Chapter 6

Discussion
6.1 Discussion

The research presented in this thesis has examined the phenomenon of salt marsh development in the Dee estuary, using approaches that encompass studies at both large and small spatial scales. Aerial photographs and multispectral remote sensing data have been used successfully to investigate large-scale spatial and temporal patterns associated with the colonisation and development of salt marsh. At a much smaller spatial scale, the environmental factors associated with the tidal regime have been experimentally shown to affect the growth and interactions between *Spartina anglica* and *Puccinellia maritima*.

In this final chapter, the key conclusions derived from the large and small-scale studies will initially be briefly reviewed, in order to provide an overview of the four preceding chapters. The next section will discuss these findings in relation to the scale of the respective studies, in an attempt to integrate the information arising into a multi-scaled view of the ecological study of salt marsh development. Finally, the implications of this study for management of the Dee estuary, particularly with respect to *S. anglica*, and the potential for future research arising from this investigation will be discussed.

6.2 Large-scale temporal and spatial variation in salt marsh vegetation

Analysis of aerial photographs dating back to 1955 revealed several key points of interest relating to the development of salt marsh in the estuary at a large temporal scale. The pattern of colonisation and development in two important areas of the estuary exhibited marked differences, related to the geographical location of the area in the context of the entire estuary.

At the apex of the current marsh, close to the English shore, salt marsh has colonised the whole of the area within the period since 1955. Initially, up to approximately 1975, this colonisation process was rapid, pioneer marsh spreading along the shoreline. Since then, however, the pattern of colonisation by pioneer marsh has changed with only a slight increase in the salt marsh further along the
shore, and with an expansion of the marsh out into the estuary, giving the appearance of a broader and blunter marsh apex. Furthermore, this change in colonisation was echoed by an accompanying change in the pattern of zonation in the marsh. Initial expansion by pioneer zone species was followed by consolidation of the marsh, between 1975 and 1997. These changes resulted in the pioneer zone being squeezed into a relatively narrow band of vegetation around the rest of the salt marsh.

In the second area studied, comprising a cross-section of the marsh elevation gradient from mudflat to high marsh zone, the pattern of colonisation derived from the sequence of aerial photographs was relatively consistent. A similar rate of expansion was determined in terms of both the area of salt marsh and the distance colonised from the sea wall in the period up to 1975 and subsequently up to 1997. In this area however, while the rate of expansion remained consistent across the sequence of photographs, the pattern of colonisation appears to have changed. A pioneer zone dominated by visible individual clumps of *S. anglica* in the 1960s and 1970s was at least partially replaced by a community co-dominated by *Salicornia europaea* in 1997.

The use of multispectral remote sensing data from the 1997 survey to map the spatial distribution of salt marsh vegetation for the whole of the area of salt marsh, provided further information pertaining to large scale patterns of salt marsh development. For example, the distribution of pioneer vegetation supports the suggestion that the marsh is reaching its current natural limits of expansion at the apex close to the English shore. A narrow band of pioneer zone in this area relative to the more southerly areas of marsh indicates that the marsh gradient is being steepened and occurs over a shorter distance. In areas of salt marsh at the southern end of the estuary, however the pioneer zone forms a broader band that indicates a shallower elevational gradient. Analysis of the Airborne Thematic Mapper data also enabled interpretation of the distribution of other zones of the marsh, such as the relative distribution of mid and high marsh zones.
6.3 Abiotic and biotic effects on *Spartina* and *Puccinellia*

In Chapters 4 and 5, ecological processes involved in the development of salt marsh were examined by investigating the effects of environmental factors associated with the tidal elevational gradient on the performance and interactions between *S. anglica* and *P. maritima*. The study of these species is particularly appropriate in relation to salt marsh development in the Dee estuary as they are dominant species of marsh zones at low and mid marsh elevation respectively. By experimentally investigating the relative effects of abiotic and biotic factors on these two species, it has been possible to analyse the processes underlying the development of salt marsh vegetation from pioneer to mid marsh communities.

In both experiments, environmental factors, manipulated in an attempt to reflect ambient marsh conditions, were found to affect the performance of the two species, with, for example, nutrient addition causing an increase in biomass of both species. Of particular interest, however, is the importance of the interspecific interactions between these species in relation to the abiotic conditions.

In both experiments *P. maritima* exerted a generally one-way competitive effect over *S. anglica*, the intensity of which varied according to the environmental conditions. The intensity of this interspecific competition was increased in environmental conditions favourable to the growth of *P. maritima*, with reduced or no significant competition in less favourable conditions. Other plant interactions were also detected in these experiments. Intraspecific competition also occurred in both species in both experiments, with the increased intensity in environmental conditions favouring the growth of the respective species, and less intense competition in less favourable conditions.

A second major finding of these experiments is that the asymmetric competitive effect of *P. maritima* on *S. anglica* also varied in intensity depending on whether the interaction was measured above or below-ground. In both experiments, competition intensity was higher above than below-ground. This suggests that the principal site of competition is above-ground and that this effect is conveyed below-ground as a less intense interaction. However, in both experiments, *S. anglica* exhibited a disproportionate below-ground response to above ground competition in conditions less favourable to the growth of *P. maritima*. In the first experiment, *S.
*anglica* below-ground biomass increased in response to less intense competition, while in the second, there was a disproportionate reduction in the interspecific competition. A corresponding increase in the number of rhizomes has resulted in this being interpreted as a potential mechanism by which *S. anglica* may be able to evade competitive neighbours at lower marsh elevations. At higher elevations, where the abiotic conditions favour the growth of neighbours, the high intensity of interspecific competition is also conferred upon the below ground biomass.

These experiments, therefore, present a potential mechanism by which *P. maritima* may be able to competitively replace *S. anglica* as the marsh elevation increases.

### 6.4 Integrating large and small-scale studies

The concept of scale is intrinsic to the approaches needed to address most ecological problems, and it needs to be considered if potentially important patterns and interpretations are not to be obscured (Blackburn & Gaston, 1998). Its importance has been related to the ability with which small-scale mechanistic processes can be scaled upwards to address large-scale issues and vice versa. It has been suggested that the complexity and attendant spatial complications inherent in addressing ecological problems is better approached using a multi-scaled view of the problem (Bissonette, 1997). In this thesis, the colonisation and development of salt marsh in the Dee estuary is examined at two contrasting scales of study, in order to combine a large-scale view with mechanistic small-scale information regarding the ecological patterns and processes involved.

The large-scale studies described here, provide important information regarding the long-term patterns of colonisation and development of salt marsh within the estuary. Additionally, it has been possible to establish a framework for objectively mapping salt marsh vegetation in the estuary at a spatial extent and detail that has hitherto not been possible.

The findings of these studies support previous studies in the Dee estuary, that identified *S. anglica* as being influential in the dramatic expansion of marsh in the estuary, particularly in the 1960s and 1970s (Marker, 1967; Hill, 1987). They also
provide evidence to corroborate previously anecdotal reports that the importance of *S. anglica* as a coloniser of mudflats was in decline (Hill, 1990). This decline may be an indication that *S. anglica* is entering a phase of ‘die-back’ as has been well documented along the south coast (Goodman *et al.*, 1959; Charman, 1990). However, the apparent decline may be a knock-on effect of the squeezing of the pioneer marsh into a narrower band of vegetation. The emergence of *Salicornia europaea*, however, in the pioneer zone of Area 2 for example (see Chapter 2), indicates that salt marsh colonisation is continuing, with *S. anglica* still present as a co-dominant species. An alternative explanation may be that the conditions for a successful expansion only rarely occur, and that given the appropriate sediment and climatic conditions seedling establishment may occur again.

Such a burst in population of *S. anglica* has been described in the nearby Conwy estuary (Gray *et al.*, 1990) and Morecambe Bay (Gray *et al.*, 1991). The causal factors for such sporadic expansions remain unclear, but are thought to require suitable sediment conditions for seedling establishment, combined with suitable climatic conditions (thought to be temperature and humidity (Gray *et al.*, 1991)) required to overcome a genetic self-incompatibility system. The temporal pattern of colonisation observed from these large-scale studies suggests that rapid expansion of salt marsh in the Dee estuary in the 1960s can be attributed to a sudden burst of population growth of *S. anglica* clumps. A change in sediment deposition towards a muddier regime has been suggested as responsible in Morecambe Bay. However, the aerial photographs from 1965 indicate that *S. anglica* was colonising light coloured sediment, indicative of sandy rather than silt or clay substrates. In the Dee estuary, therefore, the expansion may be due to an unusually successful period of seedling production, germination and establishment (Gray *et al.*, 1991). It is difficult to establish causal mechanisms using a retrogressive analysis, such as performed here. However, the questions arising from such work may warrant further investigation. For example, a finer resolution temporal analysis may reveal more information about the pattern of colonisation, providing the aerial photographs are available. Alternatively, an explanation for the expansion of *S. anglica*, and potentially other changes in patterns of development may be distinguished by stratigraphic methods where physical or chemical sediment properties may be correlated with changes in the salt marsh vegetation.
The use of remotely sensed data, therefore, illustrates the ability to interpret temporal change in spatial distribution at a relatively coarse scale through the use of aerial photographs. The emergence of multispectral technology, in the form of airborne scanners, has enabled changes at much finer spatial resolutions to be investigated. The use of ATM data to classify the vegetation from the whole marsh is an example of maintaining a large-scale study in terms of the extent of marsh, but allows a fine resolution in the definition of vegetation to be achieved. Previous surveys have been limited to estimates of distribution of salt marsh, based on surveys of sections, or very rarely, the entire salt marsh. These have involved subjective analyses of aerial photographs (Hill, 1987), or the construction of sketch maps from field observations from which estimates of area occupied by species have been made (Burd, 1989). The figure obtained for the current marsh, whilst still possessing subjective elements, represents the first estimate of the area of salt marsh using a methodology that is predominantly objective.

The use of ATM data has a number of advantages for describing the spatial distribution of vegetation in the salt marsh. For example, the extent of the area covered and the resolution obtained by the scan enabled the entire marsh to be sensed at a scale that was appropriate to the vegetation characteristics at the community level. Most attempts to derive ecologically useful information from intertidal areas have used broad band spectral data from satellites such as Landsat. These data have been applied to sediments (Yates et al., 1996), suspended materials (Baban, 1997) and extensively in salt marsh vegetation (e.g. Bartlett & Klemas, 1982; Hardisky et al., 1984; Gross et al., 1988). However, it is only with the higher spectral and spatial resolution of airborne sensors such as the ATM and CASI that the potential for detailed land cover mapping, as demonstrated here, arises (Thomson et al., 1998c).

The use of remote sensing technology, as shown in Chapters 2 and 3, is particularly applicable for describing large-scale patterns, and increasingly so for processes at a finer spatial and temporal scale. The potential for future reductions in scale of study, remains. For example, the CASI sensor, although unsuccessful in obtaining valuable data in this study, has the advantage of being versatile in the choice of spectral band selection. Thus, by manipulating the wavelengths that are specifically recorded, in conjunction with being able to manipulate the pixel size of the area of ground that is surveyed, extremely specific surveys can be designed.
The remote sensing studies described here share many of the characteristics of large scale studies, such as being inappropriate for replicated or controlled manipulations, possessing a high degree of qualitatively, and being oriented by the pattern rather than process (Wiens, 1989). In contrast, small-scale studies, characteristically have the potential for replication and experimental manipulation, are quantitative and are oriented to mechanistic modelling of the processes under investigation. The experiments in Chapters 4 and 5, dealing with effects of abiotic and biotic factors on S. anglica and P. maritima, represent examples of such studies.

The findings of these experiments, as summarised above, suggest a potential mechanism by which P. maritima can competitively replace S. anglica as the elevation of the marsh increases. Therefore by providing empirical evidence describing the mechanistic, ecological processes at the scale of the individual plant in controlled experiments, it has been possible to explain the processes involved in the successional development across one section of the marsh elevation gradient. This reflects a degree of scaling up from the level of the individual plant to the level of the marsh community.

Scaling up from small-scale studies, in a 'bottom-up' manner (Bissonette, 1997), is not necessarily a complementary approach to one involving 'top-down' explanations, where the starting from two ends of the spatial scale results in studies meeting in some common ground. In these studies, acknowledging the varying role of scale in the colonisation and development of salt marsh in the Dee estuary, has led to a holistic view of the ecological problem and has provided valuable information, from both approaches, on the ecological patterns and processes involved. Inherent, within these studies, particularly those that specifically focus on the element of temporal scale, is the premise that the current ecological status is the culmination of past ecological patterns of colonisation and development. Consequently, this premise can be extended to consider the future course of such changes. In the context of salt marsh development, these have major implications for the management of coastal environments and the strategies designed to maintain their sustainability.
6.5 Implications for management

The spread of *S. anglica*, by natural and anthropogenic means, has led it to be one of the most important management issues affecting salt marshes and subsequently the whole coastal zone. In the Dee estuary, the role of *S. anglica* as a catalyst in the colonisation of mudflats has caused it to be a priority for research and monitoring as part of the Dee Estuary Strategy (Jemmett, 1996). The findings of the studies presented in this thesis have implications for future management of *S. anglica*, as well as general development of salt marsh vegetation in the estuary.

Whilst the colonising role of mudflats played by *S. anglica* can be viewed as both beneficial and harmful, depending on the management objective of the specific coastal area, it is generally considered to be deleterious in areas of high nature conservation interest (Doody, 1990). In the Dee estuary, the anthropogenic origin of the species and its documented role in accelerating salt marsh development in the 1950s and 1960s have ensured the high management profile of the species: research and monitoring of the species has been identified as a priority in the Dee Estuary Strategy (Jemmett, 1996). These studies confirm anecdotal evidence (Hill, 1987; C. Wells, pers. comm.) that the colonising role of *S. anglica* is less influential in the current colonisation process. The reduction in expansion rate at the marsh apex and the prevalence of *Salicornia europaea* in the pioneer zone indicates the reduced importance of *S. anglica*. The large areas of monospecific *S. anglica* sward, that once occupied much of the lower marsh elevations in the Dee (Hill, 1987), are much reduced, and in most areas *S. anglica* exists as part of a mixed community with at least one other species. *S. anglica* swards have been controlled successfully using chemical methods (e.g. Taylor, 1965) and more recently using mechanical methods (Frid et al., 1999). However, control of *S. anglica* in the Dee is probably not a current practical or worthwhile course of action, given the area occupied, the potential impacts on the natural resources, including natural processes of vegetation change, the conservation of which are a guiding principle of the Dee Estuary Strategy (Jemmett, 1996). While current control measures may be unnecessary, continued monitoring is essential to ensure detection of future changes to the population. For example, if conditions suitable for a widespread establishment of *S.
anglica seedlings arose, control measures may be needed to prevent rapid marsh expansion.

The current S. anglica population in the Dee estuary, despite originating from anthropogenic introduction, can in many respects be regarded as an inextricable component of the overall salt marsh habitat. While the rate of salt marsh colonisation and development has undoubtedly been affected by the presence of S. anglica, the current area occupied by salt marsh represents the culmination of centuries of human impact in the estuary (Marker, 1967). One benefit of large-scale studies such as these is that changes at the level of the whole estuary can be taken into account. The spatial distribution of salt marsh within the estuary, for example, suggests that physiographic factors may be the overriding force in the development process. These studies suggest that the apex of the marsh on the English shore may be approaching its natural limits, with an equilibrium being reached between new colonisation and tidal erosion. Furthermore, the gradual widening of the marsh from the apex to the River Dee training wall, where the marsh spans nearly the whole width of the estuary, indicates that the reduction in power and dynamic nature of currents in the estuary may be the significant force in salt marsh development in the estuary. Should the colonisation and development of salt marsh continue in the 21st century, a more effective long-term solution, although potentially controversial, would be to advocate the partial demolition of the training wall.

A further management issue that arises from these studies is applicable to management of salt marshes at a much broader scale. The radiometric survey provided important information that allowed interpretation of the reflectance data obtained from the ATM survey. These data and their interpretation have important implications for the way in which salt marsh vegetation is classified and monitored for management purposes. The key finding of these studies is that the vegetation was classified on the basis of the amount of vegetation, which in turn can be related to the marsh zone, and also the moisture present in the respective land cover type. Of particular significance is that within species variation in reflectance data was often greater than that between species, indicating that species composition of marsh communities is difficult to resolve using remote sensing data. This has management implications in the applicability of relating such remote sensing surveys with species based classifications such as the National Vegetation Classification (Rodwell, 2000). The highly localised nature of the many British salt marshes and the deterministic
role of physiographic factors related to the tidal regime on vegetation patterns have been identified as limitations in such classifications. Further research aimed at directly relating multispectral data to the NVC and improvements in remote sensing technology may resolve these apparent discrepancies.

Colonisation and development of salt marsh is a complex, dynamic process that requires analysis from large and small, spatial and temporal scales if it is to be fully understood. In the Dee estuary, its continued development requires further monitoring, but if viewed at a large time scale in the context of predicted rises in sea level, the current extent of salt marsh in the estuary, may prove beneficial as a coastal defence. As coastal defences in low-lying areas become prone to higher storm tides, future residents of the area may be grateful for the natural barrier that the salt marsh creates.