

## THE DECLINE OF *SPARTINA* IN LANGSTONE HARBOUR, HAMPSHIRE

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### ABSTRACT

Changes in distribution of *Spartina* in Langstone Harbour, Hampshire are mapped from a series of aerial photographs taken over the past forty years. Literature which pertains to the biology and distribution of saltmarsh and to *Spartina* in particular is reviewed and the present condition of *Spartina* marsh in Langstone Harbour is described. A possible pattern of development suggested by the present condition of the marsh is postulated and compared with the map evidence. The probable consequences of the decline in *Spartina* are reviewed.

### 1. INTRODUCTION

Occasionally the introduction of a species into a country is followed by so rapid a spread that the organism becomes a pest, and then, while people are still considering how to combat the menace, the threat recedes and the organism takes its place as a normal and unremarkable constituent of the native fauna and flora.

The explanations advanced to account for this type of behaviour have usually been vague. The invading species is described as being 'aggressive' or finding an 'unoccupied niche' and then, as it declines, it is suggested that its pests and diseases have caught up with it or that the indigenous inhabitants have adapted themselves to deal with the invader. Only rarely is any experimental work done to support the general argument. Hybrid species of *Spartina* (Rice Grass) have shown this pattern of boom and recession in south coast harbours but, although a considerable quantity of thorough and competent work has been done on the species complex, events in the field suggest that none of the experimentally demonstrated interactions can explain the change from growth explosion to decline that has been observed in the Solent.

The sudden spread of *Spartina* after 1900 has become a textbook example of invasion and its subsequent decline has been investigated phys-

ologically. However, our knowledge of the full extent of the spread and decline has relied primarily on folk memory and there has been no chance of verifying the facts by objective method, for neither the Admiralty charts nor the Ordnance Survey maps provide the necessary detail.

In recent years the development of remote sensing as a tool for studying the ecology of halophytes (Gallagher 1974; Grimes and Hubbard 1971) has led to the successful application of this technique to the local harbours by members of the Geography Department of Portsmouth Polytechnic. The expertise built up during recent vegetation surveys of Langstone and Chichester Harbours plotted from aerial photographs has been extended to the interpretation of *Spartina* distribution as recorded on all the known aerial surveys of Langstone Harbour. Work done for a student project (Hall 1979) led to the extensive series of maps by Coulson against which this account by Haynes is set.

The accuracy of the interpretation of current photographs can be checked in the field but clearly this is not possible for the older photographs (see Coulson and Budd 1980, for methods). We are fortunate in possessing a vegetation survey of Langstone Harbour for 1974 in which the condition of *Spartina* was recorded at the intersection of a 75 metre square grid. This survey, carried out on foot, covered all the Harbour and provided 2700 sample points.

Two maps (Fig. 1, a, b) illustrate the extent of the *Spartina* decline.

Goodman and Williams (1961) reported die-back of *Spartina* as occurring only on the periphery of the marsh and in pans within the marsh. Die-back is a term applied to the gradual stunting of the plants, which leads ultimately to death of the aerial portion, producing a mud surface lacking living plants but bound by the tough underground rhizomes. This ultimate

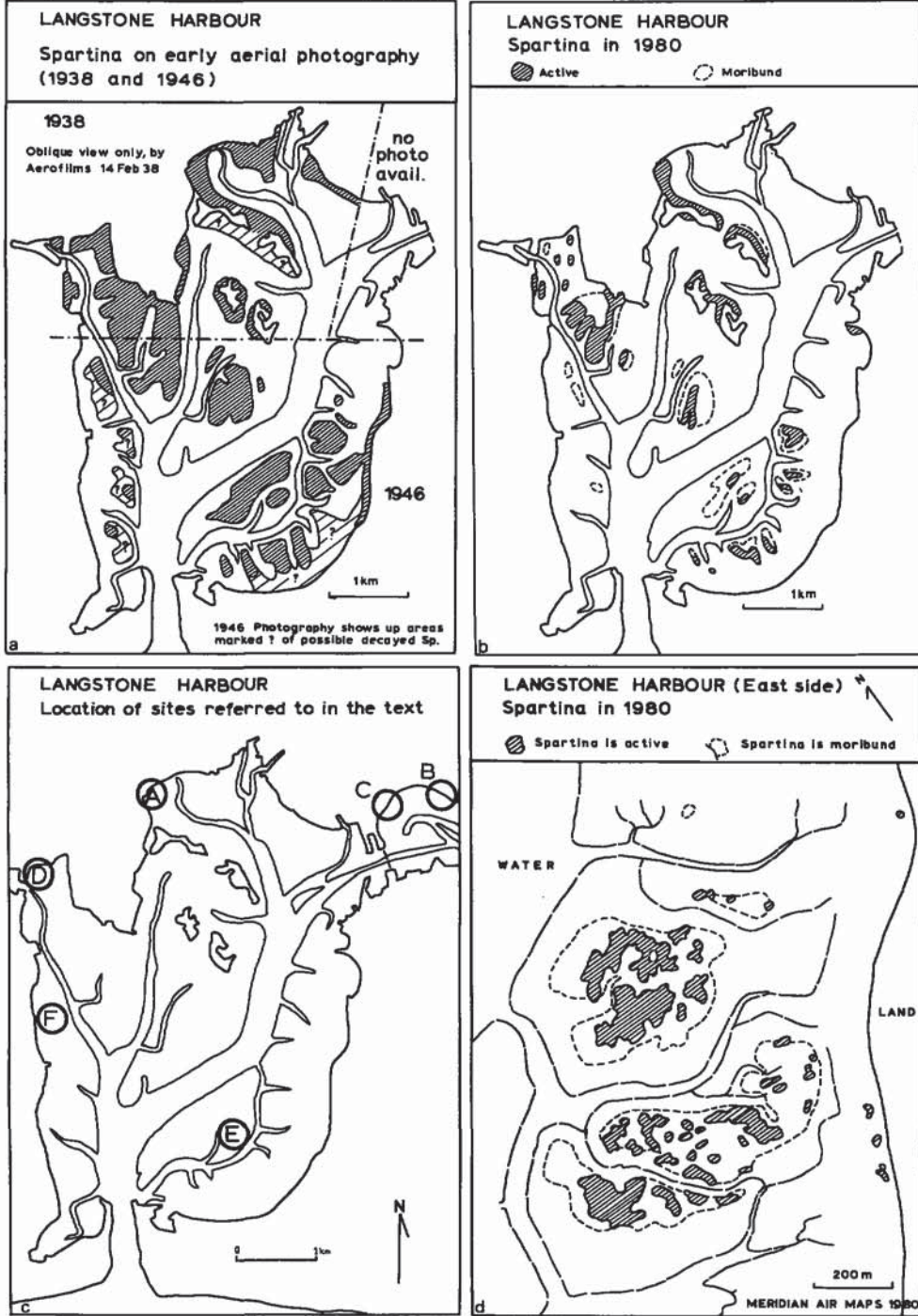


Fig. 1.

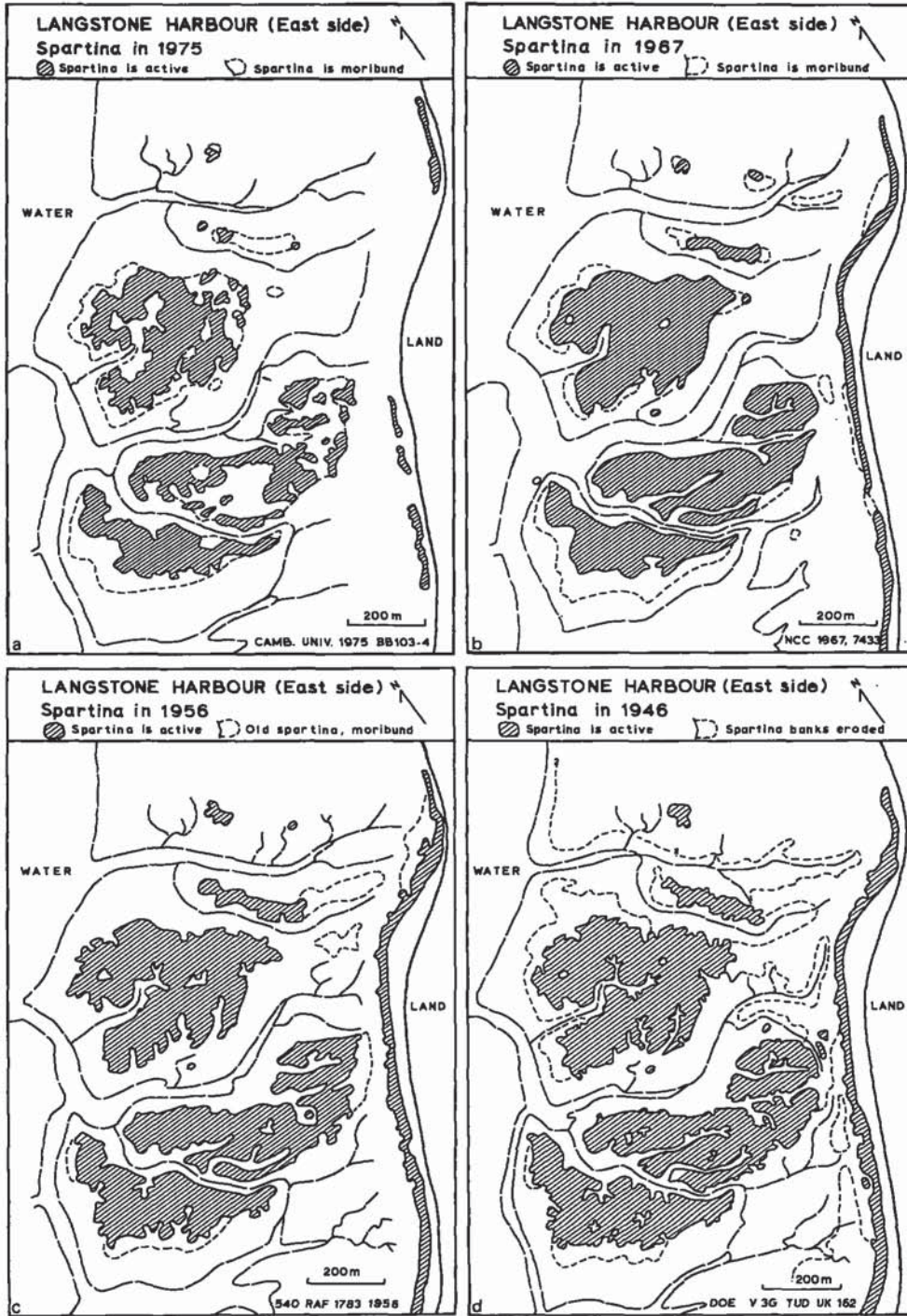


Fig. 2.

stage of die-back is referred to on the maps as 'moribund'. In the present state of the Harbour it is difficult to accept that die-back is restricted to the two locations described by Goodman and Williams. Closely, almost inextricably, linked with *Spartina* die-back are the changes in level of the muds colonised, stabilized and built up by actively growing *Spartina* and subject to erosion and re-distribution on its death.

The vegetation of the Harbour was described by Haynes in Chapter 8 of the Langstone Harbour Study (Portsmouth Polytechnic 1976). The Harbour has a large intertidal area over which *Spartina* has been the dominant salt marsh plant (Fig. 1b). The more varied collection of flowering plants which constitute a mixed or general saltmarsh is now rare in the Harbour and the stages leading to its formation have not been seen this century. Over the past fifteen years mats of green algae have covered large areas of the mudlands, their growth stimulated by the nutrients contained in the effluents discharged into the Harbour. *Zostera* (Eel grass) beds form the remaining vegetation type. Early this century *Zostera* is reported to have formed large productive beds over the muds, but the plant suffered a drastic set back in the 1930's and until recently occurred only in small quantities. Figure 3 shows the conventional pattern of plant succession and the extent to which it has been followed in Langstone Harbour.

It would seem that, at present, *Spartina* is never found below mean tide level whereas *Zostera* is primarily a plant of low-lying mudlands. *Zostera* has increased markedly during the recent rapid retreat of *Spartina* (Tubbs and Tubbs 1981). A vegetation survey in 1979 (Coulson and Budd 1979) revealed no new localities since 1974 but the scattered, overdispersed cover of 1974 had become consolidated, which leads one to ask whether the decline of *Spartina* had created the low lying mudlands suitable for *Zostera* colonisation. The implications are interesting for if all the *Spartina* which has gone once formed high-level marsh, then vast quantities of mud have been redistributed within or lost from the Harbour.

## 2. GENERAL CONSIDERATION OF SALT MARSH VEGETATION

In trying to evaluate the possible implications of the *Spartina* decline, one is constantly made aware of the inadequacies of the hypotheses which previously have been advanced to explain salt marsh development.

The concept of succession no longer seems applicable to a Harbour where only the primary colonisers remain successful (Fig. 3). It is not just *Spartina* marsh that is failing. Mixed salt marsh seems equally loathe to commence redevelopment.

Theories which suggest that different dominants prefer substrates of different particle size fail to account for the one-time success and the present failure of mixed marsh and *Spartina* marsh, or for the present success of *Zostera*, all apparently in the same type of sloppy mud.

Many of the taxa of flowering plants found between tide marks are variable in some aspect of their constitution, a feature recognisable either in their cytology (chromosome number) e.g. *Spartina*, *Salicornia*, or by the presence of hybrids e.g. *Spartina*, *Puccinellia*, *Limonium*, or in the range of ecotypes e.g. *Plantago maritima*, or by an unexplained variable morphology e.g. *Spergularia media*, *S. marina*, *Suaeda maritima*, and *Limonium vulgare*. Inherent variability of organisms in general is often matched by a parallel range of ecological preferences which permits the taxon to grow over a wide range of environmental conditions, but such flexibility is not taken into account in any of the discussions of habitat preference in published accounts of salt marsh ecology. Only in *Salicornia* has a clear relationship been established between cytological races and habitat salinity. General accounts more often give the impression of very narrow tolerance ranges, laying stress on the importance of the relative periods of submergence and emergence and emphasising the floristic changes induced by differences of only two or three centimetres in substrate height.

The causal relationship between substrate level and species distribution has been variously attributed to changes in either oxygen tension or nutrient supply. The relationship is usually indirect: slower currents deposit finer particles

and the smaller pore spaces decrease aeration; reduced periods of immersion reduce nutrient supply, etc. Experiments in which aeration is increased or fertilizer (usually nitrogen or phosphorus) is added have shown enhanced growth rates (Pigott 1968; Stewart *et al* 1972; Tyler 1967).

More recently, salinity gradients have again been considered important. Salinity of the inter-

stitial waters is claimed to be inversely related to the level of the substrate. Such a transition has renewed interest in problems of ion uptake in halophytes (e.g. Queen 1974).

It is highly probable that all these factors are of importance to the growth of salt marsh plants and combine to control their vigour, particularly when the plants are growing just below High Water Springs. However, although these ideas

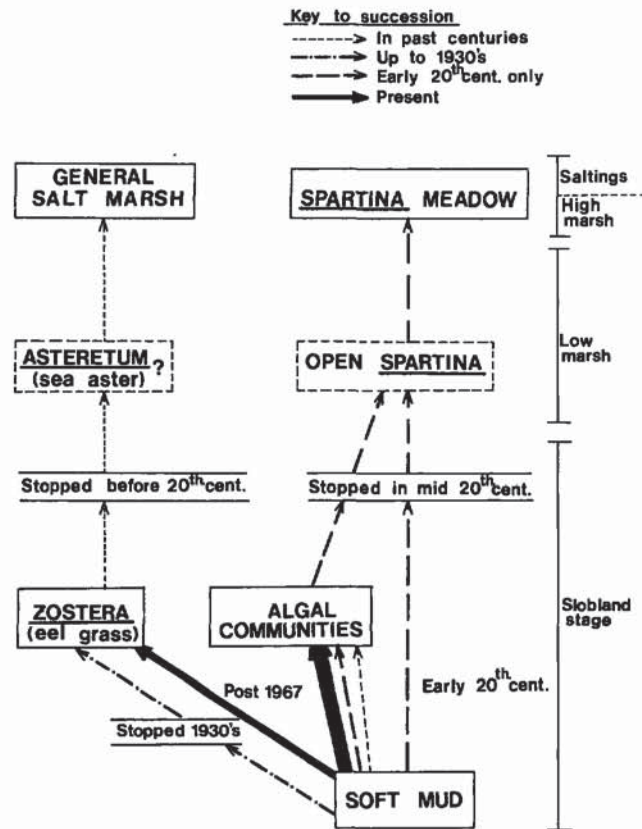


Fig. 3. Plant successions on muds of Langstone Harbour.

can be used to explain the degeneration of high level marsh left unprotected from wave action by the absence of low marsh, none of these features can account for the failure of low marsh to develop in places where it must once have been, subject as it was to constant tidal inundation, to no severe salinity, and in recent years to sea water enriched by processed sewage effluent

(Portsmouth Polytechnic 1976). Such conditions elsewhere have produced highly productive low marsh (Fahy, Goodwillie *et al* 1975). (N.B. No biocides or above-average levels of heavy metals have been recorded during the continuous and frequent monitoring of Langstone Harbour waters).

In considering the present state of the

Harbour, the two related problems of the death of high level marsh and the absence of new colonization which might lead to re-establishment, need to be borne in mind.

### 3. THE BIOLOGY OF *SPARTINA*

Four 'species' of *Spartina* have been found in Langstone Harbour (Marchant pers. comm.). They are *Spartina anglica*, *S. townsendii*, *S. maritimum*, and *S. alterniflora*. Of these *S. maritima* is indigenous, *S. alterniflora* was introduced and formed a sterile hybrid *S. × townsendii* with the indigenous species. It was the chromosome

doubling of this sterile hybrid which produced the vigorous taxon *S. anglica* which so rapidly colonised Solent harbours after 1900 and is still rapidly spreading along some parts of the Irish coast. The fertile hybrid has also backcrossed with *S. alterniflora* to give further variation (Fig. 4).

This complex story, worked out by Marchant (1968), is not such a neat and simple picture as that originally described by Huskins, whose account is enshrined in many textbooks as the classic example of the vigour of hybrids. For Huskins' theory to be acceptable the chromosome numbers would need to be 61 and 122.

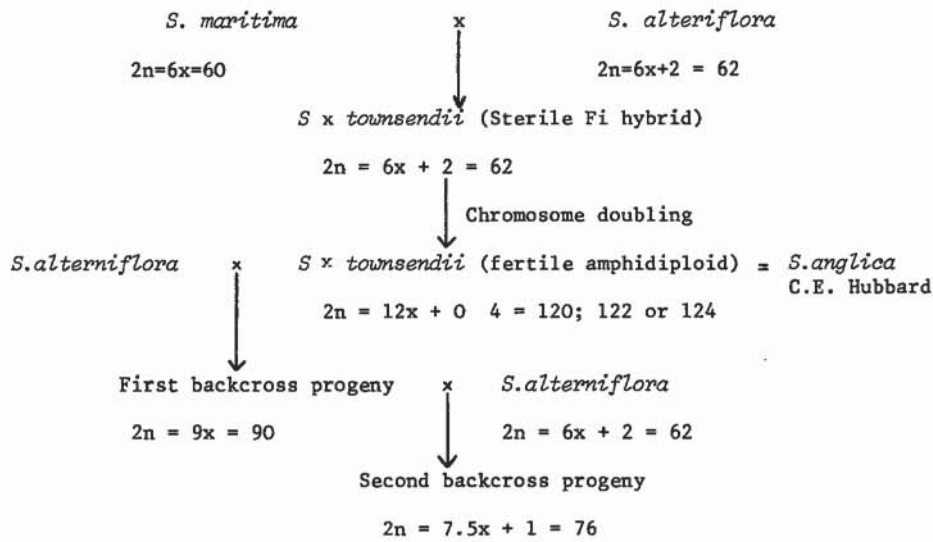


Fig. 4. Chromosomal races of *S × townsendii agg.*

When first recognised at Lymington in 1892, this fertile amphidiploid was described as vigorous. It had spread to Poole and Chichester Harbours by 1900 and by 1907 was widespread. The confusion possible with such a range of chromosomal races (the fertile amphidiploid has three) is worse compounded by the continued prevalence of the older theories in which any hybrid is identified as *S. × townsendii*. Sometimes the whole hybrid complex is described as *S. townsendii sensu lato* but in the second edition (1968) of Hubbard's book on grasses, the sterile hybrid is called *S. × townsendii* and the fertile amphidiploid is referred to as *Spartina anglica* C. E.

Hubbard. From the chromosome numbers given and comments in the text, the first and second backcross progeny are not included under any taxon.

The visual differences between the described taxa lie primarily in the flowers (character of the anthers) but they are not very great and the smaller growth of the indigenous species is of little significance in any area such as Langstone where the supposedly genotypically taller species are dwarfed. No behavioural differences (other than vigour) have as yet been reliably ascribed to the present day taxa of the Harbour and *S. anglica's* early vigour seems to have been

lost. In Langstone the complex is referred to simply as *Spartina*.

*Spartina* employs the most efficient of the various photosynthetic pathways and is capable of very high levels of production particularly in the lower marsh areas where its productivity can be twice that at higher elevations. In height *S. alterniflora* can range from 2 metres in the lower marsh to 20 centimetres on the upper marsh (Nixon and Oviatt 1973). The outstanding contribution of *Spartina* to salt marsh production has been recognised by many workers (e.g. Odum 1974; Reimold 1974) and in those localities where it grows it contributes most of the detritus supplies to the detrital feeding animals in which the marine habitat is particularly rich.

The standard explanation of *Spartina* die-back in the Solent (a decline not reported in the American literature) suggests that with the gradual rise in mud level which follows the rapid accretion of material the water current is slowed, finer material is deposited, pore spaces decrease and aeration worsens (Goodman and Williams 1961). It follows from this hypothesis that *Spartina* initially colonises coarser sediments, that there is a change in particle size with depth below *Spartina* and that the aeration along clifflets should enhance growth. None of these expected consequences applies in Langstone Harbour where *Spartina* is reported as colonising 'sloppy' mud (Perraton 1953) a substrate which is also specified in Hubbard's grass book and justified by recent observations. Nevertheless the experiments described by Goodman and Williams do support their conclusions and the occasional colonisation of channel slopes in Langstone may be attributed to increased aeration. Low concentrations of iron (Adams 1963) and nitrogen (Valiella and Teal 1974) have also been found to limit growth, but fertilizer treatment of the highest *Spartina* marsh in the U.S.A. stimulated no increased growth in contrast to the lower zones where extra nutrients induced growth comparable to that found in the most luxuriant low marsh. Some 'other factor' was assumed to control the low growth rate in these highest zones.

In experiments conducted by Dr Dancer under greenhouse conditions at Portsmouth,

*Spartina* grew better when irrigated with fresh water. Limited field trials gave support to the view that excess salinity inhibits growth. In the U.S.A. Penfound and Hathaway (1938) found that *Spartina alterniflora* grew well on sites having low 'root-medium' salinity and grew poorly on highly saline soils. More recently Nestler (1977) has shown that the growth of *S. alterniflora* is inversely related to interstitial salinity along the gradient from luxuriant low level to dwarf high level marsh in Georgia.

The difference in growth and vigour at different elevations might suggest that different genetic races of the grass may be involved. The relationship has been both claimed (Odum 1974) and denied (Shea *et al* 1972).

Preliminary investigations by Dr Dancer in 1980 suggest that there may be differences in the pattern of root and rhizome growth which are correlated with the vigour of the plants and their substrate.

#### 4. THE PRESENT *SPARTINA* BEDS OF LANGSTONE

The map of the present day distribution of *Spartina* (Fig. 1b) does not indicate the condition either of *Spartina* or of its substrate. A number of different aspects can be recognised (see Fig. 1c for the location of examples).

##### A. Mixed marsh with *Spartina*

An example of mature mixed marsh associated with *Spartina* can be found only at the north-east end of Farlington Marshes adjacent to the islands (Fig. 1c, site A). Here the associated *Spartina* remains healthy and at least as tall as anywhere in the Harbour (40–50 cm). It is rooted in the usual fine muds which, near the surface, have the denser character found on all old *Spartina* flats. Using a Pilcon, direct reading, hand vane tester, we found that the shear strength of the dense surface layer ranged from 8–15 K Pa wherever it was measured in the Harbour (To convert K Pa to Kg/cm<sup>2</sup> multiply by 0.012 and to convert to lbf/ft<sup>2</sup> multiply K Pa by 20.8854).

The marsh is dissected by a tortuously dendritic pattern of steep sided drainage channels, a

marked feature of which, at this site, is the presence of a channel, running parallel to the shore line, separating a thin littoral strand from the more extensive marsh to seaward. Such a channel is also a common feature of the patches of extant marsh in Chichester and Pagham Harbours.

To seaward this mature marsh ends abruptly in clifflets and it is clear that a considerable extent of marsh has been eroded.

#### B. Mature *Spartina* Marsh

Mature *Spartina* marsh can no longer be found in Langstone Harbour but may be seen in Emsworth Harbour adjacent to Langstone village (Fig. 1c, site B), but even there it is beginning to develop a reticulate pattern of channels by breakdown of the interfluves. *Spartina* is here the only species and such marsh was once probably common throughout the harbours.

A transect over this mature marsh to its cliffed seaward edge revealed a drop of 1 metre over 180 metres, but half of this fall occurred in the first 20 metres. A measure of *Spartina* height, known to be related to its dry weight, was taken as the distance from the mud surface to the tip of the uppermost leaf. Such measurements were made at intervals down the transect and at each site a sample of at least 30 plants was measured. The results showed there to be no correlation of plant height with the depth to which the mud surfaces are covered at high water. (There was a 95% chance ( $p=0.05$ ) that the true means of the populations sampled lay between the range of  $28\text{ cm} \pm 1.6$  to  $32.9\text{ cm} \pm 1.7$ ). Material from two patches of 'die-back' lying off the transect provided means of  $20.6\text{ cm} \pm 1.7$  and  $22\text{ cm} \pm 0.6$ . The shear strengths of the muds were all in the normal range of consolidated mature *Spartina* mud (8–12 K Pa).

Adjacent to one of the die-back sites, *Spartina* was growing vigorously ( $40.6\text{ cm} \pm 3.6$ ) along the base of an eroded gully level with the most seaward mature marsh. The mud here had a shear strength of 5 K Pa.

Thus three, distinct, non-overlapping groups of *Spartina* were present (mean heights of 30 cm, 20 cm, 40 cm) and the only observable habitat difference lay in the softer muds below the tallest

population. Caldwell (1957) reports spread by extension from clumps of *Spartina* during pioneer phases. This growth habit would result in large clones whose uniformity in stature would not be unexpected. The origin of the vigorous plants on the gully slope is unknown. Isolated plants investigated by Dr Dancer and Mr Craig in similar situations had no root or rhizome connections either with each other or the adjacent patch of dwarfier plants.

#### C. Marshland Archipelago

The map sequence (Figs. 1d, 2) shows that erosion can commence at the periphery and then it seems that the narrow channels in the marsh widen and coalesce leaving a collection of small islets separated by a reticulate pattern of lower and softer mud. The gradual break up of widespread *Spartina* marsh seems to alter the appearance of drainage channels by lowering the interfluves and softening the contours. This must certainly alter the character and direction of local tidal currents even though the main channels remain dendritic.

A convenient example of this third aspect occurs on the foreshore by Langstone Village (Fig. 1c, site C). Here, of one hundred isolated mounds, only thirty-five still have *Spartina* growing on their summits; the more compact mud, plus the binding effect of the rhizomes, resists erosion for some years even after the *Spartina* has died back. On the lower slopes of sixteen of these one hundred mounds vigorous growth of *Spartina* was to be seen.

*Spartina* height on one mound was  $22.3\text{ cm} \pm 1.5$ . This *Spartina* was growing in mud with a shear strength of 10 K Pa while on the slopes *Spartina* height was  $41.2\text{ cm} \pm 2.6$  on a mud with shear of 4 K Pa.

Shear strengths were measured down the face of a clifflet and out across the mud at the seaward edge of the hummock complex (Fig. 5).

From a few random checks in other parts of the Harbour, these readings appear to be characteristic. They re-emphasise the occurrence of dense surface muds created in the presence of *Spartina*. Such muds appear to contain low numbers of macro-invertebrates and in this they contrast with the soft muds of the

gullies and slopes where the infauna associated with *Spartina* is more similar to that of open muds.

**D. Pioneer *Spartina* areas**

In the north-west tip of Langstone Harbour (Fig. 1c, site D) is seen a smooth gently undulating mud surface with occasional patches of *Spartina* growing in the soft substrate. This appears to be a genuine modern case of re-colonisation and accretion is just commencing. Local inhabitants recollect this area as one of hummocky *Spartina* growth; a dissected mature marsh akin to that described as marshland archipelago. One sole remnant of this old marsh

survives near the bund wall north of the lake on Farlington Marshes.

Little seems to be known of the methods by which *Spartina* initially colonizes bare mud, but the patches of *Spartina* here are probably derived from plants which grew on the face of dissected mature marsh, as seen in about one sixth of the mounds by Langstone village. The plants colonising both the mud and the littoral shingle appear to be hybrids with considerable variation between plants in the viability of their pollen and in the percentage of pollen of aberrant shape.

**E. Dead *Spartina* Marsh**

The mud banks to the west of Rod Rithe in the

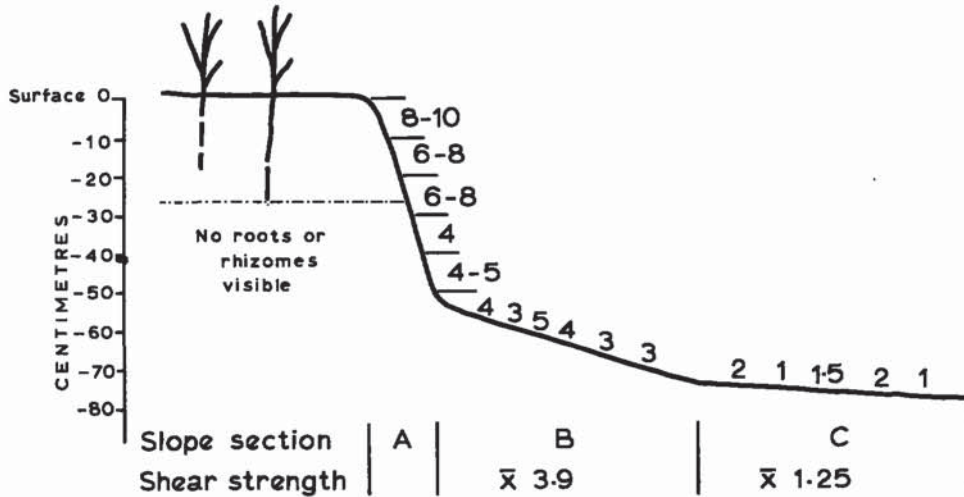


Fig. 5. Shear strengths of mud along a transect at Langstone Village (in KPa).

south-east of the Harbour (Fig. 1c, site E) present a striking contrast. This is an area of desolation, the mud not yet totally eroded below its 'mature' height but lacking any rooted vegetation and gently cratered to appear like rippled glass. In the depressions *Zostera* is common, often associated with a thin layer of silvery sand. The shear strength of the surface is 8-12 K Pa and in the depressions 5 K Pa. No *Spartina*, vigorous or otherwise, could be found in these soft muds.

**F. Channel edge marsh remnants**

Down the western side of the Harbour

elevated stands of *Spartina* occur as narrow strips lying adjacent to the main channels and separated from the coast by wide stretches of low-lying mudlands over which secondary colonisation is occasionally occurring. North of Great Salterns Quay (Fig. 1c, site F) two or three old hummocks lend credence to the view that these low lying mudlands were once at least in part covered by mature *Spartina* marsh. Erosion and decay here seem to have occurred from the landward side, perhaps originating in major drainage channels such as those seen in the mature mixed marsh (Aspect A above) or in Chichester Harbour (by Mengham Rithe on

Hayling Island and Marker Point on Thorney Island).

#### *G. Littoral fringe*

All round the littoral there are patches of old *Spartina* marsh standing on the beach as small eroding hummocks at the level of high tides. Some are made up of harbour muds, some are of coarser material and on the eastern shore some are composed of the London Clay into which the *Spartina* rhizomes appear to have penetrated with facility. The erosion of these latter hummocks suggest that here the Harbour basin is itself being extended. Most of the extant *Spartina* on the littoral hummocks is dwarf (less than 25 cm). The substrate is of a tough consistency (greater than 15 K Pa and up to 100 K Pa) and occasionally small remnants of mixed marsh may represent surfaces which pre-date the spread of *Spartina*. On the western shore some of the hummocks are layered, with bands of clay and flinty shingle reflecting a complex history of accretion.

Spasmodically round the Harbour patches of tall *Spartina* (c. 40 cm) can be seen. Each clump is uniform and probably clonal and the difference in height from the hummock populations is statistically highly significant. This tall growth always occurs on the 'new' secondary surface though there is evidence of slight accretion in some cases. Since elsewhere in the Harbour vigorous *Spartina* is only found in sloppy mud a causal relationship between such mud and vigour has to be abandoned when equal success is achieved on the littoral in both sand and shingle almost beyond the limit of tidal influence.

By the Sports Ground on Eastern Road a particularly complex mozaic of vegetation is present with a population of tall *Spartina* (44 cm  $\pm$  2.3) juxtaposed against short *Spartina* (26.0 cm  $\pm$  2.0) on shingle. All experience the same degree of tidal inundation, the muds are comparable in shear strength and the three areas have similar interstitial salinities (50% of seawater two hours after high tide on a dry cloudy day).

#### 5. SPARTINA MARSH IN THE PAST

Present observations make possible a specu-

lative description of the past and the maps can be used as indicators of the probable accuracy of the speculation.

Initial colonisation by *Spartina* appears to have occurred on low open mudlands above low water neaps. Without the stability provided by the plants the topography would have been gently undulating like that near Farlington at the present. Very rapid rates of accretion can occur, and this coupled with the vegetative spread of *Spartina* onto the higher muds would have resulted in much of the intertidal zone having become dominated by *Spartina* and having formed the 'mature' marsh. This marsh would have a gentle slope seaward (Aspect B and examples in Chichester and Pagham Harbours).

How much of the intertidal area would have been subject to a rise in mud level as a consequence of accretion is debatable. In this connection it is worth noting that a well defined low level marsh seems to be a fairly constant feature of *Spartina* localities and Odum (1969) in his discussion of the system as a 'pulse stabilised climax' is referring to an equilibrium state maintained by the constant pulse of energy and nutrient provided by the tide rather than the growth, degeneration and regrowth of marsh.

Perraton (1953) suggested that the clifflet at the outer edge of the marsh marked the ecological limit of the species but this was hardly applicable in view of his observation that *Spartina* colonises low lying muds. An accretion rate which leads to the development of a vertical clifflet of up to a metre in height is hardly feasible in view of the erosive action of waves. Clifflets are more credibly a sign of erosion and retreat, a process which must have started when Perraton did his work in the late 1940's.

During the field survey of the Harbour in 1973 to 1975 a particularly remote small islet of moribund *Spartina* (c. 1 metre high and 1 metre wide) was noticed on the east of the Harbour. It was separated by at least 100 metres of low lying mud from the nearest strand of *Spartina*. This isolated unit persisted throughout the three years of the study and bore witness to a remarkable capacity of the islets to resist erosion and highlighted the quantity of sediment which had

been removed.

Such outliers are reminiscent of the isolated hills that can be left as a scarp recedes. In geomorphology such residual surfaces are used as guides to the reconstruction of past landforms and levels. Such islets, taken in conjunction with the cliffed remnants of the littoral fringes would, even in 1980, suggest the earlier existence of considerable areas of mature marsh.

In Figs. 1d to 2d a portion of the survey maps east of Rod Rithe has been presented on an enlarged scale so that detailed comparison is possible.

If one accepts the evidence of old Admiralty charts that the major drainage pattern has changed little over many years then a generalised contour round the isolated *Spartina* remnants of 1980 (nearly all cliffed outliers in this area) (Fig. 1d) would provide a conservative estimate of the marsh shown in 1975 (Fig. 2a). Each move back in time reveals a larger mass of marsh with fringing outliers. This backward extrapolation of marsh area does not seem to have reached its full extent even in the earliest detailed survey we possess (1946). The littoral fringe almost absent in 1980 (Fig. 1d) is both continuous and obvious in Fig. 2b and the area of low lying muds between the main marsh and the littoral fringe of *Spartina* is smaller. The maps for 1956 (Fig. 2c) and 1946 (Fig. 2d) reduce this low lying mud to little more than a channel, comparable to that described separating mature marsh from the littoral in section 4A. The dotted lines in the 1946 map represent areas that do not carry *Spartina* but appear to have a different texture from that of the open muds. It could be that the photographs are discriminating between slumped marsh edge and undisturbed mud (zones B and C of Fig. 5).

Applying this backward extrapolation to 1947 on the generalised maps of the whole Harbour (Fig. 1, a and b) suggests that most of the present open mudlands were once marsh even in the south-west. Confirmation of this is provided by the single oblique photograph of 1938. The quality as well as the angle make interpretation difficult but a small 'cliff' line fringes the marsh and to seaward the muds seem to carry quantities of vegetation, perhaps algal, perhaps

*Spartina* litter, for formidable quantities must have been contributed by such a large stand of vegetation (Odum 1973; Reimold 1974). The distribution of marsh conjectured from the photograph is included in Fig. 1a.

At the present day the pioneering *Spartina* plants are rooted in soft muds, although at some stage of the development of mature marsh the surface layer becomes compact. In all cases which have been investigated the compact zone is the uppermost surface and the crust forms a relatively shallow layer (c. 10 cm). No buried surfaces of this nature have been discovered so far. It is suggested that the change is brought about during a period with little accretion perhaps because the supply of silt has run out. This could be because the system contains no more silt or because the tidal flow over the elevated and gently inclined flats would only occur at high tides. The processes which might lead to the formation of a crust during the postulated still-stand have not yet been elucidated.

Once the process of accretion ceases marginal erosion is inevitable. Small clifflets are visible in all the aerial photographs. Often erosion is preceded by the die-back of the peripheral *Spartina*. In Figs. 1d-2d the breakdown seems to be initiated at the periphery and then later there is decay within the stands.

In many cases within the Harbour the mid marsh area between the littoral and the outer beds seem to have been destroyed first. It is interesting that a number of these relatively recent zones of low lying mud have been the favoured sites for the recent spread of *Zostera*. The plants also colonise the reticulate meshwork of mud in some areas of eroding marsh. The general fall in mud levels following erosion must have created competition free sites for the eel grass at the tidal height it favours.

For the thirty years preceeding 1970 erosion seems to have been gradual and almost unnoticed, though our backward extrapolation suggests large areas of former marsh were vanishing. Since 1970 all remaining areas of *Spartina* in the Harbour have been affected and the impression of change has intensified. Only in the north-west of the Harbour are there clear signs of recolonization successful both at Far-

lington and by Langstone Village where there are vigorous plants from which future spread might be anticipated. The means by which *Spartina* spreads is now being studied.

## 6. SPARTINA AND THE FUTURE ECOSYSTEM

If the dominant role of *Spartina* is over, what might be the consequences?

*Spartina* has been variously recorded as:

1. Colonising low lying, sloppy mud and creating conditions in which rapid accretion can occur,
2. Forming a monoclimate, in which it is the only species of vascular plant,
3. Ranging from vigorous, low level marsh to dwarf, high level marsh,
4. Being the most productive of the various constituents of the flora and providing the bulk of the detritus whose export from the system indirectly supplies the food on which productive inshore fisheries depend,
5. Providing protection from the fetch of the waves,
6. Having, associated with it, a richer benthic flora than is found on open mud,
7. Providing firmer substrates which are usually aerated near the surface to a greater extent than open mud because the plants transport oxygen through their tissues,
8. Providing consolidated mud which is less aerated than open mud because the sediments are finer and the pore spaces less.

Observations in Langstone suggest that

- a. Areas of mature *Spartina* carry a less abundant macrofauna than does open mud and much less than sediments below *Zostera*.
- b. *Spartina* is responsible for less transmission of nutrients from sediment to water than *Zostera*.
- c. It has a far smaller range of epifauna than does *Zostera* and is less favourable as a breeding ground and habitat for fish than *Zostera*. It has more epifauna than does bare mud.
- d. It is not frequented by feeding waders and wildfowl as much as the open mud whereas *Zostera* is recorded as being a favoured habitat for wildfowl.

e. Birds use the high level marsh as a roost and its disappearance may make mainland roosting sites of greater importance.

f. Deep algal mats are not associated with *Spartina*, but occur within marshland archipelagos and on open muds once covered by *Spartina*. Such algal mats have a larger biomass of macro-invertebrates than open muds but are avoided by feeding birds.

In Langstone *Spartina* has formed a monoclimate but it has almost ceased to colonise and there is no low level marsh. Die-back coupled with the failure of mixed marsh could well increase fetch and hence increase coastal erosion. Maximum productivity has passed from *Spartina* to green seaweeds and *Zostera*, and it is probable that the biomass of these materials is as great as that which was derived from *Spartina*. The importance of the benthic flora is under investigation but it appears likely that in the rather eutrophic state of the Harbour the bare mud will be found to carry as rich a flora as that between vigorous *Spartina* shoots and more than in the crust of mature *Spartina* marsh. If the observations are correct then the replacement of *Spartina* by *Zostera* (which also maintains a more aerated substrate) would be an advantage if biological diversity were the criterion in the Harbour.

It must not be taken that we are forecasting the demise of *Spartina* as an intertidal constituent of the Harbour vegetation but its continued absence from areas which formerly it dominated certainly suggests that re-colonisation is taking far longer than was required for *Spartina* first to spread over the muds. It may indicate the onset of a period in which the Harbour will lack a continuous *Spartina* cover such as it once had. The original spread took about 20–30 years. If there is a cycle of build up, break down and renewed growth, its periodicity is likely to vary according to location and the result of renewed growth would eventually be a mosaic of stands of different ages representing different stages of development.

About the fate of the sediments only speculation is possible. One wonders whether the general level of the mudlands will fall if no plants of the higher marsh flourish in the system. Such a fall could have repercussions on the feeding be-

haviour of waders and wildfowl constrained to a shorter period of feeding. In the few coastal areas studied with sufficient intensity and equipment it has been found that accretion and erosion depend on local inshore patterns of water movement that are to a great extent independent of each other. This appears to be the case for the eastern Solent coastline (Harlow 1979) and thus it seems feasible that the sediments circulated by the tide in the Langstone Harbour system are not an infinite resource but finite. The limit of marsh growth may have been set by the availability of sediment and a decrease in its supply may have in some way initiated the breakdown of the marsh.

On the other hand it has been claimed that the southern coast of Britain is gradually sinking at a rate which would permit a very considerable accretion of sediments in the Solent harbours without any noticeable change in mud level (1 mm a year).

The fine sediments of the Harbour have been shown to be more stable than fine sands in response to certain types of tidal action. It is suspected that, as in the muds of the Wash, mucilage associated with diatoms and bacteria is acting as a binding agent (Coles 1979). It could be that the bare mud surfaces of Langstone are more productive and stable than has been suspected and, though the mud does persist at the high level it can attain when stabilized by marsh, the bare mud now occupying so much of the Harbour represents a new equilibrium compatible with the present vegetation of the Harbour.

Certainly, the ecosystem of Langstone has changed in the past. This century has seen not only the rise and fall of *Spartina* and the collapse and spread of *Zostera* as apparently 'natural' phenomena; but also the increase of green seaweed and the advent of *Sargassum muticum* as fortuitous results of man's activities.

Lasserns (1979) has reported on enclosed coastal waters. Langstone falls into his category of open lagoon where the sea waters are still important to the nearly closed system. He suggests that two types of ecosystem prevail. The first consists of a stable climax, presumably comparable to Odum's pulse stabilised system, whereas the second type, to which Langstone undoubtedly belongs, undergoes natural or man made perturbations. To promote the understanding of such systems he advocates an holistic approach—studies in the dynamics of natural production, in energy transformations and in the adaptation of indigenous and immigrant populations.

At Portsmouth we have been trying this approach for some years, during which time the ecosystem is changing more rapidly than we can study it. Despite over ten years of varied field study and the scrutiny of pertinent literature published about similar coastal areas in the British Isles and in other parts of the world, the multiplicity and complexity of the factors involved makes forecasting the future of our local harbours more tentative than could be desired. At least in the maps which accompany this paper we have a concrete if inexplicable record of one of the major changes which has taken place.

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