such programmes to achieve their desired objectives without wider, perhaps less desirable, effects. For more discussion on control techniques the reader is referred to Lacambra *et al.* (2004).

An intriguing situation, therefore, exists. In that *Spartina* marsh is being encouraged, protected or even planted in some areas and yet being considered for control in others. Appropriate management of this key species is likely to require consideration of the entire local saltmarsh and mudflat system, including sediment supply. It is not yet clear whether the *Spartina* marshes in the north and west will reach a mature phase and begin to die back as in the south and east. A more rapid successional replacement of *Spartina* by other species on the Ribble marshes is amongst the pieces of evidence that suggest classic die-back may not occur on most of these, generally sandier, marshes. It is not known if die-back is cyclic or whether local recolonisation will occur. Furthermore, the outcome of these processes is certain to be complicated by the rise in relative sea level presently contributing to saltmarsh erosion in the south and east.

A2.4 Saltmarshes as ecosystems

A2.4.1 Saltmarsh productivity

As an example of marsh productivity, the mean productivity of two saltmarshes in Essex and Norfolk was estimated at 450-500gm⁻² per year, with a corresponding carbon production of 180 to 200gC m⁻² per year (Boorman, 2000). The contribution of algae is included within these figures and probably accounts for between 5 and 15gC m⁻² per year. However, this figure for algae production is low due to the relatively small contribution of algae to the total biomass. In systems where macroalgae form a larger proportion of the total biomass, production can be similar to that of vascular plants. As Table A2.3 shows, productivity also varies across saltmarshes during their development. In general, there is high productivity in the pioneer zone followed by a fall in productivity in the lower marsh. Productivity then steadily increases as the saltmarsh develops into a middle marsh until, finally, it decreases in the upper reaches.

Table A2.3 Net annual primary productivity (NAPP) of the four major saltmarsh zones studied in England, France and Holland (cited in Boorman, 2003)

Marsh zone	Main species	Range NAPP Average gm ⁻² per year	
Pioneer marsh	<i>Salicornia</i>	233 -849	465
Pioneer marsh	<i>Suaeda</i>	1032	1032
Lower marsh	<i>Puccinellia</i>	317-701	485
Middle marsh	<i>Puccinellia</i>	417-824	586
Middle marsh	<i>Atriplex</i>	631-1708	1137
High marsh	<i>Elymus</i>	362-1260	593

Measurement of vascular plant productivity has been made in several ways, not all of them comparable (or even accurate), usually involving regular estimation of the living biomass by harvesting several times a year. Losses of material between harvest dates may be partly estimated by measuring rates of turnover of leaves, tillers etc., using detailed demographic analysis, but such losses are likely to lead to underestimates of productivity. Most measurements have been confined to above-ground production, but a few studies have shown that below-ground biomass may exceed that of aerial biomass. In *Spartina* grass on one Suffolk site an average of around 75% of the biomass was below ground. At the same site it was estimated that, when the turnover of shoots, roots and rhizomes between samples was accounted for, the gross primary production (at 4500gm⁻² per year) was about three times the figure estimated for net production. Variation in the seasonal growth patterns of different species (see Figure A2.6) means that estimates of the peak biomass must be made at different times for different species. Furthermore, aerial and below-ground peaks are known to occur at different times.

With these cautions in mind, it is worth noting some of the estimates of aerial primary production in some studies of a few species. *Spartina* grass, perhaps the most studied, has been estimated to produce between 475 and 700 grams of dry weight of tissue per square metre per year (gm⁻² y⁻¹) on a Suffolk saltmarsh, from 1162-1649gm⁻² y⁻¹ in a

Dutch saltmarsh and from 1600-1850gm⁻² y⁻¹ in the Ribble estuary. These figures are all much lower than that of up to 4800gm⁻² y⁻¹ of above-ground net productivity in smooth cord-grass on creek edges in the USA.

An annual net aerial primary production of 1372gm⁻² was estimated for sea club-rush on a brackish marsh in the south Netherlands. Also from the Netherlands is an estimate for saltmarsh rush vegetation of between 420 and 1050gm⁻² y⁻¹ (the below-ground primary production of the same vegetation ranged from 1010 to 2450gm⁻² y⁻¹).

A2.4.2 Saltmarsh Fauna

Invertebrates

The following is a brief description of the invertebrate species found on saltmarshes, starting on the low shore sand or mud flats and progressing up the shore to transitional vegetation types. It is largely based on studies of the saltmarshes of the Wadden Sea by workers from the University of Kiel and published in the Council of Europe review of saltmarshes in Europe (Dijkema, 1984).

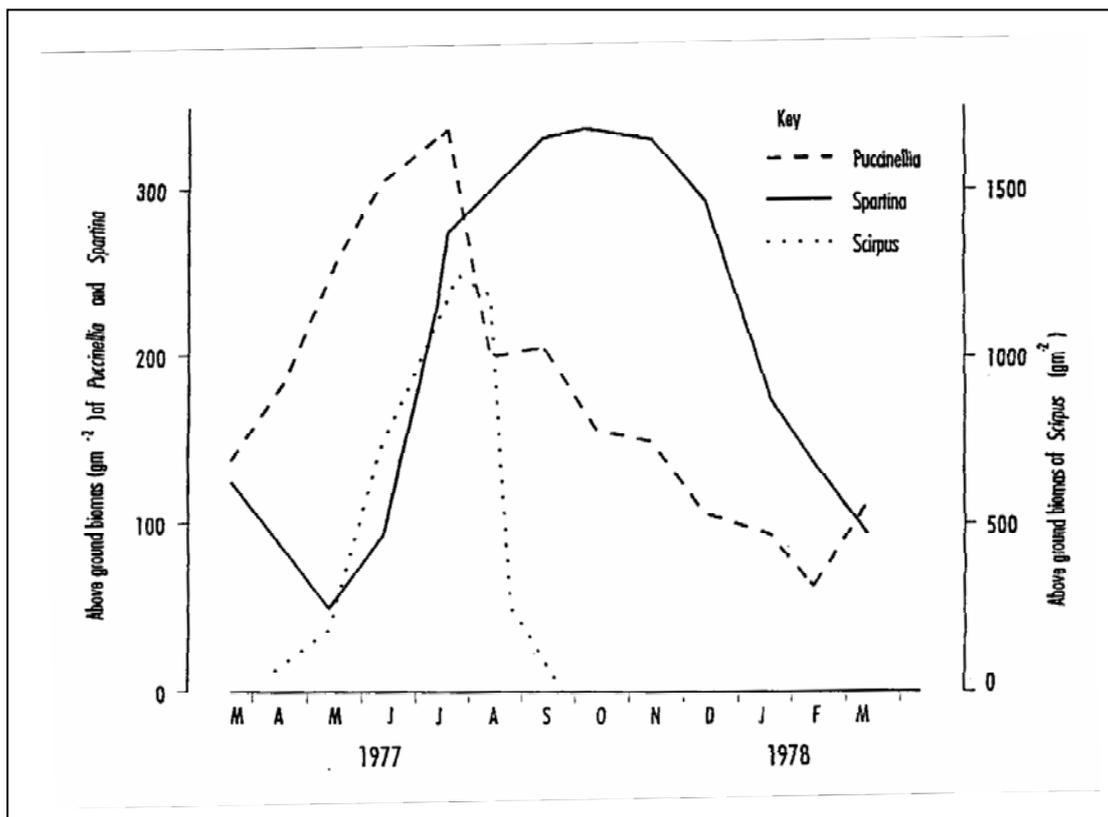


Figure A2.6 Differences in seasonal patterns of growth in three saltmarsh plant species, as indicated by aboveground biomass (based on data from Long, 1983 (Spartina and Puccinellia) and de Leeuw, 1987 (Scirpus))

Table A2.4 gives a reasonable indication of the way in which invertebrate diversity increases in the upper levels of the marsh. As might be expected, there are few plant

eating species associated with the sand and mud flats. However, it is here that the larger populations of individual species occur.

Table A2.4 Number of species of invertebrates found on different levels of saltmarsh in the Wadden Sea (from Dijkema, 1984)

Species Type	No. of Species Found		
	mud/sand flat	lower zone	middle zone
Species <1mm in size	300	350	1300
Macro species	100	500	
Plant eating	3	130	370
Detritus feeding	-	160	480
Carnivorous	-	80	200
Parasitic	-	80	250

A sharp discontinuity in faunal distribution occurs at the interface between mud/sand flat and pioneer marsh. This is caused not only by the change in structure, micro climate and food availability, but also by a change in predation pressure from birds and fish. Species which require the cover provided by denser vegetation, such as the shore crab *Carcinus maenas* and the rough periwinkle *Littorina saxatilis* become more common. In mid-upper marsh zones the burrowing amphipod *Corophium volutator* is often numerically dominant, especially where vegetation is less dense on creek edges and around pools. Higher up in the mid-upper marsh zones, invertebrates of terrestrial rather than marine origin become more frequent, especially around the better drained margins of creeks. This is reflected by the larger number of phytophagous (plant eating) species identified in the Table A2.4 above.

A further characteristic of saltmarshes is the extent to which species tolerant of tidal inundation are restricted to the different zones of the marsh. As Table A2.5 below shows, in the lower zones a majority of species are so specialised that they occur virtually nowhere else. However, in the upper and transitional zones, species which use the marsh are often those which can compete equally well in the adjacent terrestrial habitats and, therefore, the number of species restricted to the habitat is much reduced.

The burrowing activity of some invertebrate species has been proposed as an alternative theory to the prevailing theory that saltmarsh erosion is due to coastal squeeze. Bioturbation and herbivory by the ragworm *Nereis diversicolor*, has been shown to negatively affect pioneer species, such as *Salicornia*, by increasing sediment instability and exacerbating the erosion of saltmarsh creeks (Hughes and Paramor, 2004). Morris et al (2004), however, present other evidence to refute this claim.

Table A2.5 Proportion of species found exclusively within each zone

Low - mid marsh	Middle marsh	Upper transitions
75-80%	25-50%	5-10%

Large expanses of open sand flat in the upper marsh and transition zones are required specifically by a few species. The ground beetle *Bembidion pallidipenne* and the two maritime tiger beetles *Cicindela maritima* and *C. hybrida* range very widely over extensive intertidal sand flats backed by dunes. Strandline accumulations of drift litter, with or without saltmarsh species, support various assemblages of invertebrates which are dependent on the humidity and state of decay of the drift material. Accumulations of seaweed at high water mark support a wide diversity of specialist flies. One scarce beetle, *Aphodius plagiatus*, in a genus composed otherwise only of dung beetles, is associated with rotting fungi and accumulations of plant litter in saltmarsh and dunes.

As can be seen from the above, far from being restricted in the diversity of invertebrates, saltmarshes are likely to have both a diverse and abundant fauna.

Birds

Typical birds species which breed on UK saltmarshes can be found in Table A2.6. The table attempts to give a broad indication of the main habitat requirements and numbers of some of the most common species (along with Table A2.7).

Table A2.6 Habitat, geographical location and density of breeding birds on saltmarshes in Great Britain (from Cadbury, Green & Allport, 1987)

Species	Habitat	Distribution	Average Numbers
Redshank	Tussocky, moderately grazed mid-high marsh	50% East Anglia / 25% north west England	up to 100 pairs per km ² (The Wash)
Oystercatcher	Moderately grazed high marsh	Highest densities in the north west	72 pairs per km ² (the Solway)
Lapwing	Grazed grassland on high marsh	Western England & eastern Scotland	20 per km ²
Black-headed gull	Mounds on marsh	Scattered large colonies	20,000 in 1 colony (the Ribble Estuary)
Skylark	Upper grassy marsh		up to 105 pairs per km ²
Reed bunting	Edge of marsh with tall vegetation		up to 80 pairs per km ²
Meadow pipit	Upper grassy marsh		up to 76 pairs per km ²

Table A2.7 Average number of some of the most numerous birds using estuaries in Great Britain (taken from British Trust for ornithology counts, winter 1990/91)

Species	Numbers	Main feeding habitat
Knot	292 117	Tidal flats
Oystercatcher	277 091	Tidal flats
Dunlin	567 173	Tidal flats
Redshank	74 429	Saltmarsh
Pink-footed Goose	176 000	Saltmarsh/farmland

The extensive saltmarshes of The Wash, in particular, hold significant numbers of wintering passerines and Table A2.8 provides an indication of the numbers involved.

Table A2.8 Estimates of the number of individuals of some of the most numerous passerines on the saltmarshes of the Wash, winter 1985/6

Species	Estimated Numbers (Winter)
Skylark	26 000 - 32 000
Twite	up to 17 000
Reed bunting	500 - 1000
Rock pipit	1200 - 23 000