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Managing the Retreat: Understanding the transition to salt marsh in coastal realignment projects

White, Anissia

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Plymouth University

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**MANAGING THE RETREAT: UNDERSTANDING
THE TRANSITION TO SALT MARSH IN COASTAL
REALIGNMENT PROJECTS**

by

ANISSIA WHITE

A thesis submitted to Plymouth University in partial fulfilment
for the degree of

DOCTOR OF PHILOSOPHY

School of Biological Sciences
Faculty of Science and Technology
Plymouth University

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ABSTRACT

Managing the retreat: Understanding the transition to salt marsh in coastal realignment projects

Anissia White

Managed realignment is now widely seen as an important part of coastal management strategy, as an environmentally sustainable, cost-effective alternative to traditional, hard defences. However, the trajectory of salt marsh development in managed realignment schemes remains uncertain and it is unclear how sites should be managed to fulfil both coastal defence and biodiversity objectives.

In this study, the overarching aim is to find out ways in which we can create salt marshes that are self-sustaining and function as closely to natural ecosystems as possible, by considering the linked biogeomorphological processes in salt marsh ecosystems. Such an approach will improve predictions of habitat development and recommendations for future practice in managed realignment schemes.

The first important question is: How do pre-alignment plant species growing within managed realignment sites respond to salt water inundation upon re-exposure to flooding? Understanding the responses of the terrestrial vegetation community to initial seawater flooding may improve predictions of the short-term transition into salt marsh vegetation. To answer this, the effects of seawater inundation on pre-existing vegetation are initially examined in a greenhouse experiment in Chapter 3. It was demonstrated that one common plant species component of many coastal grasslands, *Trifolium repens*, responds poorly to simulated seawater soil flooding, but the response is population-, i.e. ecotype-, specific; therefore, the species consequently has an adaptive capacity to

withstand short periods of soil inundation by seawater. In addition, I look at how and why the vegetation community of a restored site transitions following the reintroduction of tidal water, including the response of the original community of non-salt marsh plant species to salt water inundation and subsequent salt marsh plant community reassembly. After three years of tidal inundation at South Efford managed realignment site (SEM), terrestrial vegetation had decreased in cover and nearly all species recorded on the adjacent natural marsh had colonised. However, the cover of salt marsh species was limited by waterlogging, caused by modifications to the tidal regime by a self-regulating tidal gate.

This leads on to the second question: How do new engineering techniques alter the tidal regime and what specific aspects of the new regime drive plant community reassembly and sedimentation patterns? In Chapters 4, 5 and 6, three years of ecological and geomorphological development are investigated in response to a variable inundation regime imposed by regulated tidal exchange at SEM. Inundation of the marsh surface was very regular, but water levels were not deep enough to encourage sufficient morphological development, sedimentation nor hydrochory. In contrast, ecological development was limited by waterlogging. Balancing the tidal regime with the drainage efficiency of managed realignment sites may be the most likely scenario under which restored salt marsh will develop with maximum biodiversity benefits. Otherwise, further management techniques, such as the excavation of tidal channels, may need to be employed to improve site drainage.

Consequently, the final question is: How can biodiversity be maximized on realignment sites through the use of different management techniques and site design? Tidal channels on a range of managed and natural sites were shown to improve the drainage efficiency of adjacent soils (particularly channels of greater width and/or higher Strahler

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AUTHOR'S DECLARATION

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Graduate Committee.

Work submitted for this research degree at the Plymouth University has not formed part of any other degree either at Plymouth University or at another establishment

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Publications:

- White, A.C., Colmer, T.D., Cawthray, G.R., Hanley, M.E., 2014. Variable response of three *Trifolium repens* ecotypes to soil flooding by seawater. *Annals of Botany* 114, 347-355 (**Chapter 3**).
- Hoggart, S.P.G., Hanley, M.E., Parker, D.J., Simmonds, D.J., Bilton, D.T., Filipova-Marinova, M., Franklin, E.L., Kotsev, I., Penning-Rowsell, E.C., Rundle, S.D., Trifonova, E., Vergiev, S., White, A. C., Thompson, R.C., 2014. The consequences of doing nothing: The effects of seawater flooding on coastal zones. *Coast. Eng.* 87, 169–182 (**Chapters 4-5**).

Conference presentations:

- White, A.C., Hanley, M.E., Masselink, G., Blake, W.H., Hoggart, S.P.G., 2012. Managing the retreat: Salt marsh development in coastal realignment projects (poster presentation). British Ecological Society Annual Meeting 2012, Birmingham University, UK.
- White, A.C., Masselink, G., Blake, W.H., Hoggart, S.P.G., Hanley, M.E., 2013. Managing the retreat: Physical and social constraints on short-term salt marsh development in coastal realignment projects. 12th International Coastal Symposium, Plymouth University, UK.
- White, A.C., Hoggart, S.P.G., Hanley, M.E., Blake, W.H., Masselink, G., 2013. A risky retreat: Fine-tuning projections of salt marsh development in managed realignment projects. The 8th International Conference on Geomorphology of the International Association of Geomorphologists (IAG/AIG), Paris, France.
- White, A.C., 2013. Compensatory habitat creation through managed realignment: Can we replace what is already lost? URBANE Final Stakeholder Workshop: “Enhancing Biodiversity in Urban Natural and Artificial Coastal Environments”, Bristol, UK.
- White, A.C., Masselink, G., Blake, W.H., Hoggart, S.P.G., Hanley, M.E., 2013. Managing the retreat: Understanding the transition to salt marsh in coastal realignment projects. ‘PHUNCH’ presentation, Plymouth University, UK.
- White, A.C., Masselink, G., Blake, W.H., Hoggart, S.P.G., Hanley, M.E., 2013. Managing the retreat: Understanding the transition to salt marsh in coastal realignment projects. Coastal Processes Research Group seminar, Plymouth University, UK.

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Chapter 1 - Introduction

1.1 Habitat restoration

For decades, attempts have been made to restore habitats that have been destroyed or degraded by human activity. Some restoration projects aim to return habitats to a precise natural or historical state, yet such a feat is increasingly recognised as a challenging, if not impossible goal.

Many modern restoration projects do not aim for natural equivalency, but instead to “recover a natural range of ecosystem composition, structure and dynamics” (Larkin et al. 2006). Therefore, the key question is: how can we improve restoration practice to achieve the latter goals? Sound habitat restoration is often hindered by a lack of understanding of holistic ecosystem functioning and a paucity of data from model case studies. Many ecosystems function as a result of multi-way environmental interactions. If the interactions and thresholds responsible for ecosystem functioning are not fully understood, then successfully restoring a habitat may prove extremely difficult. Salt marshes are particularly complex ecosystems, as their natural functioning is dependent on multiple interactions between ecological, geomorphological and chemical factors. A full picture of salt marsh functioning will only be gained when we have a complete understanding of these linkages between salt marsh processes. Information gained from a range of restoration sites (varying in degrees of success) can contribute to guidelines, which can be referred to in order to improve the practice of habitat restoration.

In this study, the overarching aim is to find out ways in which we can improve salt marsh restoration practice, by considering the linked processes in salt marsh ecosystems. Firstly, I will look at how and why the vegetation community of a restored site

transitions following the reintroduction of tidal water, including the response of the original community of non-salt marsh plant species to salt water inundation and subsequent salt marsh plant community reassembly. I will investigate the ecological and geomorphological drivers of the latter two processes and therefore speculate on how we can optimise the transition into sustainable salt marsh habitat in future restoration projects. The thesis will be synthesised by contemplating methods by which we may manipulate geomorphological aspects of the ecosystem, in order to improve overall geomorphological and ecological functioning of the restored salt marsh.

1.2 Salt marsh habitats

Salt marshes are vegetated intertidal habitats on the transition zone between land and sea. Globally, these landforms are found on temperate or high latitude coastlines, in a variety of geomorphological settings, providing low energy conditions allow fine sediments to settle out of suspension and halophytic vegetation to colonise. Salt marshes may occur in deltas, estuaries, behind barriers, on the open coast, in embayments and drowned valleys (rias). In the USA, vast salt marshes can be found in river deltas, such as the Mississippi Delta, whilst dynamic back-barrier marshes are common on the eastern coast. Salt marshes are found in a range of locations in Europe, such as in large deltas (e.g. the Ebro Delta, Spain) and even beside lagoons, such as the Venetian Lagoon in Italy. Allen (2000) describes seven different locations on the coastal fringe where salt marshes may be found in the UK (Table 1.1). Substrate may therefore vary between marsh types, but most salt marshes in the UK tend to be minerogenic, in that their accretion depends primarily on a local supply of sands and silts from neighbouring tidal flats. In the USA, organogenic salt marshes are more common, where the substrate is mainly composed of organic material from

decomposing plant litter. Such salt marshes are also found on the western coast of Ireland (Cott et al. 2013).

Type	Key features	Example
Open-coast	Sandy. Sandflats occur on exposed areas near the sea.	Thornham and Titchwell Coastal Marshes, North Norfolk
Open-coast back-barrier	Sandy-muddy. Form behind barriers where sheltered from hydrodynamic forces.	Scolt Head Island, North Norfolk
Open-embayment	Sandy. Found on edges of large embayments.	Freiston Shore, The Wash, Lincolnshire
Restricted-entrance embayment	Mixed sandy-muddy. Spits forming barriers across embayment mouth.	Morecambe Bay, north-west England
Estuary-fringing	Muddy. Open-mouthed estuaries.	Campfield Marsh, Solway Firth, Cumbria
Estuary back-barrier	Mud over sand. Behind spits closing estuary mouths	Dyfi Estuary, Ceredigion, Wales
Ria/Loch head	Muddy. Generally lower in salinity due to large fluvial influence.	Portsmouth Harbour, Hampshire

Table 1.1 - Seven main locations where salt marshes are found in the UK (based on Allen 2000).

1.3 A Simplified Biogeomorphological Model

Salt marshes are highly complex landforms with a number of sensitive links and feedbacks existing between plants and geomorphological systems (Viles et al. 2008). In Fig. 1.1, I propose a simplified model of some of these key relationships of major importance to salt marsh development. Aspects of the tidal regime (e.g. inundation frequency, duration) have a major control on the supply of sediment to a developing

marsh (Pye 1995; Boorman et al. 2001), which increases the elevation of the marsh surface once deposited. Marsh elevation, seed supply and soil redox potential (all influenced by the inundation regime) ultimately determine the composition and density of vegetation that colonises (Rand 2000; Wolters et al. 2005; Huiskes et al. 2012). In turn, vegetation development impacts geomorphological and geochemical processes in feedback loops, such as hydrodynamics and soil redox potential. These effects, however, are species and density-dependent (Leonard & Luther 1995).

Biogeomorphological systems are extremely sensitive to disturbance due to the vast array of linkages and feedbacks between processes (Townend et al. 2011). Alterations to one process can therefore have a ‘domino’ effect throughout the whole system, affecting both ecological and geomorphological processes and ultimate salt marsh development (Belluco et al. 2006; D’Alpaos 2011).

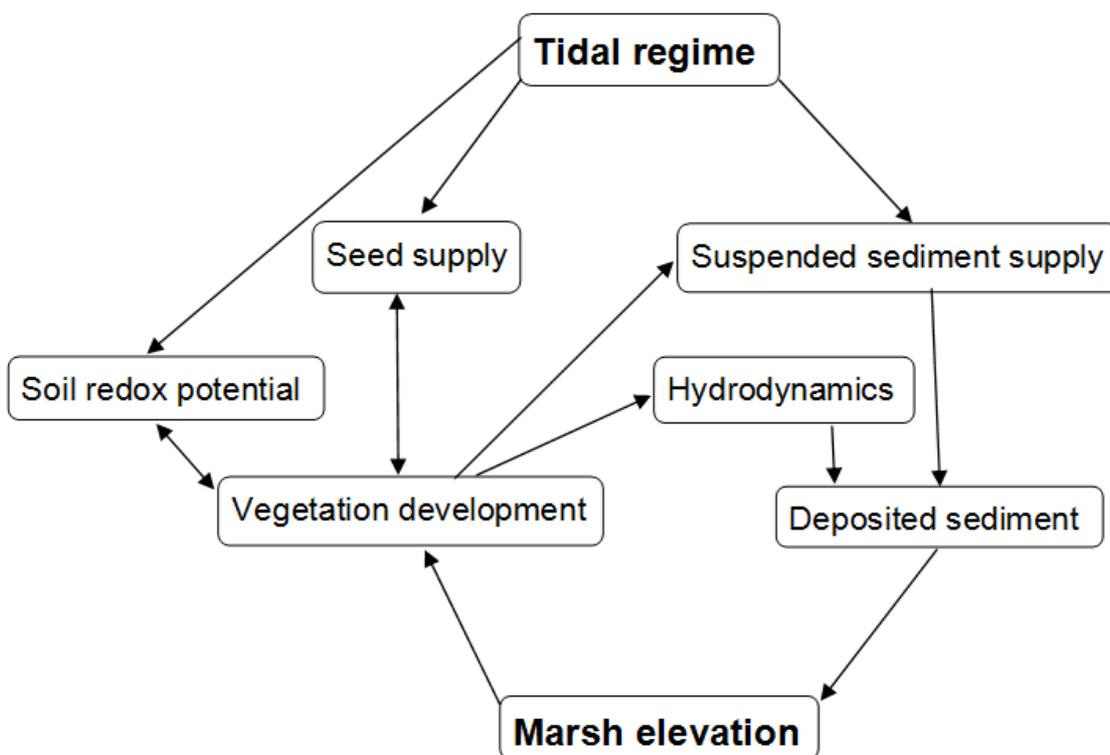


Figure 1.1 – A simplified biogeomorphological model of a salt marsh system. Marsh elevation and the tidal regime are indirectly linked via many geomorphic and ecological processes.

1.3.1 The role of geomorphology in salt marsh evolution

Adnitt et al. (2007) state that salt marshes should be considered as a part of a hierarchy of landforms. Estuaries, bays and deltas are the largest landforms in the hierarchy and salt marshes and mudflats occur along their banks. Within salt marshes, there are additional geomorphological landforms that are smaller in scale, such as salt marsh platforms and tidal channels. Tidal channels have a central role in salt marsh functioning, as they deliver sediment and seeds to the marsh platform on the flood tide, whilst water drains from the salt marsh into channels on the ebb tide. The latter function prevents marsh soils from becoming saturated.

Small-scale geomorphological features contribute to the natural topographic heterogeneity, or high spatial variation in elevation within salt marshes (Larkin et al. 2006). Topographic heterogeneity affects abiotic functioning, which ultimately determines the vertical and horizontal zonation of salt marsh vegetation (Zedler & Callaway 1999). Abiotic conditions at lower elevations in the tidal frame are harsh due to more frequent and longer saline inundations (Townend et al. 2011), which also cause lower soil oxygen concentrations and low soil redox potentials (Silvestri et al. 2005). Only halophytic pioneer species that have evolved to tolerate such harsh conditions are able to colonise these areas. Although they are relatively stress-tolerant, pioneer halophytes are generally ineffective competitors; therefore at higher elevations in the tidal frame, a greater diversity of salt marsh species that are more sensitive to saline inundation and waterlogging are able to outcompete pioneer halophytes. The upper/outer extent of salt marsh vegetation is therefore determined by interspecific competition between terrestrial species and halophytes (Allen 2000). Similarly, there

may be horizontal zonation of plant species on a salt marsh in response to spatial patterns in drainage. This is based on the adaptations of plant species to waterlogging, affected by proximity to tidal channels and sediment composition (Zedler et al. 1999; Mossman et al. 2012b).

1.3.2 The role of vegetation in salt marsh evolution

According to Reed et al. (1999), the catalyst of salt marsh development is the colonisation of vegetation. Pioneer species such as *Salicornia europaea*, *Spartina anglica* and *Suaeda maritima* are usually the first species to colonise (Reed et al. 1999; Wolters et al. 2008; Garbutt & Wolters 2008; Mossman et al. 2012a) due to their adaptations to harsh abiotic conditions. In turn, these species can facilitate the growth of less robust species that are more specifically adapted to higher salt marsh elevations (Townend et al. 2011), by stimulating marsh elevation rise and providing shelter. Further to this, Ursino et al. (2004) highlight the positive effects that pioneer plants can have on soil aeration through evapotranspiration, which can prevent the development of anoxic soils. Indeed, salt marsh pioneers have been frequently labelled as ‘ecological engineers’ (Jones et al. 1994), as without their facilitative effects, the colonisation of higher plants may be limited by harsh abiotic conditions at lower elevations (Allen 1990; Langlois et al. 2003).

Reed et al. (1999) state that elevation rise is dependent on the indirect and direct mechanisms provided by plant growth. In order for marsh elevation to rise in relation to the tidal frame, settlement of suspended inorganic and organic sediment must exceed the rate of total subsidence (Cahoon et al. 1995), which occurs due to compaction (Kaye & Barghoorn 1964). The aboveground biomass of some plants indirectly contributes to elevation rise through attenuating wave energy (Möller et al. 1999) and reducing current

velocities (Leonard & Luther 1995; Koch et al. 2009). Leonard and Luther (1995) demonstrated that on first encounter with marsh vegetation, water flow energies can be reduced by one order of magnitude and may be further reduced with increased densities of vegetation. Inorganic sediment grains transported in suspension are subsequently deposited following the reduction of flow energies (Leonard & Luther 1995; Yang et al. 2008). Plant biomass also contributes organic matter directly to the soil surface, which can be a significant constituent of the net sediment input (Cahoon et al. 1995; Day Jr et al. 1999; Belluco et al. 2006; Santín et al. 2009).

Plant roots help to bind this newly accreted sediment and aboveground biomass provides shelter, therefore inhibiting re-suspension of sediment and aiding marsh elevation rise (Friedrichs & Perry 2001). Reed et al. (1999) emphasise the value of plant roots in stabilising creek banks and therefore in the design of creek networks during salt marsh restoration. Such vegetation growth encourages sedimentation, leading to the formation of small levées bordering the creeks (Murray et al. 2008). In contrast, Vandenbruwaene et al. (2011b) demonstrated how clumps of vegetation may also be significant in the initial formation of creeks. In a large-scale flow facility, water flows were shown to accelerate between clumps of *Spartina anglica*, potentially causing the erosion of sediments and the formation of deep channels (Bouma et al. 2009).

1.4 Ecosystem services

Ecosystem services are defined as the multiple benefits provided to human society from ecosystems (Millennium Ecosystem Assessment, 2005). The Millennium Ecosystem Assessment (2005) highlighted the great global importance of ecosystem services in sustaining human life, but also revealed that such services are being lost/degraded as continued damage is being caused to ecosystems. As a result of these findings, the UK

National Ecosystem Assessment (Jones et al., 2011) was conducted in order to identify and assess the services provided by ecosystems in the UK. In this assessment, the total value of ecosystem services provided by coastal margins (of which salt marshes cover the second greatest land area after sand dunes) was stated as an estimated £48 billion. Table 1.2 shows the many provisioning, regulatory and cultural services that can be derived from salt marshes.

Service group	Ecosystem service	Example
P	Crops, plants, livestock, fish, etc. (wild and domesticated)	E.g. Meat (sheep/cattle); wild food
P	Trees, standing vegetation and peat	E.g. Turf/peat cutting
P/R	Wild species diversity, including microbes	E.g. High diversity or rare/unique plants, animals and birds, insects; nursery grounds for fish; breeding, overwintering, feeding grounds for birds
R	Climate regulation	E.g. Carbon sequestration
R	Hazard regulation – vegetation and other habitats	E.g. Sea defence
R	Waste breakdown and detoxification	E.g. Immobilisation of pollutants
R	Purification	E.g. Water filtration: surface flow
C	Environmental settings: religious/spiritual and cultural heritage and media	E.g. Sites of religious/cultural significance
C	Environmental settings: aesthetic/inspirational	E.g. Paintings; books
C	Environmental settings: recreation/tourism	E.g. Walking; fishing; birdwatching
C	Environmental settings: physical/mental health and security and freedom	E.g. Opportunities for exercise; personal space
C	Environmental settings: education/ecological knowledge	E.g. Resource for teaching; scientific study

Table 1.2 – *Ecosystem services provided by salt marshes; P = Provisioning services, R = Regulatory services, C = Cultural services (based on Jones et al., 2011).*

A valuable regulatory service provided by salt marshes is their role in coastal defence, as plant roots stabilise marsh sediments, preventing erosion (Friedrichs & Perry 2001) and aboveground plant biomass attenuates wave and tidal current velocities (Möller et al. 1999). In reference to salt marshes in Essex, UK, King and Lester (1995) even claim that as the area of salt marsh increases before a sea wall, maintenance and construction costs for the coastal defence decrease. Many other ecosystem services can also be provided by salt marshes, including plant biodiversity conservation (Lefeuvre et al. 2003), carbon sequestration (Viles et al. 2008), fish nurseries (Barbier 1994), bird breeding grounds (Mander et al. 2007) and recreational opportunities (Klein & Bateman 1998) (Table 1.2). The economic value of these ecosystem services has been increasingly recognised in recent years (Costanza et al., 1998; Millenium Ecosystem Assessment, 2005; Jones et al., 2011) and within the UK National Ecosystem Assessment it is recommended that salt marshes must be conserved and restored in order to retain these services (Jones et al. 2011).

All plant species have different functions within salt marshes (Zedler et al. 2001). For example, Bouma et al. (2005) found that species with stiff shoots dissipate hydrodynamic energies three times more efficiently than species with flexible leaves. However, other species may be more efficient at increasing soil nitrogen content (Sullivan et al. 2007) or stabilizing marsh soils with an extensive root network (Cox et al. 2003). Therefore, vegetation community composition may impact the provision of ecosystem services from salt marshes (Spencer & Harvey 2012).

1.5 Salt marshes and coastal management

Over hundreds of years, the spatial extent of salt marsh habitat has been significantly

reduced in the UK. Historically, losses were primarily a result of land reclamation, where large areas of salt marsh were drained to make them suitable for agricultural use. In addition, the British Isles are undergoing isostatic readjustment as a result of a release of pressure from the melting of glacial ice on the Scottish Highlands. This means that whilst northern parts of Britain are rising, the southern end is sinking into the sea, causing a gradual increase in sea levels. Hard coastal engineering has traditionally been employed to protect sections of vulnerable coastline from erosion and flooding in the UK. Under increasing threats of sea level rise, policy-makers have been forced to accept that there are physical and economic limits on the height and size of hard defences (King & Lester 1995; Nicholson-Cole & Riordan 2009). Additionally, hard defences prevent the adaptive inland movement salt marshes. As the seaward edge of a salt marsh is eroded by the rising tide, it may be severely reduced in width if unable to extend landward due to the barrier of a sea wall or embankment (Fig. 1.2; French 1997). Consequently, 'coastal squeeze' has severely reduced the extent of valuable salt marsh habitat along the UK coastline, exacerbating historic losses to agriculture (King & Lester 1995) and isostatic readjustment (Boorman 2003).

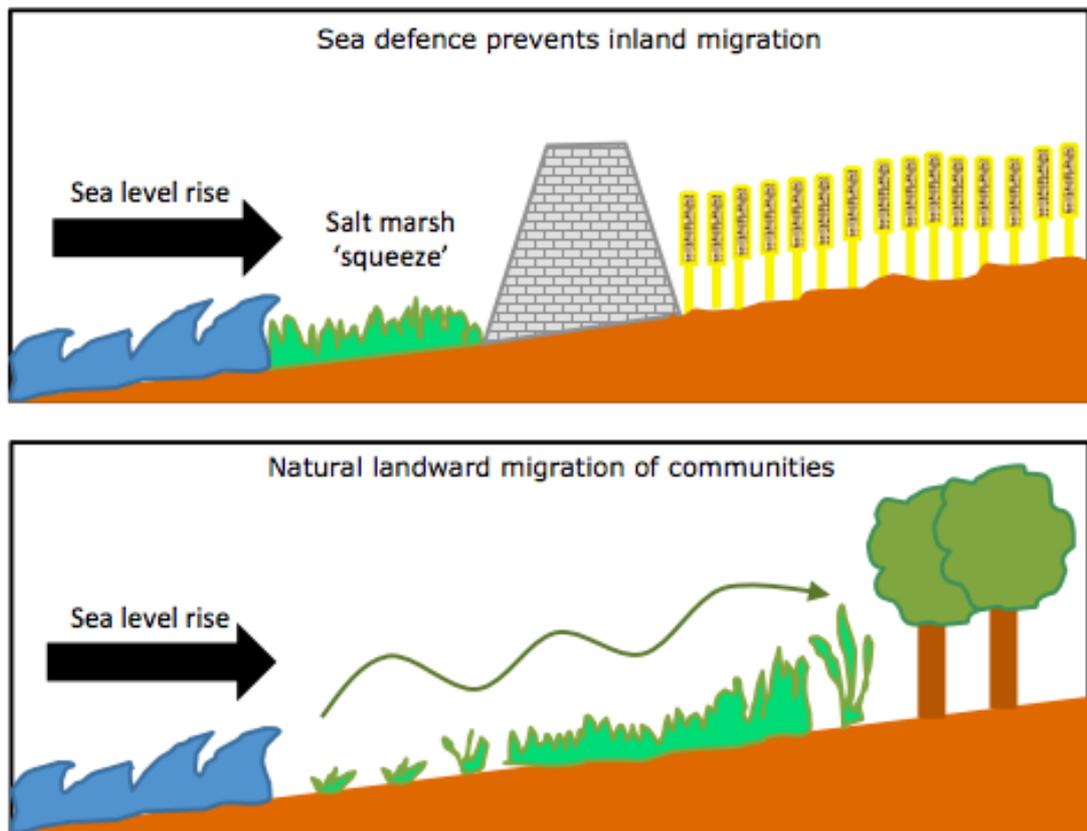


Figure 1.2 – Decreasing width of salt marsh habitat as a result of coastal squeeze (above) as opposed to natural ‘rollover’ of salt marsh habitat where no barriers are present (below).

Salt marshes are now legally protected under the European Union Habitats/Birds Directive. The directive seeks to maintain no-net-loss in total habitat area, by ensuring habitat with ‘equivalent biological characteristics’ is created in place of salt marsh lost through coastal squeeze and land reclamation. Additionally, the UK’s Biodiversity Action Plan (BAP) commits the UK Government to develop strategies to conserve and, where possible, enhance biodiversity (UK Biodiversity Group 1999). Importantly, as part of BAP, the Government has set a challenging target to create/restore at least 300 hectares of intertidal habitat (salt marsh and tidal flat) (Ridgway & Williams 2011). The development of deep-sea ports is now the main direct threat to salt marsh habitat, yet the EU Habitats/Birds Directive declares that in order for plans to proceed, the development must have Imperative Reasons of Over-riding Public Interest (IROPI) and a commitment to creating/restoring sufficient compensatory habitat. Quite often a

development is decided not to have IROPI. For example, Associated British Port proposals for a container port at Dibden Bay in Southampton Water were rejected in 2004, even though compensatory intertidal habitat had been included in the proposals. The planning inspector decided that development at Dibden Bay was not economically necessary and the proposed compensation was regarded as inadequate. Dibden Bay was regarded as the first major test case for compensation requirements in the EU Habitats/Birds Directive (Defra 2012).

1.6 Coastal realignment: the main habitat replacement option in the UK

Coastal realignment has recently come to the forefront of coastal engineering and policy as a sustainable and cheaper alternative to traditional, hard defences (French 2006). In coastal realignment, terrestrial land on the coastal fringe is flooded accidentally (e.g. storm breach) or deliberately, as defences are no longer maintained or sea walls and embankments are deliberately breached (French 2006). As sea levels rise, an increasing number of coastal realignment sites are appearing on formerly reclaimed land. In these areas, there is potential for areas of salt marsh to (re-) establish and compensate for prior losses. If successful, coastal realignment can therefore address stipulations of the EU Habitats/Birds Directive and contribute to the implementation of the UK Biodiversity Action Plan (BAP) for salt marshes, by conserving and enhancing biodiversity (UK Biodiversity Group 1999).

1.6.1 Managed realignment

Managed realignment is the deliberate or anticipated flooding of land situated behind coastal defences. There are now over 50 managed realignment sites in various coastal/estuarine locations across the UK (ABPmer Online Marine Registry 2014). Sites are mainly concentrated in the east/south east of England, as this is where most losses have occurred (see section 1.5), but also occur as far southwest as Hayle, Cornwall to as

far north as Nigg Bay on the Cromarty Firth, Scotland. Managed realignment is most commonly implemented to create new areas of intertidal habitat, in order to alleviate losses from coastal squeeze (Fig. 1.3). However, a substantial number of managed realignments are also implemented for reasons of habitat compensation (from development), improved flood defence and reduced defence costs.

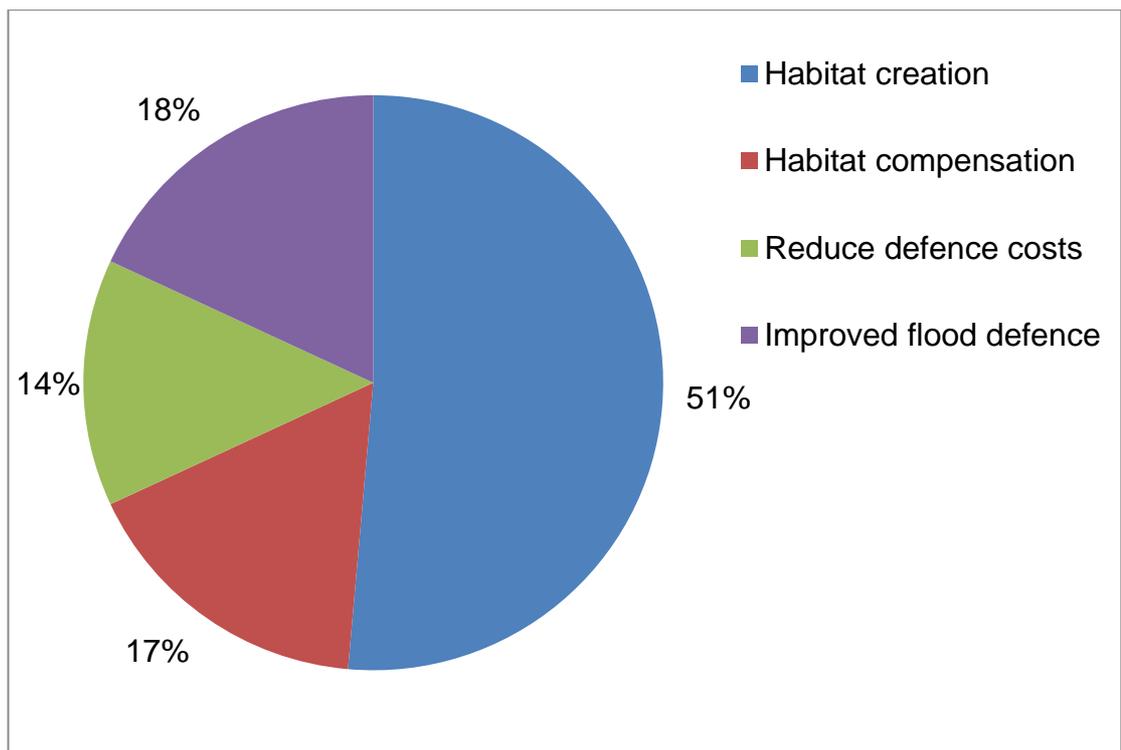


Figure 1.3 – Reasons given by site managers for the implementation of managed realignment, on 51 sites in the UK (Data source: ABPmer Online Marine Registry 2014)

1.6.1.1 Simple breach

Simple breaches are the most common form of managed realignment (ABPmer Online Marine Registry 2014). This is where machinery is used to either remove or lower a section of the pre-existing line of defence. As the remainder of the coastal defence is left in situ, the managed realignment site is generally more sheltered from prevailing estuarine hydrodynamics, which can prevent excessive erosion of the marsh surface (Crowther 2007). However, simple breaches occasionally erode rapidly and expand in

width in order to accommodate the natural tidal prism (Friess et al. 2014). Examples in the UK include Paull Holme Strays (Humber Estuary, Yorkshire) and Freiston Shore (the Wash, Lincolnshire).

1.6.1.2 Defence removal

This is where the entire defence is removed, allowing the land to become a fully integral part of the estuary. This is often used to increase the tidal prism of an estuary, which alleviates flood risk in other locations (ABPmer Online Marine Registry 2014). Defence removal is a less commonly used practice in the UK, as such sites are initially expensive and generally slow to form salt marsh habitat due to their high exposure. However, defences were entirely removed at Welwick managed realignment site (Humber Estuary, Yorkshire), in order to initiate tidal flat development (Mazik et al. 2010).

1.6.1.3 Regulated tidal exchange

A significant issue in managed realignment is that there are often differences in elevation between reclaimed land and adjacent, natural saltmarsh. This is generally caused by compaction of the land and a lack of natural sedimentation on the reclaimed land, as hard defences have prevented the natural rollover and expansion of salt marsh inland (Burd 1995). As a result, many realignment sites lie at elevations too low in the tidal frame to support salt marsh vegetation (Paramor & Hughes 2005; Vandenbruwaene, Maris, et al. 2011).

On managed sites, engineering techniques are often used to accelerate or enhance the transition into salt marsh after realignment in an attempt to overcome problems caused by variations in elevation. Regulated tidal exchange is one such technique, where the exchange of seawater through a breach in a sea defence is regulated through engineered structures. A range of different structures is currently used, such as tide-gates and

sluices, which exert a high level of control over the amount of water entering the restored area (Environment Agency 2003). The Environment Agency has recently recognised the value of the self-regulating tide-gate (SRT), where a float system is adjusted to open the gate until a specified water level is reached, after which the SRT will close (Ridgway & Williams 2011). These designs ensure maximum control over water levels in the restored area and minimum flood risk to nearby populations (Adnitt et al. 2007). Similar SRT designs have been used by the Environment Agency at two different locations in Devon to create different saline habitats. At Black Hole Marsh, near Seaton, the SRT is adjusted to flood the restored area on spring tides over three to four days to fill a saline lagoon. This water then partially drains until the next cycle (Ridgway & Williams 2011). Meanwhile, at Goosemoor (Exe Estuary, near Exeter), the same SRT system allows water into the restored area on every tidal cycle but regulates the maximum water level at 1.69m ODN, aiming to create salt marsh habitat but prevent extreme flooding (ABPmer Online Marine Registry, 2014).

RTE can be used as part of a ‘phased realignment’ scheme (Environment Agency, 2003). This technique has been employed at Abbott’s Hall, Essex, to create 20 hectares of salt marsh. It is essential that high rates of sediment accretion be attained in RTE sites (Environment Agency, 2003), in order to allow the site to increase in elevation in accordance with sea level rise. When the restored surface is sufficiently raised, the RTE mechanism may be removed and a more natural tidal regime reinstated.

1.6.2 Unmanaged realignment

This type of coastal realignment is where no management takes place at all. If sea defences are gradually damaged by wave activity or breached in a storm, salt marsh may start to develop on the newly flooded land behind the old defences, providing no repairs take place. At Porlock Weir, Somerset, a long gravel barrier was breached in a

storm in 1996. The National Trust made the decision not to repair the breach and adopt a policy of ‘Working with Nature’; therefore, salt marsh has since developed on the landward side of the breach (Crowther 2007).

1.7 Practical challenges

Salt marshes are biogeomorphic systems, where multi-way interrelationships exist between many geomorphological and ecological processes (Naylor et al. 2002; Viles et al. 2008). Disturbance to geomorphological functioning (e.g. reintroduction of tidal flow) can therefore directly affect vegetation development and also indirectly, through its influence on biochemical functioning. It is still not understood how the reinstatement of tidal flows affects restored salt marsh functioning, especially as the management of realignment sites remains experimental and uncertain, due to the novelty of the technique (French 2006). In particular, regulated tidal exchange is a highly experimental technique due to its novelty and a general lack of understanding of how the whole system responds to direct process alterations (French 2006).

The practice of managed realignment by retreating the line of defence and allowing landward spread of marsh may be seen as reinstating natural processes. However, the starting point of managed realignment sites is far from that of natural salt marshes. Under natural adjustment to sea level rise, an established marsh would slowly move landward and upward along a natural profile. When a site is re-aligned, this landward movement occurs as one large ‘jump’ rather than allowing the site to evolve over time and sedimentation to naturally take place (French 2006). Additionally, it is thought that de-watering reclaimed land and using it for agriculture affects the sub-surface soil structure, which significantly alters soil biogeochemistry once flooded (Spencer & Harvey 2012). Indeed, the establishment of vegetation in many realignment sites has been shown to be extremely slow or incapable of matching the composition of natural

reference marshes (Garbutt & Wolters 2008). In a recent study in which plant community composition of deliberately realigned, accidentally realigned and natural reference marshes were compared, Mossman et al. (2012b) claimed that deliberately realigned sites do not fulfil legislative requirements of biodiversity enhancement and habitat creation, such as within the EU Habitats Directive. Restored soils were generally lower in redox potential at equivalent elevations in the tidal frame, which led to a dominating pioneer vegetation community.

Differences in vegetation community composition may well impact the provision of ecosystem services (described in section 1.4) from restored salt marshes (Spencer & Harvey 2012), as all species have different functions within the marsh (Zedler et al. 2001). Additionally, communities with higher biodiversity are more resilient to disturbance and therefore more sustainable in the long-term (Tilman et al. 1997; Loreau et al. 2001; Folke et al. 2004). This is highlighted in an ecomorphodynamic model by D'Alpaos et al. (2007), where it is proposed that under a constant sea level, there is a positive feedback between the colonisation of multiple species and elevation rise due to the accretion of organic sediments. The accompanying variety of species adaptations in a multispecies marsh allows the land to remain vegetated at different elevations, until reaching a maximum level above the mean high water line (MHWL). Although *Spartina* marshes accumulate much more rapidly, both through inorganic sediment trapping and organic contributions, elevation rise is limited by a negative feedback when it reaches the point (below MHWL) of maximum productivity for the species.

If not accurately controlled, alterations to the tidal regime may prevent establishment of the desired vegetation communities, affecting both geomorphological and geochemical processes which ultimately feed back to control vegetation development (Fig. 1.1). Therefore any geomorphological hindrance to vegetation development in the early

stages of managed realignment schemes could ultimately affect ecosystem functioning and long-term sustainability of realigned areas (Cooper et al. 2004; Viles et al. 2008). This fundamental uncertainty has economic and social implications for current and proposed managed realignment schemes (Nicholson-Cole & Riordan 2009). Consideration of the initial responses of both pre-alignment vegetation and new halophytic colonisers to different levels of inundation and associated sediment biochemical alterations would inform the specific habitat creation objective of techniques such as regulated tidal exchange (Spencer & Harvey 2012).

Sedimentation and seed dynamics may also be affected by alterations to the tidal regime. Sediment grains and seeds from external sources are generally transported in suspension into the realigned area via tidal flow and are subsequently deposited following a reduction of flow energies (Leonard & Luther 1995; Yang et al. 2008). The resulting elevation rise is essential for the realigned marsh to keep pace with sea level rise (Reed 2002) and also for the spatial development of characteristic patches of vegetation (zonation) according to species adaptations to abiotic conditions (Silvestri et al. 2005). However, care must be taken to avoid unnaturally high rates of sedimentation, through suitable site selection and appropriate regulation of the hydroperiod. At Orplands, on the Blackwater Estuary (Essex), excessive sedimentation caused the burial of vegetation and anoxic conditions to develop on the marsh, limiting the colonisation and establishment of pioneer species (Macleod et al. 1999).

In regulated tidal exchange sites, controlling water levels suitable to the elevation of the site should ensure a sufficient supply of sediment and seeds to the site, providing there are adequate sources nearby. However, in a study by Reed et al. (1997), significantly less sediment was deposited on sites with tidal mechanisms in place than natural control sites. It is of high importance that patterns of sedimentation on realigned marshes are

investigated, especially on sites where new tidal gate designs are being tested. Likewise, monitoring seed deposition and the occurrence of halophytic colonisers may indicate whether certain seeds are prevented from entering the MR area by the tidal gate. For example, Huiskes et al. (2012) suggest that seeds with shorter buoyancy periods are generally move along the channel bed (e.g. *Salicornia* spp.), whilst those with longer buoyancy periods float on the water surface (e.g. *Spartina anglica*), which may affect their entry into the site.

It has also been suggested that restored sites are less topographically heterogenous than natural salt marshes (Elsley-Quirk et al. 2009). The development of tidal channel networks is extremely variable on restored sites and pre-realignment morphology may often remain stagnant for many years (Bowron et al. 2011). This can influence vegetation community composition by reducing the vertical range of species present on elevation gradients (Zedler et al. 1999). Additionally, as creeks have a valuable drainage function (Crooks et al. 2002), horizontal vegetation zonation may be reduced on managed realignment sites (Zedler et al. 1999). In order to understand the potential effects that creeks have on plant community composition, more research needs to be conducted on the geomorphological and ecological functioning of creek networks in both restored and natural salt marshes. This may inform the management practice of creek construction prior to realignment, i.e., could excavating creeks enhance salt marsh biodiversity on managed realignment sites and if so, is it worth considering creek morphology in excavation design?

Future management of coastal realignment sites will require a better understanding of the key interrelationships between abiotic and biotic processes that determine salt marsh development. The incorporation of such research into a predictive framework for habitat development following realignment would be extremely useful in the planning and

implementation of restoration projects. Such a framework could help to predict both the temporal and spatial development of restored salt marshes and ultimately fine-tune management techniques that are often employed to accelerate or enhance the transition into the specific desired habitat after realignment.

1.8 Aims and thesis outline

Practical applications of managed realignment remain highly experimental (French 2006). It is clear from previous studies that restoring the vegetation community composition of salt marshes to historical or natural equivalency is extremely challenging, if not impossible (Mossman, Davy, et al. 2012; Garbutt & Wolters 2008). However, previous studies have often neglected to focus on the important links between geomorphological and ecological processes in salt marsh ecosystems. In this study, the overarching aim is to find out ways in which we can create salt marshes that are self-sustaining and function as closely to natural ecosystems as possible, by considering the linked biogeomorphological processes in salt marsh ecosystems. Such an approach will improve predictions of habitat development and recommendations for future practice in managed realignment schemes.

The effects of seawater inundation on pre-existing vegetation are initially examined in a greenhouse experiment in Chapter 3. The aim of this chapter is to elucidate responses of a glycophyte (*Trifolium repens*) to short duration soil flooding by seawater and recovery following leaching of salts. The impact of short-duration seawater soil flooding (8 or 24 hrs) on short-term changes in leaf salt ion and organic solute concentrations were monitored, as well as longer-term impacts on plant growth (stolon elongation), and flowering. Plants were cultivated from parent ecotypes collected from a natural soil salinity gradient; therefore, of high relevance is whether *T. repens* has a natural adaptive capacity for tolerance of short-duration seawater soil flooding. This kind of experiment

will not only improve spatial and temporal predictions of the immediate response of glycophytic vegetation to seawater inundation following realignment, but also indicate how glycophytes on coastal grassland on the inland fringes of salt marshes may respond to occasional seawater flooding as a result of storm surges and rising sea levels.

In Chapters 4, 5 and 6, three years of ecological and geomorphological development are investigated in response to a variable inundation regime imposed by regulated tidal exchange at South Efford managed realignment site (SEM), south Devon, UK. These three chapters aim to generate recommendations for the future management of the site, with particular regard to the tidal regime. Seawater inundation is known to be a major driver in the complex biogeomorphological model of salt marsh dynamics, therefore Chapter 4 specifically aims to investigate whether there are temporal and spatial differences in the tidal regime at SEM in comparison with the adjacent natural salt marsh and tidal flat in the estuary. The influence of a new self-regulating tidal gate (SRT) design on tidal exchange will be discussed and the implications of imposed hydrodynamic variations on salt marsh development will be explored.

Subsequently, Chapter 5 aims to investigate whether patterns of spatial and temporal vegetation development at SEM have developed in relation to the tidal regime, including the reduction in terrestrial vegetation cover (linking back to Chapter 3) and the colonisation of halophytes. The management technique of transplanting salt marsh species on realignment sites in order to enhance vegetation development will also be explored.

Sediment and seed deposition are integral to salt marsh development, but also highly controlled by certain aspects of the inundation regime (Reed et al. 1999). Therefore, Chapter 6 aims to find out whether sufficient sediment accretion and hydrochory are occurring at SEM in relation to the tidal regime imposed by the new SRT. Additionally,

are there any particular characteristics of the controlled tidal regime that could be limiting sedimentation rates? Patterns of seed and sediment deposition on SEM will be compared with the natural salt marsh at South Efford and a nearby unmanaged realignment site in order to decipher the potential implications of a regulated tidal regime.

It has been suggested in recent literature that managed realignment sites may not be as topographically heterogeneous as natural salt marshes and tidal channel networks can be particularly slow to develop (Zedler 2005; Brooks et al. 2015). Therefore, in Chapter 7, the aim will be to investigate the effects that tidal channels have on drainage and on subsequent plant diversity on multiple restored and natural sites in South West England. The effects of varying creek morphology will also be discussed. This will improve general understanding of the functioning of restored sites and indicate how tidal channels may be excavated on future sites to enhance the establishment of a greater diversity of salt marsh vegetation.

As geomorphological and ecological processes are highly linked in salt marsh systems, the chapters described above are all linked in various ways (Fig. 1.4). For example, regulation of the tidal regime on managed realignment sites (Chapter 4) controls the decline of glycophytic vegetation (Chapter 3) and therefore the transition into salt marsh vegetation (Chapter 5). Sediment deposition and hydrochory (Chapter 6) are also controlled by the tidal regime (Chapter 4), but sediment accretion will also feedback to increase the elevation of the marsh surface in the tidal frame; therefore, altering the tidal regime. Initial creek development (Chapter 7) is controlled by the tidal regime (Chapter 4), whilst creek networks potentially influence sediment delivery (Chapter 6) and vegetation zonation (Chapter 5). These multidirectional links between the chapters become clear throughout the progression of the thesis.

The final chapter (Chapter 8) synthesizes results from the previous chapters and provides suggestions for the management of future sites by integrating information gained from this research with current literature. Future areas of interest are also discussed.

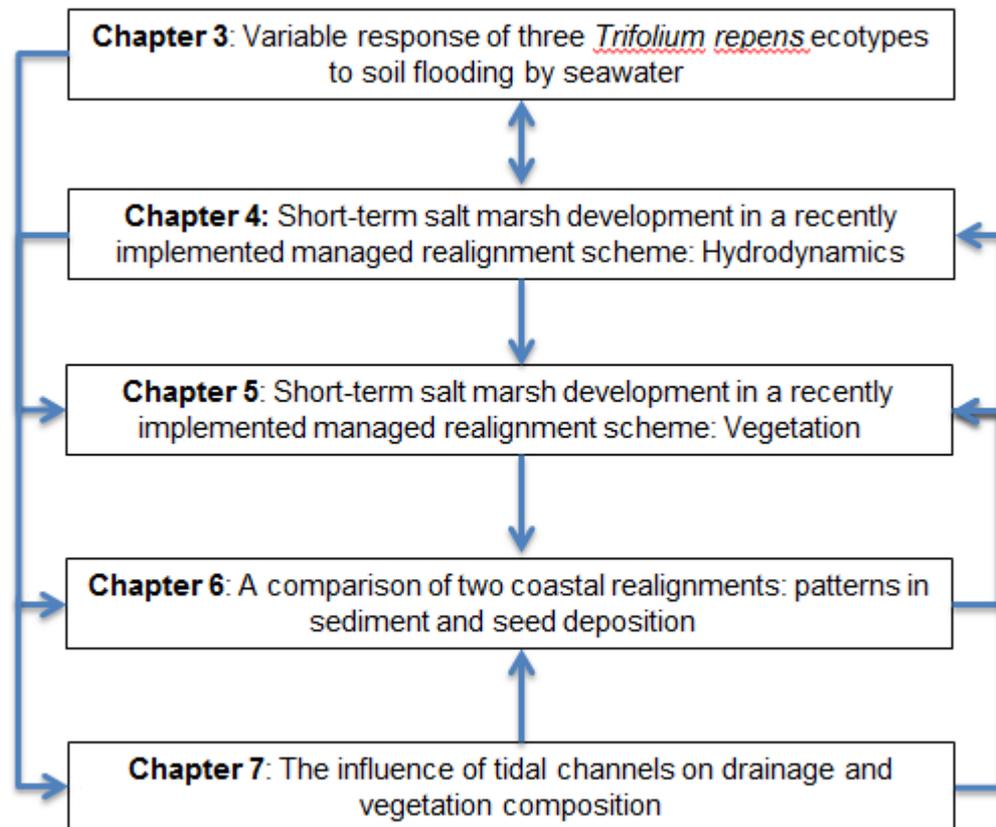


Figure 1.4 – Thesis outline (experimental chapters only). The directions of the arrows indicate where processes from one chapter may influence those within another chapter.

1.8.1 Summary of the main questions

Results from the various investigations described above will aim to answer three overarching questions: -

- Question 1: How do pre-alignment plant species growing within managed realignment sites respond to salt water inundation upon re-exposure to flooding?

This question will be tackled in a manipulated greenhouse experiment in Chapter 3, but field-based observations will also be made in Chapter 5.

- Question 2: How do new engineering techniques alter the tidal regime and what specific aspects of the new regime drive plant community reassembly and sedimentation patterns?

This question follows onto the next chronological stage of realignment, investigating the drivers of important ecological and geomorphological change in a tidally controlled setting. This question will be examined in Chapters 4, 5 and 6.

- Question 3: How can biodiversity be maximized on realignment sites through the use of different management techniques and site design?

This question is investigated throughout the thesis, but the use of regulated tidal exchange is particularly focused on in Chapters 4, 5 and 6, whilst the benefits of tidal channels to managed realignment sites are investigated in Chapter 7.

Chapter 2 - The Study Sites

South Efford managed realignment site (SEM) was inundated for the first time in July 2011, providing an excellent opportunity to investigate factors influencing the transition of formerly reclaimed land into salt marsh from initial realignment (Section 2.1). SEM is therefore the main site in focus throughout the thesis, featuring in all chapters. The site features exclusively, albeit remotely, in Chapter 3, as plants were collected from the pre-realignment vegetation in 2011 to be used in greenhouse experiments. In Chapter 4 and 5, the focus is again on SEM, with comparisons drawn from adjacent natural habitats. A nearby unmanaged realignment site (Section 2.2) is also introduced in Chapter 5, as an additional location for transplanting experiments. This unmanaged site is used alongside SEM in Chapter 6, allowing sediment patterns to be investigated and compared between an unmanaged and managed site in similar geographical locations. In Chapter 7, tidal channels were surveyed at SEM and the adjacent natural salt marsh (SEN) (Section 2.1), with data also collected from two additional managed realignment sites and adjacent natural salt marshes in South West England (Sections 2.3 and 2.4). This allowed for patterns of variability to be compared both within and between sites in different geographical locations, of both managed and natural origin. The locations of all study sites are shown in Fig. 2.1.

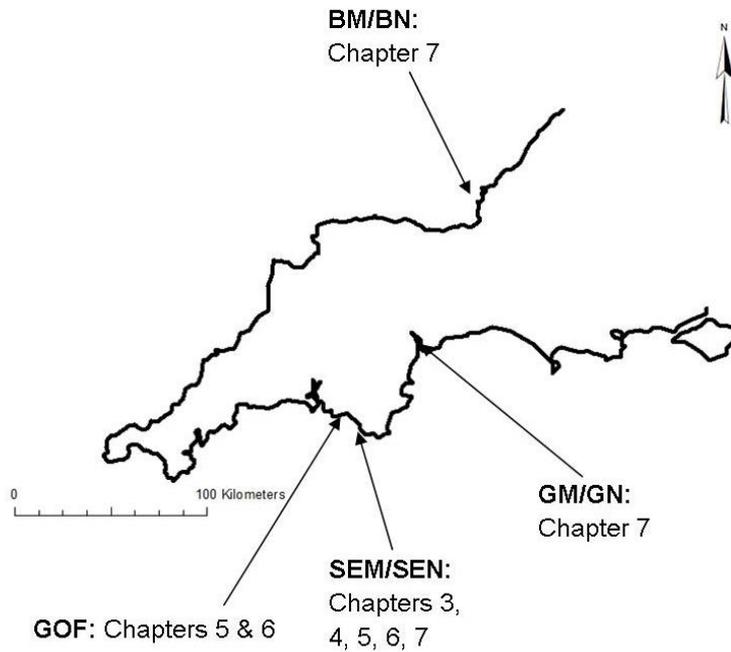


Figure 2.1 – Study site locations in South West England and their corresponding chapters. For site descriptions, see Sections 2.1 for SEM/SEN (South Efford managed realignment/natural sites); 2.2 for GOF (Great Orcheton Fields); 2.3 for GM/GN (Goosemoor managed realignment and natural sites) and 2.4 for BM/BN (Bleadon Levels managed realignment/natural sites).

2.1 South Efford managed realignment, Avon Estuary

South Efford managed realignment (SEM) is a regulated tidal exchange site located on the southern side of the upper Avon Estuary, near to Aveton Gifford (south Devon, UK, 50°18'14"N, 3°50'59"W; Fig. 2.1 and 2.2a). A natural salt marsh (SEN) with a highly dendritic creek network lies adjacent to the site, on the southwestern side of the embankment (Fig. 2.2b). The estuary generally flows over Devonian slates/grits and similar to the majority of estuaries in South West England, is a drowned river valley (ria), inundated by Holocene sea level rise (Masselink et al. 2009). The River Avon

originates ~460 m above sea level on the Aune Head mires on south Dartmoor and stretches 37 km to the estuary mouth at Bantham and Bigbury-on-sea. The mean spring tidal range on the open coast is 4.3m (Uncles et al. 2007). Only 7.8km of the river is tidal (Davidson 1991), therefore SEM is located just within the maximum tidal limit at Aveton Gifford weir. Freshwater discharge is measured at Loddiswell, approximately 3km upstream from SEM. Uncles et al. (2007) showed that seasonal cycles in freshwater discharge occur in the Avon, with a monthly average of 7 cumecs (m^3s^{-1}) in winter and 1 m^3s^{-1} in summer.

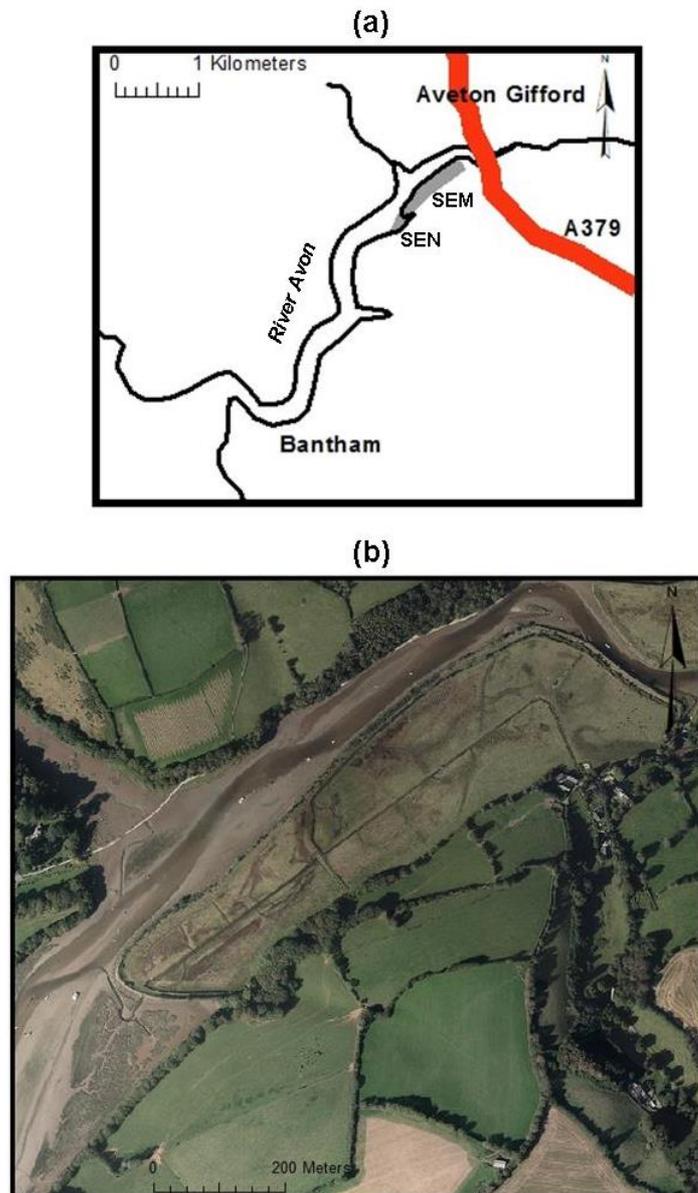


Figure 2.2 – (a) Location of SEM and SEN (grey shaded areas) on the Avon Estuary; (b) SEM surrounded by embankment, SEN on the southwestern edge. Aerial imagery (2012) courtesy of Channel Coastal Observatory (www.channelcoast.org).

Originally natural salt marsh, SEM was reclaimed for pastureland in 1760, when an embankment was constructed to isolate 14.6ha of intertidal area from the sea. In the Second World War, a bomb was dropped on the bank of the site, which created a crater that filled with seawater on every high tide. Although the damaged portion of the bank was re-built in 1956, a slight crater still exists today. In 1994, an additional breach occurred in the southwestern end of the site. On this occasion, the bank was re-built by the river authority, at great expense (Doughty 2014). In addition, the drainage channels were realigned in the 1990s. The highly linear, central channel is visible in Fig. 2.2b.

In 2009, the Environment Agency bought the 17ha site, which was then leased to Devon Wildlife Trust, as part of the Environment Agency's South West Regional Habitat Creation Programme. Regional Habitat Creation Programmes are partnership schemes between the Environment Agency, Local Authorities, Natural England and private landowners, aiming to create/restore habitats at a local level, in order to compensate for national losses. The aim at South Efford was to re-instate tidal influence and within five years restore 7ha of salt marsh habitat. This habitat would consist of low-marsh communities on the lowest elevated areas of land, such as annual *Salicornia* species (British National Vegetation Classification SM8). This would gradually transition back to typical mid-elevation species, such as *Atriplex portulacoides* (British National Vegetation Classification SM14) and then to species typical of higher elevations, such as *Juncus gerardii* (British National Vegetation Classification SM16) and species

typical of freshwater grazing pasture, such a transition ensuring a biodiverse plant community.

The average elevation of the restored marsh surface is <1 m ODN, at least half a meter lower than the adjacent natural marsh on the southern, outer side of the SRT, due to restricted sediment accretion post-reclamation (see Fig. 4.1 in Chapter 4). Therefore, the EA installed a single self-regulating tidal gate (SRT) at SEM, which became operational in July 2011 (Fig. 2.3). The new design produced by the Environment Agency is known as a ‘stop-go-stop’ mechanism, where a metal plate, controlled by a flotation device, closes over the 900 mm diameter culvert at low water levels (as shown in Fig. 2.3), moves anticlockwise on the rising tide to uncover the culvert and a second plate closes over the culvert at higher water levels. The floats can be adjusted to fine-tune the water levels at which the SRT opens and closes. Tidal exchange is therefore highly controlled and inundation of the realigned area can be regulated (at optimum levels to encourage salt marsh establishment), whilst flood risk is kept to a minimum. The SRT links a large channel from an adjacent natural salt marsh creek network with linear drainage ditches in the realigned area, relics of former agricultural land use. With the exception of annual lightly-stocked cattle grazing on the landward half of the site between April-October, no further management has taken place.



Figure 2.3 – Photograph of the SRT on the seaward side of South Efford Marsh. The green float rises and falls with the tide, which controls the position of the metal plates and therefore the amount of water entering the realigned area. Photo taken at low tide.

At SEM, the high level of control the gate provides is considered by the EA to be key to the future success of the project. Initial plans for the scheme were met with a large amount of controversy and resistance within the local community of Aveton Gifford; therefore, ensuring a smooth transition from previously valuable grazing marsh to functioning salt marsh habitat is crucial for trust and confidence to be maintained in the EA.

2.2 Great Orcheton Fields unmanaged realignment, Erme Estuary

Great Orcheton Fields (GOF) is located in the upper reaches of the Erme estuary, near Modbury (south Devon, UK, Lat: 50.332 Long: -3.931; Fig. 2.1 and 2.4a). This estuary is also a ria, the majority of which is underlain by the Dartmouth Beds, with overlying Staddon Grits and Meadfoot Beds (Gehrels et al. 2001). The source of the River Erme is 430m above sea level, on Stall Moor mires, south Dartmoor. The river flows for 24 km before reaching the sea at Wonwell and Mothecombe. The mean spring tidal range on the open coast is 4.7m (Gehrels et al. 2001). GOF lies just within the maximum tidal extent at Flete (~6km inland).

In December 2007, extreme high tides occurred in the estuary as a southwesterly storm surge coincided with sustained rainfall. The swollen river caused a breach in the wall on the eastern side of the estuary (Fig. 2.5), flooding six fields (28 ha) of reclaimed pastureland on GOF (Fig. 2.4b). Cattle had grazed this reclaimed land since Napoleonic prisoners of war built the wall in 1800. After the storm, the decision was made by Natural England and the landowner (Anthony Mildmay-White) to ‘work with nature’,

i.e. not to repair the former stone wall defence and to allow the site to develop as salt marsh.

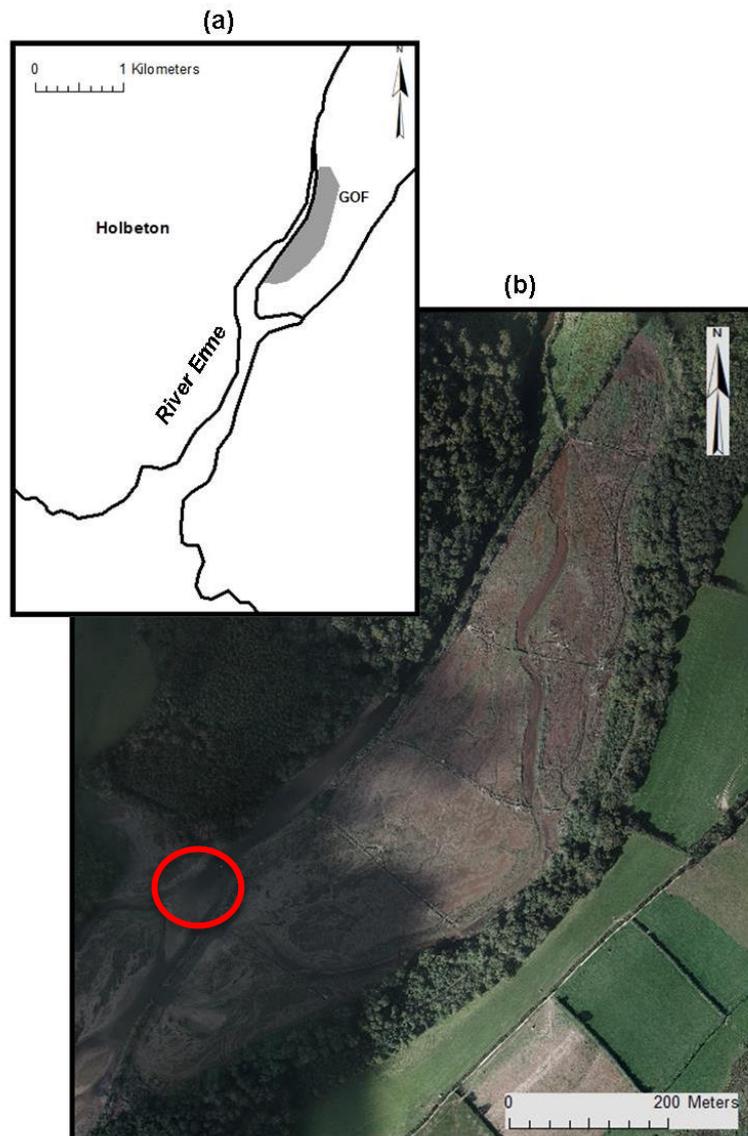


Figure 2.4 – (a) Location of GOF (grey shaded area) on the Erme Estuary; (b) Flooded fields at GOF (breach is in southwestern corner). Red circle shows breach in the stone wall surrounding the site. Aerial imagery (2012) courtesy of Channel Coastal Observatory (www.channelcoast.org).

By 2010, the landowner had reported that *Salicornia europaea* had replaced many terrestrial species within the flooded area (Mildmay-White, pers. comm.). By 2013, the site was dominated by saltmarsh plants with a number of different species having colonised (pers. obs.) and *Salicornia europaea* is currently harvested commercially. However, as the site is within a Site of Special Scientific Interest (SSSI), AONB and part of the south Devon Heritage Coast, there are limits on the amount of *Salicornia europaea* that can be harvested and the species must be harvested by hand, leaving roots in situ.



Figure 2.5 – *The breach at GOF, looking seaward (south west).*

2.3 Goosemoor managed realignment, Clyst (Exe) Estuary

Goosemoor managed realignment site (GM) is located on the southwestern side of the Clyst, near Topsham (south Devon, UK; 50°40'92"N, 3°27'21"W; Fig. 2.1 and 2.6a) not far from where it meets the Exe estuary. The River Exe is comparatively large,

rising at ~440m above sea level at Exe Head near Simonsbath on Exmoor and flowing southwards for ~80km before reaching the south Devon coast at Exmouth and Dawlish. The mean spring tidal range at the mouth is 3.72m. The Exe is tidal up to Countess Wear, 15 km from the mouth. Approximately 5km from here, the Clyst meets the Exe at Bowling Green Marsh, south of Topsham. The Clyst rises near Clyst William, near Cullompton and flows for 28 km before meeting the Exe.

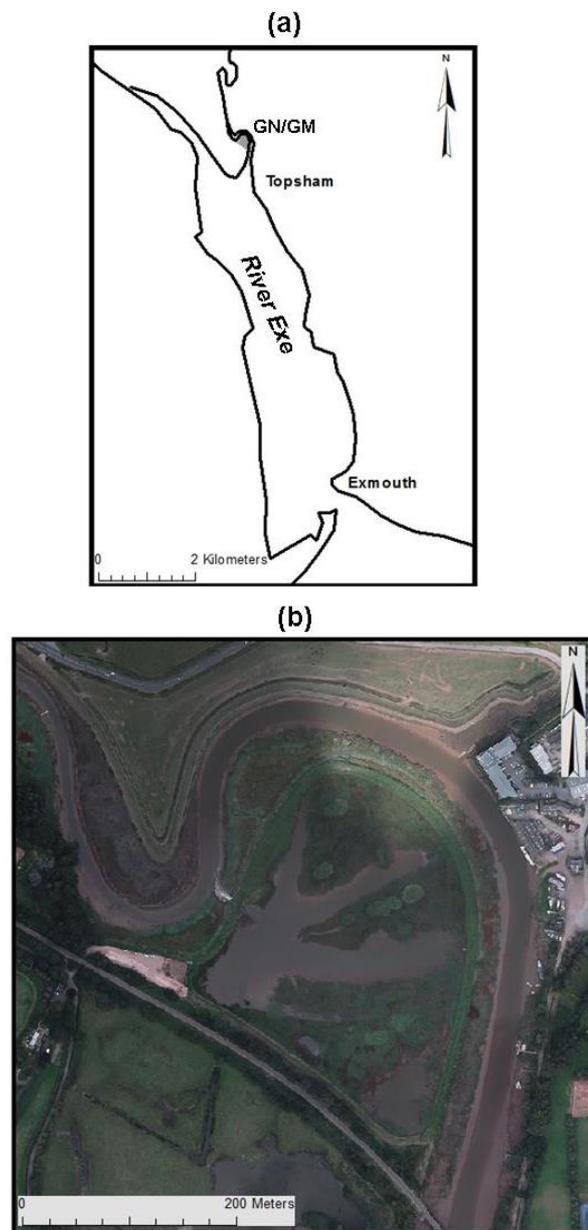


Figure 2.6 – (a) Location of GM and GN (grey shaded areas) on the Clyst (Exe) Estuary; (b) GM surrounded by embankment (SRT on the western side), GN on the outer perimeter of the embankment. Aerial imagery (2012) courtesy of Channel Coastal Observatory (www.channelcoast.org).

Goosemoor managed realignment site was originally drained for agricultural use when an embankment was constructed in the 1840s. During this time, the site reverted to wet grassland, dominated by *Agrostis stolonifera* (Lyons & Ausden 2008). In November 2004, the 8.1ha site was inundated by seawater again as part of the South West Regional Habitat Creation Programme, in partnership with the RSPB, DEFRA, Environment Agency and Natural England (Fig. 2.6b). As the land was low in elevation due to the lack of sediment accretion during realignment and there was high risk of flooding of the nearby railway without construction of an expensive sea wall, an American Waterman SRT with a 1 m culvert was constructed in the old embankment (ABPmer Online Marine Registry 2014). Floats cause the SRT to open and close at defined tidal heights so that seawater flows into the site on the rising tide and flows out on the ebb tide. During the first year of realignment (November 2004 – October 2005), maximum water levels on the site were 1.57m AOD, rising to 1.69m AOD from October 2005 – March 2006. Thereafter, the float arms were removed from the SRT, so that natural tidal flows entered the site. However, the flap is still prompted to close on spring tides. Prior to realignment, a small ditch network was excavated to maximize tidal flows into the site (ABPmer Online Marine Registry 2014).

The nearest natural salt marsh (GN) is situated immediately adjacent to Goosemoor managed realignment site and in fact lines the old embankment surrounding the site (50°41'02"N 3°27'23"W; Fig. 2.6b). Historical maps show that the natural marsh has expanded since the embankment was constructed in the 1800s and is now at its maximum extent (Mike Williams, pers. comm.).

2.4 Bleadon Levels managed realignment, Axe Estuary

Bleadon Levels managed realignment site is located on the eastern side of the Axe estuary, near Uphill, north Somerset ($51^{\circ}18'68''\text{N}$ $2^{\circ}59'05''\text{W}$; Fig. 2.1 and 2.7a). Water drains from the Mendips to where the River Axe rises at Wookey Hole, after which the river flows through permeable limestone into underground caves. The river mouth is at Weston Bay on the Bristol Channel (Fig. 2.7a). The mean spring tidal range in Weston Bay is 11.2m and the tidal limit of the estuary is 4km from the mouth, at Brean Cross (Royal Haskoning 2013). There is a high amount of suspended sediment in Weston Bay, mainly due to the high loads in the Bristol Channel, but also contributed from the River Axe (Royal Haskoning 2013).

Bleadon Levels is close to the upper limit of the estuary, positioned ~3km from the mouth of the estuary (Fig. 2.7a). As part of the Somerset Levels, salt marshes in this area started to be reclaimed by the Romans, continued throughout the Middle Ages and into the 17th century (Royal Haskoning 2013). However, in winter 1999/2000, a 13ha site was realigned by Wessex Water, mitigating for the construction of a nearby sewage treatment works. Two breaches were made in the old embankment, the width of the northern breach approximately 39m and the southern breach approximately 25m. Two creek networks were excavated in the shape of herringbones, leading from each breach (see Fig. 2.7b). In the first year of realignment, some salt marsh species had colonised. After three years, a basic salt marsh community had established. Since then, the site has developed a high marsh community dominated by *Elymus repens* (Ellen McDouall, pers. comm.).

The nearest natural salt marsh to BM is located approximately 2km downstream, in the lee of the Carboniferous limestone promontory of Brean Down ($51^{\circ}19'26''\text{N}$ $3^{\circ}0'01''\text{W}$; Fig. 2.7a and 2.7c). This 18 ha site could therefore be described as an 'estuary back-barrier' salt marsh, as it is protected from westerly swells.

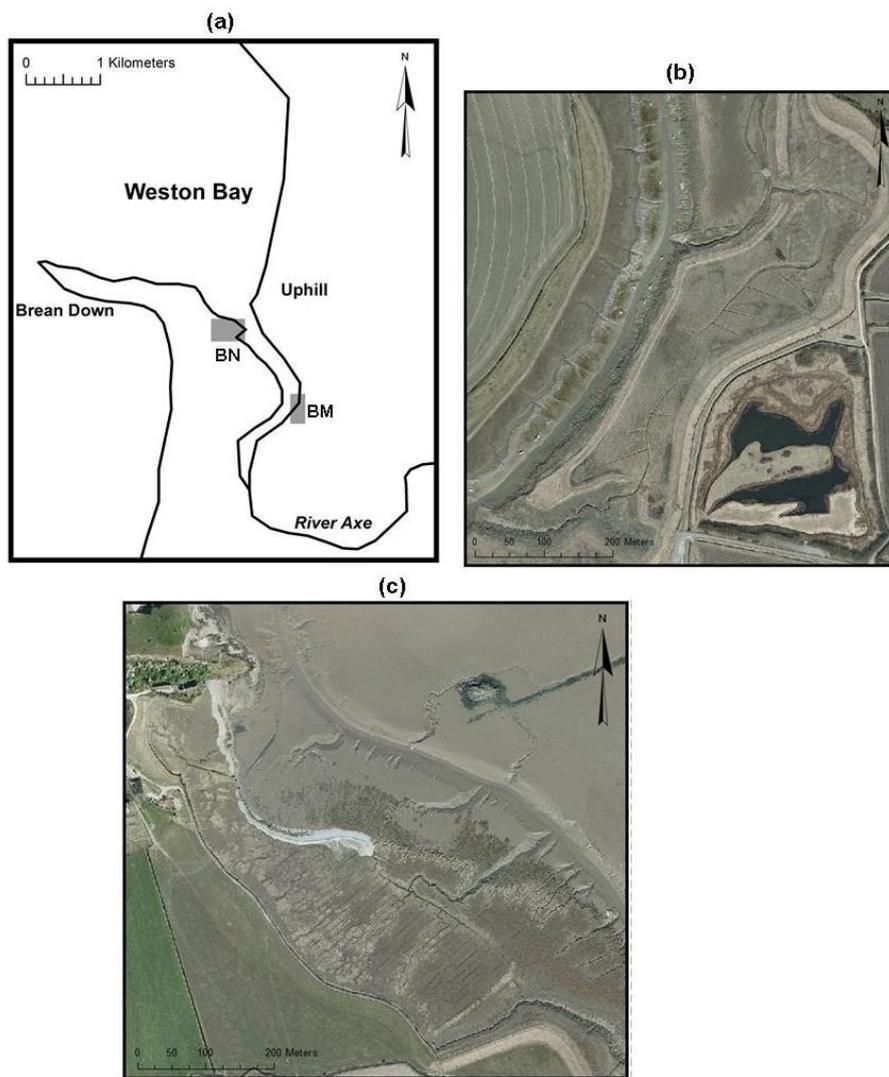


Figure 2.7 – (a) Location of BM and BN (grey shaded areas) on the Axe Estuary; (b) Herringbone creek formations within the embanked area of BM, with the breach to the south and freshwater marsh to the east); (c) BN at the base of Brean Down. Aerial imagery (2008) courtesy of Channel Coastal Observatory (www.channelcoast.org).

Chapter 3 - Variable response of three *Trifolium repens* ecotypes to soil flooding by seawater

3.1 Introduction

A combination of sea level rise and the increased likelihood of storm surge events associated with anthropogenic climate change is likely to result in more frequent and severe episodes of salt water inundation into low-lying coastal vegetation (Nicholls & Cazenave 2010; Martin et al. 2011; Zappa et al. 2013). In coastal realignments, terrestrial land is often deliberately flooded, with the intention of creating salt marsh habitat. In the initial stages of realignment, it is essential for unvegetated microsites to occur in the pre-existing terrestrial vegetation, allowing halophytes to colonise in the absence of interspecific competition. If pre-alignment vegetation remains for a prolonged period, the establishment of new halophytic species may be inhibited by competitive exclusion (Erfanzadeh et al. 2009; Jacobs et al. 2009). Predictions and management of salt marsh restoration projects would therefore benefit from an increased understanding of how glycophytic species in coastal grasslands respond to sudden seawater inundation.

In addition, areas of coastal grassland on the inland perimeter of managed realignment sites will become increasingly vulnerable to occasional flooding as sea levels further increase. Coastal grasslands are both economically and ecologically important. Not only do they provide protection against the sea for urban areas and agro-ecosystems in-land (Hanley et al. 2014), they offer refuge for many plant and animal species excluded by intensive agriculture (Rhymer et al. 2010; Fisher et al. 2011). Consequently the ecological response of these coastal habitats to seawater inundation may have important ramifications not only for conservation, but also shoreline management.

The potential impact of sudden seawater inundation may be particularly acute for grazing marsh and coastal pasture since unlike salt marshes, these ecosystems are not naturally susceptible to the periodic intrusion of sea water. Salt stress and inundation regimes are known to affect productivity and plant zonation in estuarine marsh/grassland transitions (Guo & Pennings 2012; Janousek & Mayo 2013), and also influence plant survival, growth, and reproduction in freshwater macrophytes (Van Zandt & Mopper 2002; Van Zandt et al. 2003; Middleton 2009; Pathikonda et al. 2010). However, our understanding of the impact of salt stress on coastal mesophytes is limited to the effects of sea spray on cliff and strandline vegetation (Malloch et al. 1985; de Vos et al. 2010; Rogers & Wisser 2010). This contrasts markedly with a rich literature documenting salinity tolerance in halophytes (Zhu 2001; Flowers & Colmer 2008; Weston et al. 2010) and the impact of salinity on growth and yield of crop species (Munns & Tester 2008; Flowers et al. 2010).

The tolerance of wetland plants to freshwater flooding has been studied extensively (see reviews by Bailey-Serres & Voesenek 2008; Colmer & Voesenek 2009), but knowledge of plant response to seawater flooding is limited (Colmer & Flowers 2008; Bennett et al. 2009; Hanley et al. 2013) and for the most part focusses on how increased tidal flooding affects halophytes in salt marsh systems (e.g., (Janousek & Mayo 2013; Valentim et al. 2013). In addition to impeded gas exchange and chemically-reduced compounds in flooded soils (Armstrong 1979), flooding by seawater also imposes osmotic and ionic stresses; the osmotic stress limits the plant's ability to absorb water and the ionic stress can result in toxicity through the accumulation of Na^+ and Cl^- in tissues (Munns & Tester 2008). In order to cope with the challenge of salinity the plant must prevent or alleviate damage caused by the high concentration of salt ions (Na^+ and Cl^-) and re-establish homeostatic function (e.g. for K^+). Salt tolerance is often achieved by the accumulation of stress metabolites (e.g. compatible solutes) and the regulation of

tissue ions to exclude or compartmentalize the potentially damaging Na^+ and Cl^- , but even if successfully achieved, this can impose a cost on plant growth (Munns & Tester 2008).

Any change in the frequency and severity of seawater flooding might therefore be expected to influence greatly the vegetation of low-lying coastal ecosystems. Nonetheless, our ability to predict the impact of anthropogenically-induced changes in managed realignment scenarios on coastal vegetation is limited by the paucity of information on how component species respond to salt water inundation (Hoggart et al. 2014; but see Redondo-Gómez et al. 2011; Hanley et al. 2013). Here I investigate how one common and economically important coastal grassland species, *Trifolium repens* L., responded to simulated short-term seawater inundation of the soil. Although some coastal populations of this species have been shown to be relatively tolerant of salinity, all previous work has exposed plants to a range of salt concentrations imposed for several weeks (Ab-Shukor et al. 1988; Rogers et al. 1997), rather than looking at the effects of a simulated, short-duration seawater soil flooding event and subsequent recovery. Given the lack of information on plant response to salinity stress following sudden inundation, the primary goal was to elucidate how exposure to a relatively short pulse of seawater soil flooding affected plant survival, immediate onward growth, and flowering. In addition, as plant performance and response are likely influenced by the accumulation of salt ions and organic solutes (Munns & Tester 2008; Flowers & Colmer 2008), post-immersion changes in the tissue concentrations of Na^+ , Cl^- and K^+ and organic solutes (sugars, sugar alcohols, and proline) were investigated.

I also examined whether response to seawater immersion varied for plants cultivated from clonal fragments taken from a natural salinity gradient, stemming from the hypothesis that likely natural adaptation for salt tolerance (Munns & Tester 2008) would influence the response of *T. repens* plants to short-duration soil immersion in

seawater. Environmental gradients across even small distances can facilitate the evolution of local ecotypes; i.e., genetically distinct populations adapted to local environmental conditions (Turesson 1922). Population-specific variation in morphological or physiological responses to environmental factors such as climate are well-known (Fernández-Pascual et al. 2013; Quilot-Turion et al. 2013), but our understanding of ecotype-specific variation in response to salinity stress is largely confined to halophytes (Huiskes et al. 1985; Blits & Gallagher 1991 - but see Ab-Shukor et al. 1988; Van Zandt et al. 2003). This is the first study to examine ecotypic variation in response to simulated seawater soil flooding in a terrestrial, coastal glycophyte. Firstly, how does short-term exposure to seawater flooding affect plant survival, growth and flowering? Further to this, is there any variance in the way plant ecotypes respond to salinity stress?

3.2 Materials and Methods

3.2.1 Plant species, collection and cultivation

Naturally distributed throughout Europe, North Africa and Asia, *T. repens* has been widely introduced elsewhere as a pasture forage plant (Grime et al. 2007). It is also a very common component of coastal grasslands likely to be affected by sea-level rise and storm-surge events, or otherwise deliberately realigned. In June 2011, parent plants were collected from grassland pasture at South Efford near Aveton Gifford, Devon, England (SEM; see Chapter 2.1 for full site description). Plants were collected at locations approximately 25, 200, and 700 m away from the most southerly point of the site. At 25 m, seepage under the sea wall favoured the development of a semi-halophytic community (containing *Puccinellia maritima* and *Spergularia media*) as well as common pasture species like *T. repens* and *Agrostis stolonifera*. At 200 m the plant community was more typical of a terrestrial pasture (dominated by *A. stolonifera* and

Ranunculus repens), and at 700 m, the sward was dominated by similar species, but also including common pasture grasses such as *Holcus lanatus* and *Cyanosurus cristatus*. The variation in the plant community with distance from the sea wall suggested a salinity gradient (confirmed by electrical conductivity measurements of the soil - described below), with which to test the hypothesis that natural adaptation for salt tolerance would influence plant response to short-duration soil immersion in seawater.

In mid-June 2011, 12 individual plants were sampled per distance, collecting large, branched (circa 100 mm diameter) fragments with multiple rooting points. All parent plants were at least 5m apart and taken from distinct patches to reduce the likelihood of collecting from the same individual (Ab-Shukor et al. 1988). The plant fragments were transplanted into 110 × 110 × 120 mm plastic pots containing John Innes No. 2 potting compost and cultivated in a sheltered outdoor area. Three soil cores (10 cm depth, 5 cm diameter) per distance were also collected at random intervals to quantify soil electrical conductivity. Three 20 g subsamples were taken from each core and mixed with 100 ml deionised water on a rotational mixer to provide a 1:5 soil:water extract (British Standards Institution 1997). An electrical conductivity reading was then obtained for each subsample using a WTW Cond 330i handheld conductivity meter with a WTW TetraCon 325 probe (Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany). One-way ANOVA was used to determine variation in soil electrical conductivity from these samples.

3.2.2 Experimental treatments

In November 2011, 10 stolons (about 20 mm long with 1 root node) were removed from each of 12 parent 'stock' plants per distance group and these were individually transplanted into 70 x 70 x 80 mm pots containing John Innes No. 2 potting compost. Plants were subsequently grown in a naturally lit, heated greenhouse in Plymouth,

England (mean daily temperatures varying between $10.7\text{ }^{\circ}\text{C} \pm 0.2$ min and $26.3\text{ }^{\circ}\text{C} \pm 0.6$ max, with daily watering with tap water), until late April 2012.

On April 24th 2012, established ramets were selected such that each of 12 parent ‘stock’ plants was represented by up to 6 clones, each uniform in size and appearance. Clones were allocated to a different treatment group such that we aimed to subject two ramets from each parent ‘stock’ plant to the same soil immersion treatment with seawater collected from Plymouth Sound (electrical conductivity = 47.9 mS/cm at $23.8\text{ }^{\circ}\text{C}$) for 8, or 24 h, or were retained as untreated controls. This arrangement ensured that genetic variation across all soil immersion treatments was minimised within all distance classes. However, due to some plants failing to establish, replication fell below the target of 6 clones per parent for the 200 m and 700 m distance groups, affecting the number of replicates used in the onward growth and flowering experiment (see below). By immersing to pot-level (in large plastic tubs) we simulated short-term soil waterlogging. Although we recognise that in some cases, initial seawater inundation following managed realignment or flooding of adjacent coastal grassland in a storm surge would potentially also result in shoot submergence, our approach allowed us to focus on the effect of ionic imbalance in the root-zone rather than the combined effects that could also arise if shoots experienced oxygen deficiency by submergence. At SEM, initial water levels were regulated at such a low level (see Chapter 4) that plant stems were rarely completely inundated. Additionally, while seawater flooding of coastal grassland following storm surge events might also be expected to persist longer than 24 h, records from along the UK coast suggest a 1 d long seawater flooding event is typical (Environment Agency 2014).

Immediately after immersion in seawater, pots were allowed to fully drain before being arranged randomly on a wire mesh-topped bench inside the greenhouse; the wire mesh allowed free drainage and prevented cross-contamination of any leachates between pots.

3.2.3 Tissue ion and metabolite analyses

One fully expanded, non-senescent leaf was removed from each of 12 individual clones per ecotype per immersion treatment 2 d after soil immersion. These samples were frozen in liquid nitrogen and freeze-dried. Samples were then stored in sealed containers with desiccant in a freezer at -80 °C until analysis. These plants were then discarded.

Dried samples were digested in 5 mL dilute (0.5 M) nitric acid while suspended on a shaker in dark conditions for 2 d at room temperature prior to determination by flame photometry of Na⁺ and K⁺ and by chloridometry of Cl⁻ (Munns et al. 2010). This procedure was applied to 4 replicate leaf samples per soil immersion treatment/ecotype group (minimum sample mass = 26.7 mg). A reference tissue taken through the procedures confirmed the reliability of these measurements.

The remaining leaf samples were bulked (by adding two samples together) such that 4 replicate samples were created for each soil immersion treatment/ecotype group (minimum sample mass = 54.3 mg). Tissue metabolites were extracted from these using 5 % (w/v) perchloric acid and neutralised extracts were analysed using HPLC (Fan 1996). Neutralised extracts were filtered (0.22 µm) and stored at -80 °C. The initial HPLC analysis of organic solutes (glycinebetaine, proline, prolinebetaine and trigonelline), soluble sugars (fructose, glucose, sucrose) and sugar alcohols (sorbitol, mannitol and pinitol) was adapted from Slimestad and Vågen (2006). The HPLC system (Waters, Milford, MA) consisted of a 600E pump, 717plus autosampler and a 996 photo-diode array detector (PDA). As detection of fructose, glucose and sucrose with the PDA at 195nm is very insensitive, an Alltech (Deerfield, IL, USA) evaporative light

scattering detector (ELSD) was also used to improve sensitivity by minimum 100 fold. Separation was achieved at 22 ± 1.0 °C on a Prevail ES Carbohydrate column (250 x 4.6 mm i.d. with 5 μ m packing; Alltech) using a gradient elution profile of acetonitrile (Eluent A) and water (Eluent B) at 1 ml min⁻¹. Samples in the autoinjector were held at 10 °C, the ELSD drift tube held at 85 °C and eluent nebulisation with high purity N₂ gas at a flow rate of 2.6 min⁻¹.

Quantification was based on PDA peak area for organic solutes, and ELSD peak area for soluble sugars and sugar alcohols. Calibration curves were generated from peak area versus the mass of standard analyte injected, with linear relationship for the PDA and a power relationship for the ELSD output. A standard was analysed every 10 samples to check for any instrument/detector drift. Retention times of standards were used to identify analytes in the sample extracts with the PDA spectral data and peak purity used to confirm organic solutes. Typical sample injections were 20 μ l and runtime was 20 min per sample with Empower™ 2 software (Waters) used for data acquisition and processing.

Due to the fact that pinitol co-eluted with fructose, a second HPLC approach was needed to separate and quantify these two analytes and the method described by Naidu (1998) was followed. The Sugar-Pak column (300 \times 6.5 mm i.d.) was held at 90 ± 0.5 °C and separation achieved using a mobile phase of 2.5 mg l⁻¹ Ca-EDTA at 0.6 ml min⁻¹. Detection and quantification of pinitol was undertaken with the PDA as this offered good sensitivity as well as peak spectral and purity comparisons with the standards.

Following application of the Cochran test for homogeneity of variance, and (log_N) data transformation where necessary (Underwood 1997), the effect of immersion on tissue ion and solute concentrations was examined using a two-way ANOVA with 'Immersion Time' and 'Distance' as fixed factors, with the tests for an 'Immersion Time' \times

‘Distance’ interaction included to examine any evidence for distance-specific variation in response to immersion duration.

3.2.4 Plant survival, growth and flowering

Plants not used for chemical analysis were watered to capacity 48 h after salt water immersion (using tap water), and then every two days thereafter for a further 70 d (5th July 2012). Greenhouse air temperatures during this phase of the experiment were: 11.3 °C ± 0.3 min and 29.9 °C ± 0.9 max. Due to some clones failing to establish before immersion, replication fell below the target of 12 plants for the 200 m (0 hr = 9 plants, 8 h = 9 plants, 24 h = 8 plants) and 700 m (24 h = 11 plants) distance groups.

The number of inflorescences on each plant were monitored weekly, so that the total number of inflorescences produced per plant (‘Flowering Effort’) and the percentage of plants that produced open inflorescences (‘Percentage Flowering’) could be quantified at the end of the experiment. Elongation of a representative, randomly selected shoot on each plant, measured from a node marked with loosely tied cotton thread, was quantified at 14 days and 42 days (‘Stolon Growth’). Plant mortality was recorded daily. Subsequently, the effects of ‘Immersion Duration’ and ‘Distance’ on ‘Flowering Effort’ were examined using a two-way ANOVA with ‘Immersion Duration’ and ‘Distance’ as factors, with the tests for an ‘Immersion Duration’ × ‘Distance’ interaction included to examine any evidence for distance-specific variation in response to immersion duration. The effects of ‘Immersion Duration’ and ‘Distance’ on ‘Stolon Growth’ at 14 d were analysed in the same way. Data transformation of the 42 d ‘Stolon Growth’ data could not avoid deviations from normality and homogeneity of variance; therefore Kruskal Wallis tests were applied. Pearson’s chi-squared test was performed on ‘Percentage Flowering’ data to assess the effects of immersion within ‘Distance’ groups, where assumptions of the statistical test were met.

In order to quantify the leaching of salts from the potting compost, four pots were randomly chosen from each soil immersion treatment and water passing through collected and electrical conductivity measured as described above for 5 weeks.

3.3 Results

3.3.1 Electrical conductivity of soil samples from transects

One-way ANOVA indicated significant variation in soil electrical conductivity (of 1:5 soil:water extract, $EC_{1:5}$) between sample sites ($F_{(2,27)} = 39.61$, $P < 0.01$). Post-hoc SNK comparisons revealed that soil electrical conductivity declined with distance from the sea wall embankment, with a mean $EC_{1:5}$ of 6.96 ± 1.35 mS/cm at 25 m, 1.29 ± 0.40 mS/cm at 200 m and 0.19 ± 0.02 mS/cm at 700 m. We therefore conclude that soil salt concentrations were higher at 25 m due to likely seawater seepage through the sea wall and/or deposition of salts from sea spray.

3.3.2 Accumulation in leaves of salt ions and stress metabolites

There was substantial accumulation of Cl^- and Na^+ in leaves following soil immersion in sea water (Table 3.1). Post-hoc SNK tests showed that leaf tissue Cl^- concentrations significantly increased following 24 h sea water immersion compared with both control and 8h treatments, irrespective of original parental distance from the sea wall. There was also a significant increase in Cl^- concentrations in the 8 h treatments compared with control plants. A similar effect of ‘Immersion Time’ was evident for Na^+ although there were also additional ‘Distance’ and ‘Immersion Time’ \times ‘Distance’ effects. However, SNK tests indicated that these were a manifestation of relatively high leaf Na^+ levels in 200 m control plants, and generally relatively low leaf Na^+ levels in 25 m plants following soil immersion. There was no effect of ‘Immersion Time’ on K^+ concentrations; the significant ‘Distance’ effect denoted the inherently higher leaf K^+

concentrations in plants cultivated from the 200 m parent population.

Distance	Treatment	N	Chloride		Potassium		Sodium	
			$(\mu\text{mol g}^{-1} \text{DM})$		$(\mu\text{mol g}^{-1} \text{DM})$		$(\mu\text{mol g}^{-1} \text{DM})$	
			Mean	SE	Mean	SE	Mean	SE
25 m	Control	4	134 ^{A1}	12	476 ¹	41	216 ^{A1}	18
	8 h	4	966 ^{B2}	47	383 ¹	82	663 ^{B1}	46
	24 h	4	1261 ^{C3}	233	502 ¹	81	1049 ^{C1}	129
200 m	Control	4	138 ^{A1}	16	797 ²	30	273 ^{A2}	29
	8 h	4	1025 ^{B2}	77	712 ²	112	929 ^{B2}	34
	24 h	4	1598 ^{C3}	67	693 ²	76	1126 ^{C1}	30
700 m	Control	4	110 ^{A1}	17	466 ¹	66	202 ^{A1}	28
	8 h	4	1047 ^{B2}	36	457 ¹	66	814 ^{B1}	39
	24 h	4	1805 ^{C3}	59	518 ¹	20	1454 ^{C2}	49
Results of two-way ANOVA	Factor		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
	Distance (DF = 2,27)		1.1	0.358	14.9	0.000	5.0	0.014
	Immersion time (DF = 2,27)		471.0	0.000	0.7	0.498	289.6	0.000
	Interaction (DF = 4,27)		2.3	0.084	0.5	0.753	3.2	0.027

Table 3.1 - Ion concentrations of leaf tissues taken from *Trifolium repens* plants 2 d after root-zone immersion in seawater. Significant differences (post hoc S-N-K tests, $P < 0.05$) in the accumulation of Cl⁻, Na⁺ and K⁺ following two-way ANOVA are denoted by different letters for immersion time (0, 8 or 24 h) and different superscript numbers for parent plant location along a natural salinity gradient (25 m most saline, 700 m least saline; described in 'Results' section).

We found detectable amounts of the amino acid proline, the sugars fructose, glucose and sucrose, and the sugar alcohol pinitol, in leaf extracts (Table 3.2). Of these, proline and sucrose increased in all distance groups following soil immersion, but no other treatment-specific trends were located for organic solutes.

Distance	Treatment	N	Proline ($\mu\text{mol g}^{-1}$ DM)		Fructose ($\mu\text{mol g}^{-1}$ DM)		Glucose ($\mu\text{mol g}^{-1}$ DM)		Sucrose ($\mu\text{mol g}^{-1}$ DM)		Pinitol ($\mu\text{mol g}^{-1}$ DM)	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
25 m	Control	4	ND	-	84	11	57	5	9 ^A	2	166	31
	8 h	4	14 ^{AB}	8	74	16	75	12	155 ^B	19	138	18
	24 h	4	28 ^B	10	85	42	74	16	148 ^B	32	125	16
200 m	Control	4	ND	-	42	5	36	3	14 ^A	2	160	28
	8 h	4	16 ^B	3	68	12	63	8	54 ^B	10	148	13
	24 h	4	45 ^C	5	30	9	45	6	61 ^B	9	163	8
700 m	Control	4	ND	-	77	33	55	15	21 ^A	7	137	11
	8 h	4	22 ^B	4	61	18	57	6	142 ^B	15	131	9
	24 h	4	55 ^C	8	45	22	58	8	107 ^B	18	118	16
Results of two- way ANOVA	Factor		F	P	F	P	F	P	F	P	F	P
	Distance (DF = 2,27)		3.3	0.054	1.9	0.174	3.4	0.047	13.8	0.001	1.8	0.183
	Immersion time (DF = 2,27)		44.0	0.000	0.4	0.649	1.9	0.171	73.9	0.000	0.9	0.436
	Interaction (DF = 4,27)		1.6	0.198	0.5	0.735	0.6	0.697	4.8	0.005	0.4	0.790

Table 3.2 - Organic solute concentrations of leaf tissue taken from *Trifolium repens* plants 2-d after root-zone immersion in seawater. Significant differences (post hoc S-N-K tests, $P < 0.05$) between treatment means for each solute are denoted by different letters following two-way ANOVA showing how immersion time (0, 8 or 24 h) and parent plant location along a natural salinity gradient (25 m most saline, 700 m least saline; described in 'Results' section) affected solute accumulation. ND denotes failure to detect any quantity above the detection limit, which were: proline ($12 \mu\text{mol g}^{-1}$ DM), fructose ($14 \mu\text{mol g}^{-1}$ DM), glucose ($20 \mu\text{mol g}^{-1}$ DM), sucrose ($6 \mu\text{mol g}^{-1}$ DM), and pinitol ($36 \mu\text{mol g}^{-1}$ DM).

3.3.3 Plant survival, growth, and flowering

Water collected from control plants remained at an average electrical conductivity (EC_w) of 2.37 ± 0.03 mS/cm. Leachates from pots immersed for 8 and 24 h recorded similar levels of EC_w 2 d post-immersion (12.53 ± 3.28 mS/cm and 11.05 ± 5.61 mS/cm respectively) and declined at a similar rate until 35 d. At this point, stabilisation of EC_w occurred in both treatments (Fig. 3.1).

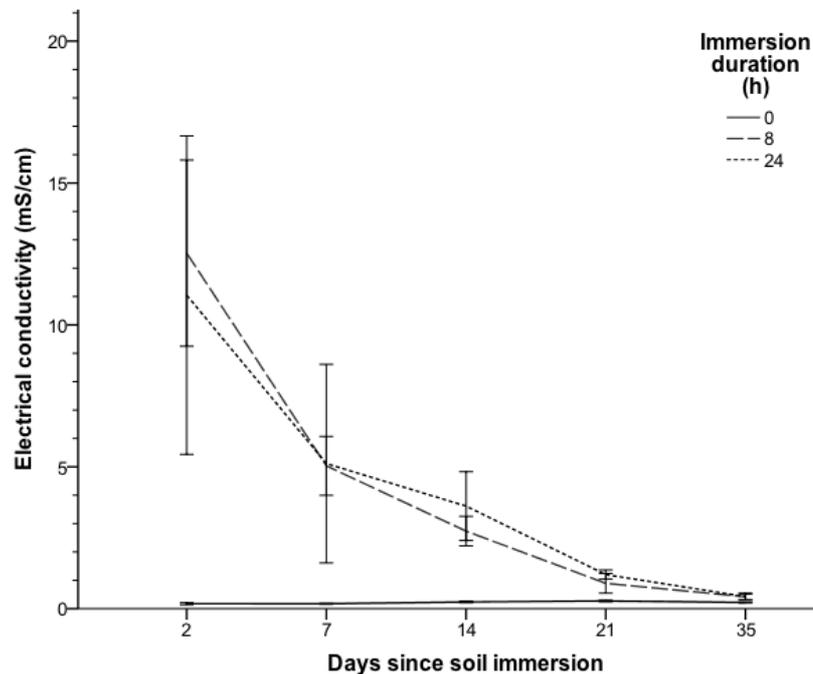


Figure 3.1 - Average electrical conductivity ($mS\ cm^{-1}$) of water passing through pots (i.e. of collected leachates following watering) after sea water soil immersion for the durations of 0 (control), 8 and 24 h.

Only four plants died during the experiment, these were all in the 24 h sea water soil immersion treatment; three from the 700 m ecotype and one from the 200 m ecotype. All plants from the 25 m ecotype survived 24 h soil immersion. At 14 d after the short-durations of soil flooding, ‘Stolon Growth’ was greatly reduced by ‘Immersion’ for all distance groups ($F_{(2,91)} = 50.25$, $P < 0.01$), with post-hoc SNK tests indicating the greatest reduction after 24 h soil immersion treatment ($P < 0.01$) (Fig. 2a). ‘Distance’

also had a significant effect on ‘Stolon Growth’ ($F_{(2,91)} = 3.40, P < 0.05$); likely due to a generally greater stem growth of 200 m plants and much reduced growth of 700 m plants following soil immersion. There was no interaction between ‘Immersion’ and ‘Distance’ ($F_{(4,89)} = 1.78, P > 0.05$). The loss of cotton thread markers used to identify stolons reduced effective replicate number (see Figure 2b) at 42 d, nevertheless the ‘Immersion’ effect remained apparent ($H_{(2)} = 35.22, P < 0.01$), but ‘Distance’ had no significant effect on ‘Stolon Growth’, as average growth of 25 m plants increased to similar rates as 200 m ($H_{(2)} = 2.15, P > 0.05$). However, average stolon growth of 700 m plants appeared to be much reduced even at 42 d after the longer duration (24 h) of soil immersion (Fig. 2b).

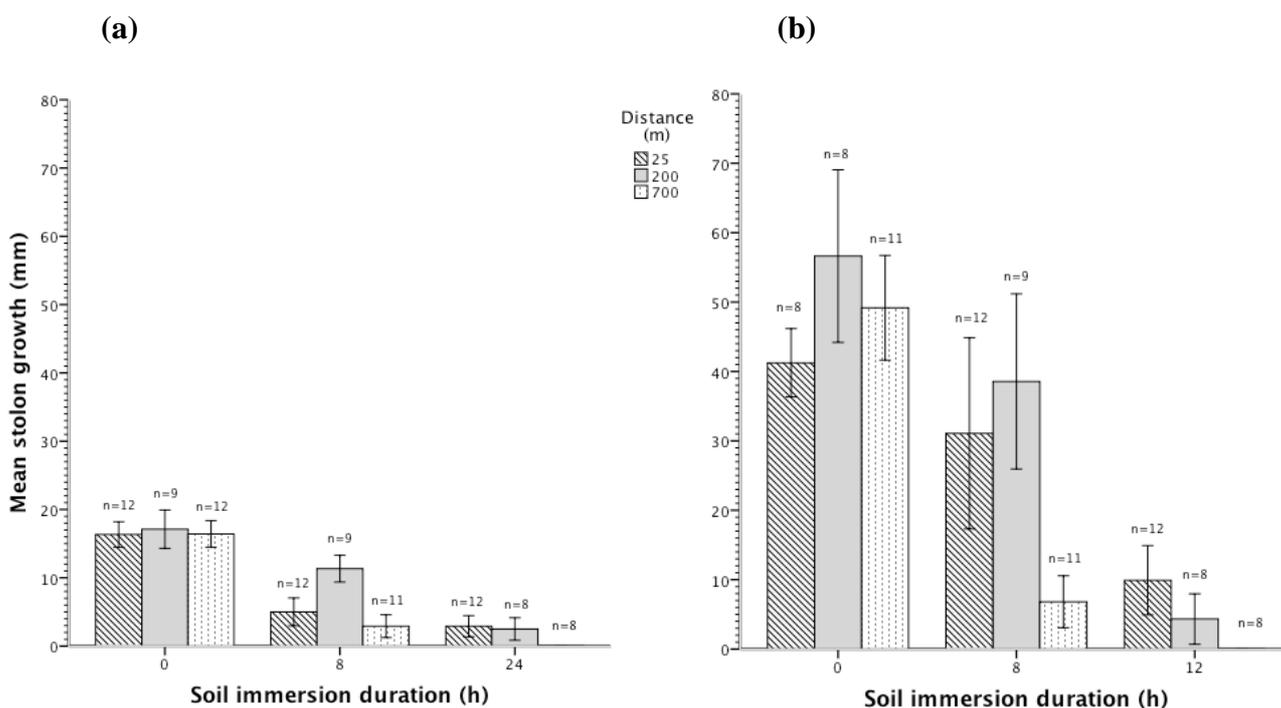


Figure 3.2 - Mean stolon extension ($\text{mm} \pm \text{SE}$) of *Trifolium repens* clones cultivated from parent plants from different locations along a natural salinity gradient (25 m is most saline, 700 m least saline; described in ‘Results’ section), (a) 14 d and (b) 42 d after the root-zones of plants were immersed in sea water.

While both ‘Immersion’ ($F_{(2,92)} = 14.18, P < 0.01$), and ‘Distance’ ($F_{(2,92)} = 6.12, P < 0.01$) had a significant effect on ‘Flowering Effort’ (Fig. 3.3), there was no interaction between ‘Immersion’ and ‘Distance’ ($F_{(4,90)} = 0.69, P > 0.05$). Post-hoc SNK tests revealed that the mean number of inflorescences per plant (‘Flowering Effort’) produced by the end of the experiment were reduced in both the 8 and 24 h soil immersion treatments ($P < 0.01$). The significant ‘Distance’ effect could be explained by greater number of inflorescences produced by the 200 m and 700 m control plants compared with the 25 m control plants, suggesting that these populations naturally produce more flowers. However, ‘Flowering Effort’ in the 200 m and 700 m plants was nonetheless greatly reduced by 24 h soil immersion. Similar patterns were observed for ‘Percentage Flowering’ (Fig. 3.4); 700 m plants produced more open flowers than plants in the groups collected at 200 m and 25 m. Pearson’s chi-squared test revealed that ‘Percentage Flowering’ in the 25 m plants was reduced by soil immersion ($\chi^2_{(36,2)} = 16.94, P < 0.01$). Although the same test could not be performed on 200 m and 700 m plants (over 50 % of cells in the test matrix had expected values of less than 5), there was a trend for reduced flowering in both these distance groups following soil immersion.

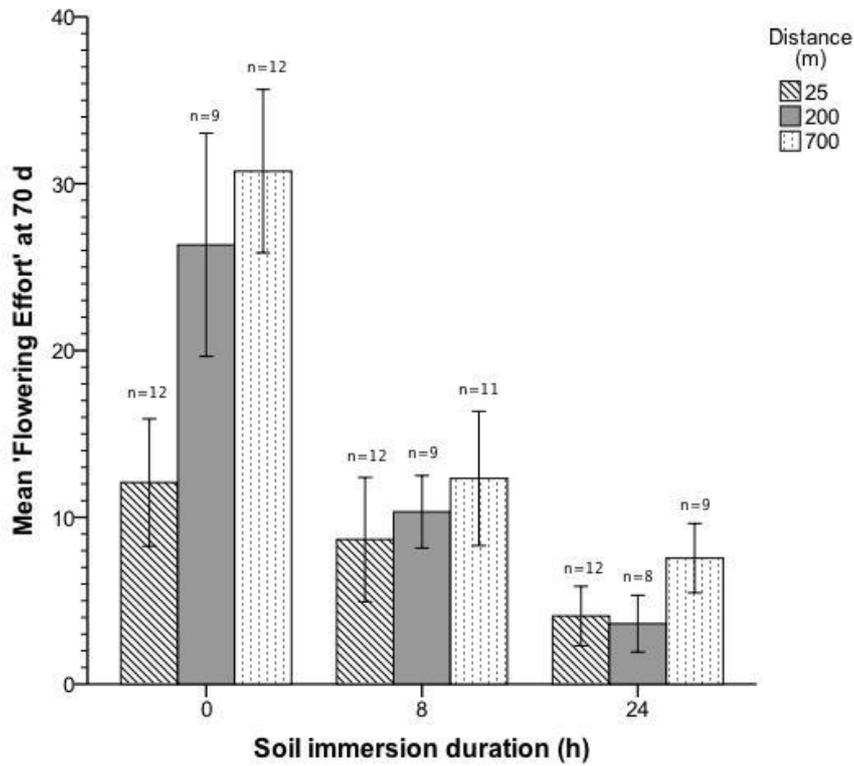


Figure 3.3 - The effects of immersion time on the mean (\pm SE) number of inflorescences ('Flowering Effort') produced by *Trifolium repens* clones cultivated from parent plants from different locations along a natural salinity gradient (25 m is most saline, 700 m least saline; described in 'Results' section) 70 d after root-zone immersion in sea water.

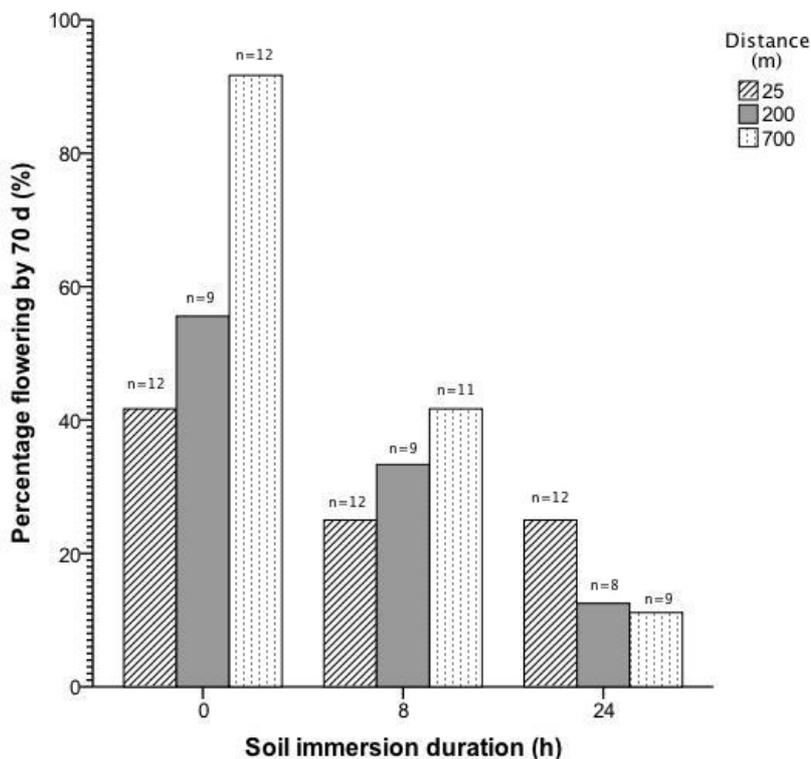


Figure 3.4 - The effects of immersion time on the proportion of *Trifolium repens* plants that had flowered by 70 d after root-zone immersion in sea water. Clonal fragments were cultivated from parents from different locations along a natural salinity gradient (25 m is most saline, 700 m least saline; described in 'Results' section).

3.4 Discussion

This experiment to simulate the effects of transient saline soil waterlogging yielded consistent ecophysiological and plant performance responses; two days after soil immersion, all plants exhibited higher leaf concentrations of Na^+ and Cl^- , concentrations of some organic solutes significantly changed (e.g. sucrose and proline increased), and longer-term plant growth and flowering potential were reduced. The fact that growth and flowering responses also varied according to the location of the parent plants along a natural salinity gradient, suggests that our study plants were displaying natural ecotypic variation to the short-duration salinity stress.

The accumulation of Na^+ and Cl^- in leaf tissues is commonly observed in salt-stressed plants which in-turn leads to the accumulation of organic solutes to counter the resulting osmotic imbalance (Wyn Jones & Gorham 2002; Flowers & Colmer 2008). It was interesting to note, however, that despite having different growth and flowering responses to seawater soil immersion, the accumulation of Na^+ and Cl^- in leaf tissues did not vary for plants from different locations along the natural salinity gradient. Unlike Rogers et al. (1997) who documented that tolerance of *T. repens* to longer exposures to salinity was associated with ‘exclusion’ of Cl^- from the shoot, the apparent salinity tolerance of plants we collected from the 25 m population could not be linked to differences in leaf ion concentrations (the trend in the present study for lower leaf Na^+ and Cl^- in ecotypes collected from closer to the sea wall was not statistically significant - Table 1). Moreover, in addition to regulation of leaf ion concentrations, other traits such as differences in “tissue tolerance” can also influence overall plant salinity tolerance (Munns & Tester 2008). Maintenance of tissue K^+ concentration, which can decrease in plants exposed to excess Na^+ , to retain a favourable K^+/Na^+ ratio of the cytoplasm for enzyme functioning, is also of importance for salt tolerance (Maathuis & Amtmann 1999), but for the short-term salinity exposures in the present experiment on

T. repens there was no significant treatment effect on leaf K^+ (Table 1). In addition to regulation of leaf ion concentrations, organic solutes that are compatible with enzymes and therefore accumulated in the cytoplasm are also of importance for adaptation to salinity (Munns & Tester 2008; Flowers & Colmer 2008). Organic solutes in plants can include various sugars, sugar alcohols, betaines, and amino acids, many of which accumulate with increasing plant exposure to NaCl, but the types and concentrations vary in different species (Flowers & Colmer 2008). *T. repens* leaves contained constitutively high concentrations of pinitol, whereas proline and sucrose concentrations rose dramatically in the salt-stressed plants (Table 2). The increased organic solute accumulation is likely a response to provide the osmotic balance needed in the cytoplasm for Na^+ and Cl^- accumulation in the vacuole.

The reduction in plant growth reported here mirrors that of plants in salinized agricultural systems (Bennett et al. 2009; Flowers et al. 2010). Simulated seawater soil flooding not only reduced vegetative growth, measured here for *T. repens* as stolon growth, but had the added effect of causing reduced flowering potential. Exposure of the roots to seawater is expected to exert a negative effect on plant growth and reproductive allocation via ionic and osmotic stresses; salt stress impacts on cell division and photosynthesis as an osmotic imbalance leads to stomatal closure and reduced CO_2 uptake and so less photosynthesis (Zhu 2001). Therefore, greater stress will be exerted on plants enduring longer root immersion as Na^+ and Cl^- ions have more time to accumulate in leaf tissues (as was observed here for all plants subject to 24 h soil immersion when compared to the 8 h treatment). This is reflected by the greatest reduction in stolon growth and flowering potential of *T. repens* occurring as a result of 24 h seawater soil immersion despite the fact that salt levels in the growing media were roughly comparable for 8 and 24 h treatments after removal from seawater and subsequent leaching due to watering.

Growth and flowering responses to seawater soil immersion also varied according to the location of the parent plant along a natural salinity gradient. After 24 h of seawater soil immersion, stolon growth of 700 m plants was severely limited, while 25 m and 200 m plants were less affected and seemed to return to similar rates of growth by 42 d. Similarly, although 'Flowering Effort' and the percentage of plants with flowering inflorescences were reduced for all distances, the effects were particularly marked for 700 m plants. Ecotype-specific variation in flowering as a consequence of long-term salinity exposure is well known for halophytes like *Aster tripolium* (Gray et al. 1979) and *Sporobolus virginicus* (Blits & Gallagher 1991), but ours is this first study to demonstrate this effect for a glycophyte from a natural salinity gradient when exposed to short-duration seawater soil flooding. Our results indicate that the 25 m- and to some degree the 200 m-ecotype, were resilient to transient seawater soil immersion presumably as a consequence of a local population adaptation to the higher soil salinity near to the sea wall embankment. Interestingly, a trade-off between salinity tolerance and reproductive allocation might be evident, as flowering potential in the 25 m ecotype was lower than in the 700 m population.

Plant adaptation to salinity has been shown for species in many hypersaline semi-arid/arid areas (Munns & Tester 2008), but such local adaptation also occurs in coastal plant populations exposed to salt spray and long-term accumulation of salt ions in the soil (Lowry et al. 2009), including *T. repens* (Ab-Shukor et al. 1988; Rogers et al. 1997). Our study is considerably different, however, in that we applied a one-off, short-term, salinity pulse via soil flooding in an attempt to mirror seawater inundation in a storm surge event or in the initial stages of managed realignment. Consequently, our plants experienced an immediate salinity shock followed by a gradual reduction of salt ions around the roots as freshwater diluted and leached salt from the potting media. Where the tidal regime has been reintroduced in managed realignment sites, soil salinity

is unlikely to decrease over time, unless freshwater input exceeds seawater input, in periods of heavy rainfall or where tidal levels are over-regulated by engineered mechanisms. However, in the latter occasions, or where coastal grasslands are flooded in a one-off event, the dissipation of salt ions over time may allow plants to recover from the initial impact of ionic and osmotic stress. This effect is not only likely to vary between plant species and ecotypes, but also with season and local weather conditions. The effects of seasonality and species identity remain to be elucidated, but we demonstrate here population-level variation in plant response to seawater soil flooding. Although ecotype-specific response to salinity stress has been demonstrated at the regional scale for *T. repens* (Ab-Shukor et al. 1988), our study evidences the presence of different salinity-tolerant ecotypes over relatively small distances within a single coastal site. If salinity-tolerant ecotypes are a widely-distributed feature of coastal plant species, supra-littoral vegetation may be naturally buffered to some extent against predicted sea-level rise and increased incidence of storm-surge events over coming decades. Indeed, this effect may also cause spatial variation in the transition of managed realignment sites into salt marsh vegetation. In areas that have not been previously exposed to salinity, less salinity-tolerant ecotypes may disappear more quickly than more salinity-tolerant individuals on soils previously exposed to higher levels of salinity. Unvegetated microsites may be more likely to appear in the former areas, where halophytes are able to colonise and establish in the absence of interspecific competition. The existence of flooding-tolerant ecotypes may also be important in developing salt-tolerant cultivars for use in saline soils (Ab-Shukor et al. 1988; Rogers et al. 1997; Bennett et al. 2009), and any coastal pastures susceptible to future episodes of seawater flooding.

3.5 Conclusion

As sea levels continue to increase, coastal realignments (both unmanaged and managed) in low-lying areas are likely to increase in frequency. As salt marsh development following coastal realignment is highly uncertain and trajectories for vegetation development are lacking, there is an increasing need for research into the initial responses of pre-existing coastal vegetation to sudden seawater inundation. Additionally, the increased likelihood of storm surge events over coming decades (Martin et al. 2011; Zappa et al. 2013), the international conservation importance of low-lying coastal vegetation and the role these areas play in coastal defence (Rhymer et al. 2010; Fisher et al. 2011; Hanley et al. 2014), call for a more detailed understanding of the structural and functional responses of coastal vegetation to periodic seawater flooding. It is demonstrated here that one common plant species component of many coastal grasslands and dune systems, *T. repens*, responds poorly to simulated seawater soil flooding, but that the response may be population-, i.e. ecotype-, specific and that the species consequently has an adaptive capacity to withstand short periods of soil inundation by seawater. Whether the likely increased selection pressure for plants resistant to seawater flooding impacts on other plant traits (e.g. growth, N-fixing capacity, anti-herbivore defence, reproductive potential) and thus the ecological role and economic value of this species is worthy of future attention. In addition, the impact of short-duration seawater flooding on multi-species mixtures and subsequent community assembly and function could yield many useful insights into the likely responses of coastal vegetation to rising sea-levels and the anticipated increased frequency and severity of saline flooding events.

Chapter 4 – Short-term salt marsh development in a recently implemented managed realignment scheme: Hydrodynamics

4.1 Introduction

Tidal regime is the most important driver of salt marsh habitat development (Allen 2000; Cooper et al. 2004; Spencer & Harvey 2012). In many biogeomorphological models of salt marsh functioning, hydrodynamics are considered to have a large degree of external control over a range of physical and chemical processes, which have ultimate internal control over vegetation zonation on the marsh surface (Allen 2000; Viles et al. 2008; Spencer & Harvey 2012). When suitably coupled with internal biotic processes, the tidal regime will boost ecosystem productivity and functioning (Odum 1995). However, certain inundation characteristics may restrict salt marsh development if not kept within pre-determined thresholds (Cooper et al. 2004).

The tidal signature of a salt marsh is a function of marsh morphology and tidal levels, i.e., the elevation of the marsh surface elevation in relation to the tidal frame. A large proportion of tides will flood and ebb in the main channels and creeks, but when water levels are raised above a certain level (often MHWS), seawater may spill over the marsh edge and channel banks, covering the marsh surface ('overmarsh' tide) (Lawrence et al. 2004). The lower the elevation of the marsh surface in the tidal frame, the higher the frequency of overmarsh tides in relation to the total number of high tides, and also the longer the period of tidal inundation ('hydroperiod'). Inundation frequency controls the import of seeds ('hydrochory'), sediment and nutrients to the marsh surface (Friedrichs & Perry 2001), all crucial in salt marsh development (see Fig 1.1, Chapter 1.2). The lower marsh undergoes the fastest rate of change in elevation as it attempts to reach equilibrium in the tidal frame (Allen 1990). At the same time, the ebb of an overmarsh

tide is important in the export of sediment and nutrients to neighbouring salt marshes (Odum 1988).

During an overmarsh tide, surface current velocities vary spatially and temporally with the depth of tidal inundation (Lawrence et al. 2004). Maximum current velocity occurs where tidal amplitude is greatest (i.e., lower marsh) and when the rate of the falling tide during ebb is fastest (at the time of salt marsh submergence and emergence) (Bouma et al. 2005; Friess et al. 2014). This is primarily determined by the size of the tidal prism, whilst the latter is also determined by how efficiently the marsh surface drains on an ebb tide (Friess et al. 2014). Sufficient current velocities are required for the erosion and expansion of salt marsh creek networks (Williams et al. 2002; Murray et al. 2008; Friess et al. 2014), which improves drainage of the local area, preventing waterlogging and ultimate soil reduction; factors which may otherwise result in reduced inhibit vegetation establishment (see Chapter 7; Ursino et al. 2004).

The term hydroperiod has been inconsistently defined in many papers (Nuttall 1997), but is defined here as the length of time over which the marsh surface is inundated during a single tidal cycle (Rowe & Dunson 1995; David 1996). Inundation duration is very significant in its relation to vegetation community composition: if a marsh area is inundated for a lengthy time period, oxygen levels may be reduced, causing the accumulation of toxic sulphides, reduced iron and manganese and lowered soil redox potential (Ingold & Havill 1984). Consequently, alterations to soil biogeochemistry are often the main cause of differences in vegetation community composition between managed realignment sites and natural salt marshes (Mossman et al. 2012b). Additionally, a single extended flooding event may cause stress responses in certain plant species, which can affect the growth and reproductive functioning of certain species (see Chapter 3; White et al. 2014), or even cause widespread death and

decomposition of vegetation, which can further lower soil redox potential (Baldwin & Mendelsohn 1998). In contrast, if a site is not flooded enough, a salt marsh community may not develop as a result of competitive exclusion by terrestrial species (see Chapter 5). However, seed germination and establishment may benefit from occasional long periods of exposure between tidal submergence. For example, Chapman (1960) found that seedlings of *Aster tripolium* could only establish if it had an exposure period of >5 days during neap tides, during which time the seedlings grew a root system to anchor the plant to the substrate.

Following managed realignment, the type and extent of habitat that develops is determined by the tidal regime, due to the specific abiotic preferences and competitive ability of different types of salt marsh vegetation (Cooper et al. 2004). According to the Environment Agency (2003), salt marsh will develop where intertidal areas are inundated by 80 to 450 high tides per year, with the species composition varying according to inundation frequency. Where an area is inundated in excess of 450 high tides per year, an unvegetated tidal flat is likely to develop. However, these are very simplistic guidelines, as different hydrological characteristics have varying degrees of influence on certain geomorphological and ecological processes in a salt marsh.

Although site hydrology is recognized as a key driver in salt marsh development, research is lacking into the hydrology of restored areas and therefore guidance on how best to implement the tidal regime in managed realignment sites is sparse (Montalto & Steenhuis 2004). In managed realignment schemes where the aim is to restore or create salt marsh, site-specific hydrodynamics need to be fully understood so that the tidal regimes can be controlled to create the desired type and extent of salt marsh, whilst reducing the risk of creating unvegetated tidal flat (Montalto & Steenhuis 2004; French 2006; Beauchard et al. 2011). In some cases, the tidal regime may be reinstated by

creating a simple ‘hole in the wall’ or even complete removal of the defence. However, as described in Chapter 1.5.1.3, reclaimed land is often significantly lower in elevation than adjacent natural marshes due to subsidence, sediment compaction and the absence of a sediment supply whilst used as agricultural land. Natural inundation of land so low in elevation would quickly lead to the development of tidal flat (French 2006).

In recent years, regulated tidal exchange (RTE) techniques have been employed to overcome elevation differences in managed realignment sites. This umbrella term includes many different types of engineered structures, such as sluice gates, spillways, pipes and culverts (Environment Agency 2003). The structure regulates the water level in the restored area according to the elevation of the site so that habitat creation is more controlled and flood risk is reduced (Ridgway & Williams 2011). However, Beauchard et al. (2011) suggest that in order to re-create an intertidal gradient, it is necessary to at least mimic the tidal signatures of nearby natural salt marshes, including simulation of spring-neap variability. Additionally, in many managed realignment sites, such as Goosemoor, on the Exe estuary in Devon, RTE is used as part of a ‘phased realignment’, where RTE mechanisms are used for a specified number of years, to instigate sediment accretion and salt marsh development, before removal and ultimate exposure of the site to a natural tidal regime (Chapter 1.5.1.3; (Environment Agency 2003). It is therefore imperative that the RTE site is able to adjust to local hydrodynamics, to become ‘self-regulated and integrated within its landscape’ (Middleton 2009).

In 2011, a new design of self-regulating tidal gate (SRT) was installed at a site on the Avon estuary near Aveton Gifford, south Devon, UK. SRTs typically allow variation between tidal cycles by using a float, which opens and later closes a valve or culvert at a predetermined water level. Although the mechanism has been used to create a saline

lagoon at Black Hole marsh, on the Axe estuary, East Devon, the aim is now to employ its versatility to create salt marsh (Ridgway & Williams 2011).

This study examines a three-year time series of hydrodynamic data collected at South Efford in comparison with data collected from an adjacent natural salt marsh and tidal flat. The dataset will be analysed to investigate how various hydrological characteristics are modified by the SRT over time and also in comparison with the adjacent natural salt marsh and tidal flat. I aim specifically to investigate the ways in which single tidal cycles are altered by the SRT mechanism and how temporal and spatial patterns in water levels may vary on the restored site. Consequently, how does this impact on specific characteristics of the tidal regime? As morphological change is highly dependent on site hydrodynamics, I will lastly assess whether there have been any significant morphological changes in the restored area. The implications of modified tidal characteristics on salt marsh development will be discussed and then investigated in detail in Chapters 5 and 6.

4.2 Materials and methods

4.2.1 Study sites

The study took place at South Efford managed realignment site (SEM), south Devon, UK (see Chapter 2.1 for full site description). The managed realignment site is 0.5–0.6 m lower in elevation than the adjacent natural salt marsh in the estuary, as the accretion of the managed realignment site was restricted following reclamation in the 1800s (Fig. 4.1). Therefore, instead of a simple breach, which would heighten flood risk in the local area as well as excessively flood the potential habitat and inhibit the development of salt marsh, a single ‘stop-go-stop’ SRT mechanism was installed in the embankment by the Environment Agency. The SRT is controlled by a flotation device, which causes a metal plate to close over a 900mm (EA) diameter culvert at low water levels (at this point, the

SRT is at an angle of 48°). The plate moves anticlockwise as water levels rise, which opens the culvert, then a second plate moves over the culvert at higher water levels (see Fig. 2.4 in Chapter 2.1). When the second plate fully closes over the culvert, the SRT is at an angle of 109° . Adjusting the float can alter the water levels at which the SRT opens and closes.

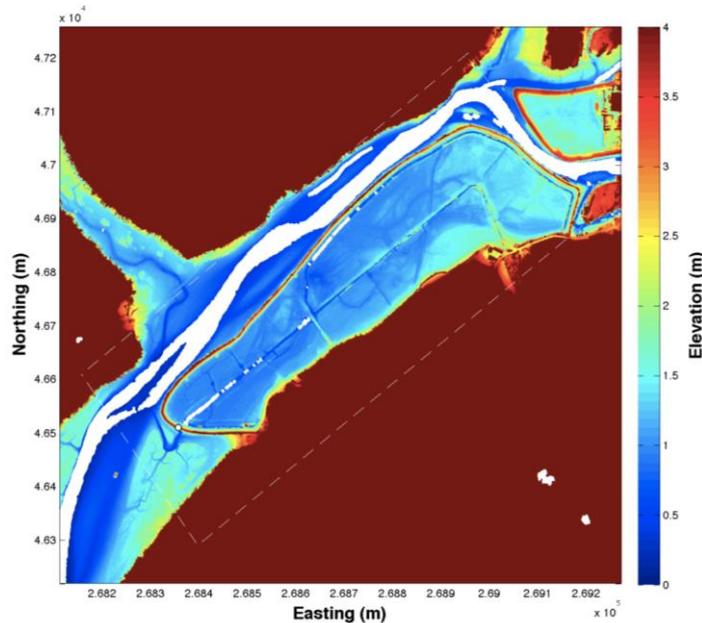


Figure 4.1 – Digital elevation model of South Efford based on PCO LiDAR data. The managed realignment site is surrounded by an embankment (>3.5 m), within the outline of the white polygon. Natural salt marsh lies to the south west of the site, adjacent to the embankment. Tidal flat fringes the natural marsh. LIDAR data courtesy of Channel Coastal Observatory (www.channelcoast.org).

4.2.2 Morphological development

In 2011, prior to initial inundation of the managed realignment site, a measurement grid was established using a laser total station (Trimble Total Station 5600). The measurement grid has the SRT as the origin and the x -axis and y -axis represent the length and width axis of the marsh, respectively (Figure 4.2). A total of 11 across-marsh measurement transects were established, with one of these crossing the natural salt marsh (SEN) to the south of the restored marsh site. Benchmarks were established along

the margin of the site and were used for re-sectioning the total station during repeated surveys in May 2012, July 2013 and May 2014.

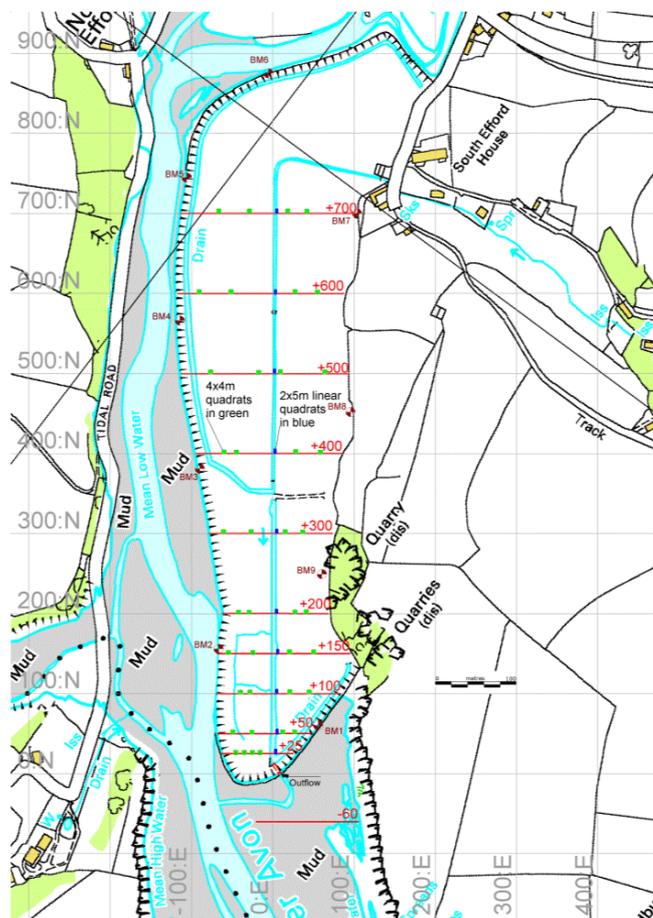


Figure 4.2 - South Efford managed realignment site displayed in the site local grid. The self-regulating tidal gate, indicated on the southern margin of the marsh ('outflow'), is the origin of the measurement grid. Morphological transects are marked by red lines and are positioned at increasing distances from the tidal gate.

4.2.3 Hydrodynamics

Water levels in the managed realignment site and the natural salt marsh were recorded from 1st September 2011 to 31st May 2014, using Impress S12C pressure transducers with data being logged at 15-min intervals. These data were firstly examined to identify differences in the tidal signatures of the managed realignment site and the natural salt marsh.

Secondly, the tidal data were used in combination with the elevation of the restored salt marsh surface, the natural salt marsh surface and the adjacent tidal flat surface to enable comparisons to be drawn between the three habitats. On examination of the baseline total station survey and a digital elevation model (DEM) created from LIDAR data collected by the Environment Agency (Fig. 4.1), the average elevation of the restored salt marsh surface was assumed to be 0.9 m ODN, whilst the natural salt marsh and tidal flat surfaces were assumed to be 1.5 and 1.0 m ODN, respectively. This enabled different hydrological characteristics to be computed per average month. The average month was calculated for all specific periods examined, to avoid between-month variability in descriptors caused by differences in the lengths of months. The following hydrological characteristics were calculated: -

- Inundation frequency, i.e., the number of overmarsh tides (N_{otide})
- Total duration of tidal inundation (D_{otide})
- Average hydroperiod, i.e., inundation duration during an average overmarsh tide, or $D_{\text{otide}}/N_{\text{otide}}$ (T_{otide})
- Longest period of tidal submergence (D_{sub})
- Longest period of exposure (D_{exp})
- Average rate of falling tide, i.e. speed at which the ebb tide falls ($\langle dh/dt \rangle$)

One-way analyses of variance (ANOVA) followed by post-hoc Tukey's HSD tests (reduces Type I error when comparing multiple, large sets of means) were employed to compare hydrological characteristics between the restored area, natural salt marsh and tidal flat, for different time periods (defined by hydrodynamic variability in the restored marsh, as outlined in the Results section). In addition, spatial patterns in tidal inundation duration per month and the extent of flooding were examined and compared between specific time periods by using tidal data in conjunction with the DEM of South Efford.

The analyses and graphical representation of all data were produced using MATLAB 2011a (The Mathworks, Inc., Massachusetts, United States).

4.3 Results

4.3.1 Hydrodynamics

The SRT has a major impact on the tidal signature of the restored area. Figure 4.3a displays water levels in the estuary and restored area on 11th February 2013 (a spring tide), with the position of the SRT shown in Figure 4.3b. The culvert was closed by the first metal plate at an angle of 50.4° whilst water levels in the estuary and restored area were low (low tide at approximately 3.45am). The SRT started to open with the rising estuary level, prompting water levels in the restored area to rise. However, as the estuary level reached ~1.1 m ODN, the second metal plate moved over the culvert to fully close the SRT again at 115°, approximately 1 hour after the marsh level started rising. This acts to ‘cut off’ the natural high tide maximum in the restored area. Levels in the restored area continued to rise very slightly, due to freshwater input, therefore high tide in the restored area occurred 3 hours after estuary high tide. At this point on the estuary lowering tide (1.43 m ODN), the SRT started to open again, causing water levels in the restored area to decline. After 2.5 hours, lower water levels were occurring in the estuary (0.69 m ODN), prompting the first metal plate to close over the culvert again. Over the next four hours, estuary and restored levels slowly declined to low tide.

On a neap tide, such as that on 18th February 2013 (Fig. 4.4a), there was a slower rate of rising tide in the estuary and the estuary high tide was relatively low, only 0.23 m above the restored marsh high tide. This caused the SRT to move more gradually, to stabilise at high tide in a partially ‘open’ position of 88.8°. The SRT did not remain in this position for long, as water levels in the estuary declined shortly after high tide, prompting the gate to start closing and water levels in the restored area to decline.

Therefore, the SRT lowers tidal amplitudes in the restored area compared to those in the estuary. Additionally, there are conspicuous differences in tidal amplitude between spring and neap tidal cycles in the estuary, whilst tidal amplitudes in the restored area do not seem to vastly differ between spring and neap tides, as high tide levels remain fairly consistent. For example, on 11th February, average spring tidal amplitude in the estuary was 4.85 m, with high tide levels of 2.83 m ODN and 2.5 m ODN respectively per tidal cycle (Fig. 4.3a). In contrast, average neap tidal amplitude in the estuary on 18th February was less than half of the spring tidal amplitude examined above, at 2.37 m, with much lower high tide levels of 1.32 m ODN and 1.22 m ODN respectively per tidal cycle. In the restored area, the investigated spring and neap tidal amplitudes were very similar, at 1.69 m and 1.8 m respectively and high tide levels remained the same on spring and neap tides, at 1.09 m ODN for the first high tide and 1.07 m ODN for the second.

However, water levels did appear to remain elevated for a longer period of time on spring tides in the restored area. Water levels remained above 0.9 m ODN for 7 hours on the first spring tidal cycle of 11th February in the restored area (Fig. 4.3a) due to the closed position of the SRT retaining high waters in the restored area between 5.15 - 9.30am (Fig. 4.3b). In contrast, on the first neap tidal cycle of 18th February, water levels remained above 0.9 m ODN for only 4 hours (Fig. 4.4a).

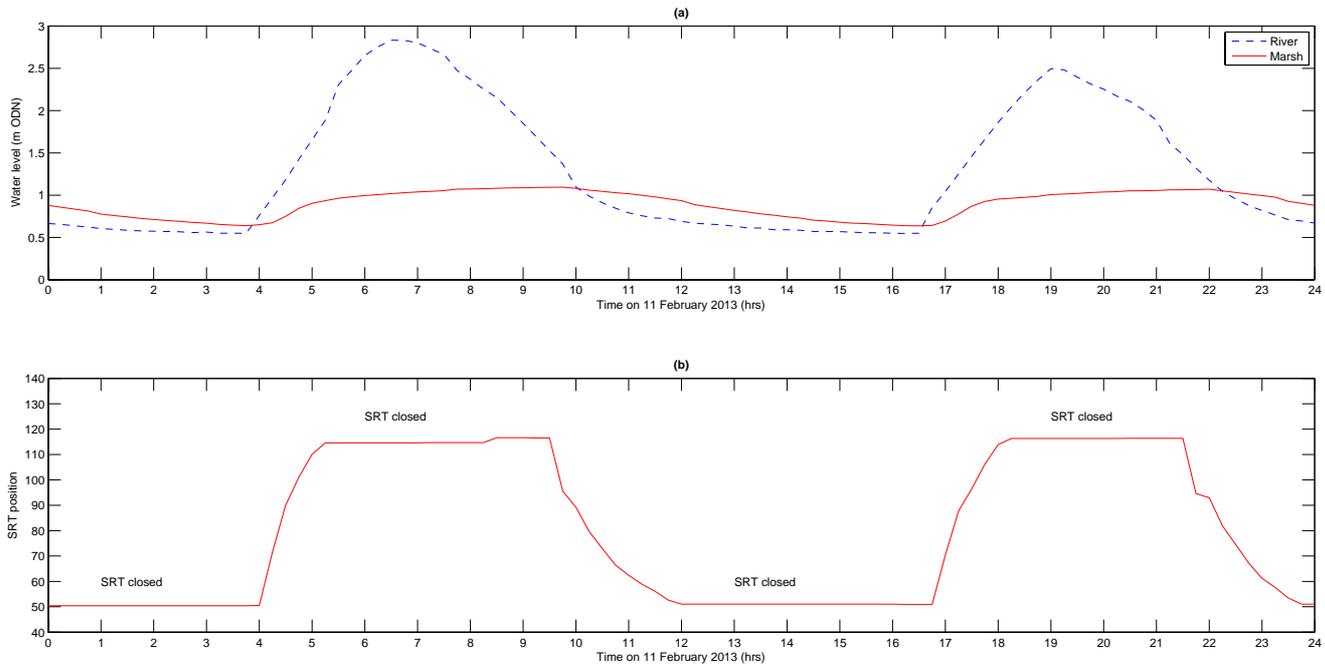


Figure 4.3 – (a) Water levels (m ODN) in the restored area ('Marsh') and in the estuary ('River') during a spring tide on 11th February 2013; (b) Position of the SRT over the same period.

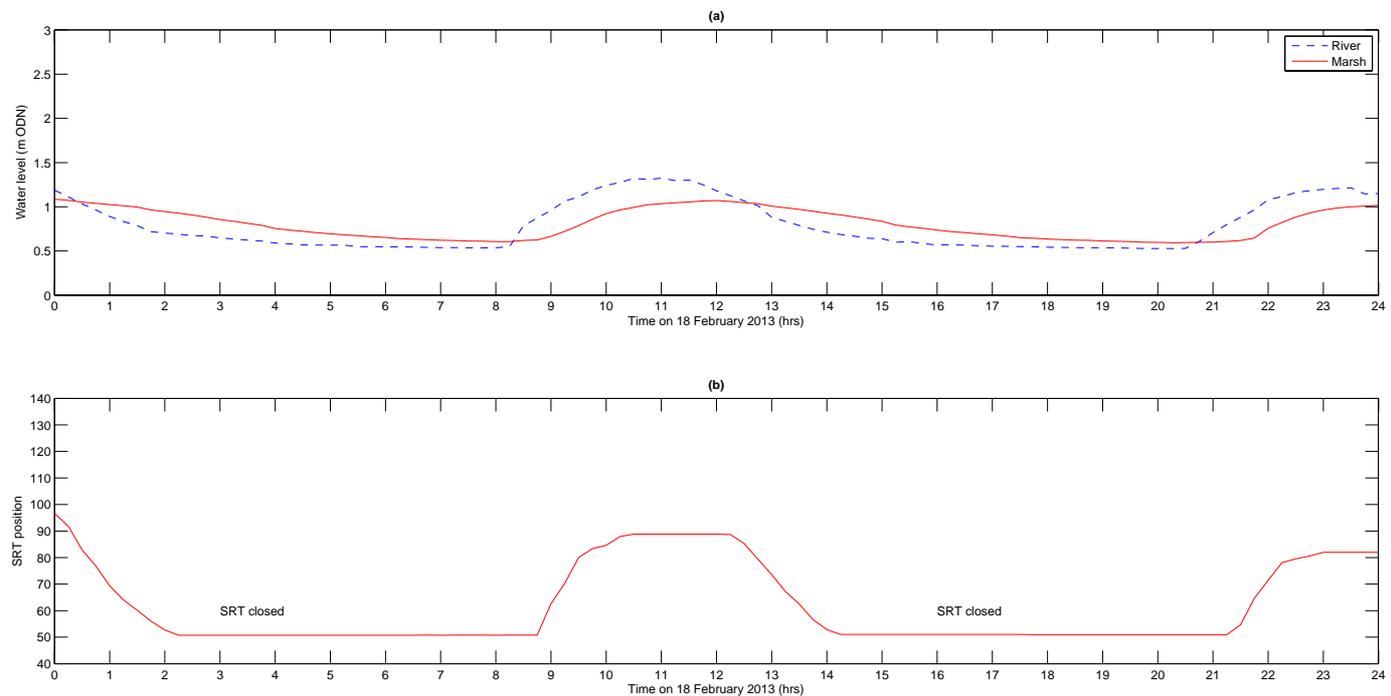


Figure 4.4 – (a) Water levels (m ODN) in the restored area ('Marsh') and in the estuary ('River') during a neap tide on 18th February 2013; (b) Position of the SRT over the same period. Periods of SRT closure indicated.

Fig. 4.5 displays time series of (a) water levels in the estuary; (b) water levels in the restored area and (c) the SRT position from September 2011 – May 2014. To re-iterate findings from the above investigations into single tidal cycles, spring-neap variability is clearly visible in the estuary time series, whilst such patterns are not seen in the restored time series, except during the period June – October 2013 when the SRT was malfunctioning. The SRT time series is highly temporally variable, partly due to adjustments made to the SRT settings by the Environment Agency, but also due to malfunctions, such as large debris obstructing movement of the SRT plate. As water levels in the restored area are controlled by the SRT, they are also highly variable.

It is possible to identify certain periods of tidal characteristics. During September 2011 – May 2012, high tide levels were 0.8 – 1 m ODN. Three months of water level data from the restored area are missing (from 21 June to 30 September 2012) due to a malfunctioning pressure sensor, although observations suggest high tide levels were similar to the preceding months (White, pers. obs.). From October 2012 to May 2013, high tide levels increased to c. 1.1 m ODN following adjustments to the SRT. From June 2013 – October 2013, high tide levels generally exceeded 1.1 m ODN and often reached 1.2 m ODN, but this is likely due to SRT malfunctioning. From November 2013 – January 2014, high tide levels were highly variable, but generally exceeded 1.2 m ODN. Tide levels were particularly high in December 2013 – February 2014 during a period of sustained heavy rainfall, which caused unusually high tide levels in the estuary as well as maximum high tide levels in the restored area of 1.74 m ODN. Water levels remained elevated in the restored area until April 2014, possibly due to limited drainage through the SRT whilst the estuary was in spate. The SRT data shows erratic patterns during February 2014, but this is likely due to inaccurate recording by a malfunctioning sensor, which stopped working during March and April 2014. However,

water levels in both the estuary and the restored area appeared to have returned to pre-flood functioning by May 2014.

For the same time period, a time series of monthly tidal statistics for the restored site, natural salt marsh and tidal flat are presented in Figure 4.6. Results for the natural marsh (Fig. 4.6b) and tidal flat (Fig. 4.6c) are relatively consistent in comparison to results for the restored site, which are highly variable. Some general patterns can be extracted from the restored site data though (Fig. 4.6a). Although the number of overmarsh tides between September 2011 and May 2012 was generally low; by November 2012, the SRT had been adjusted to allow more frequent inundation of the restored marsh surface (Fig. 4.6a). Similarly, the total length of time that the area was inundated, the average hydroperiod and longest period of submergence were also low in the first few months, but all gradually increased in later months. The rate of falling tide is the only tidal characteristic that remains fairly consistent throughout the whole time series, ranging between 0.04 cm min^{-1} and 0.09 cm min^{-1} .

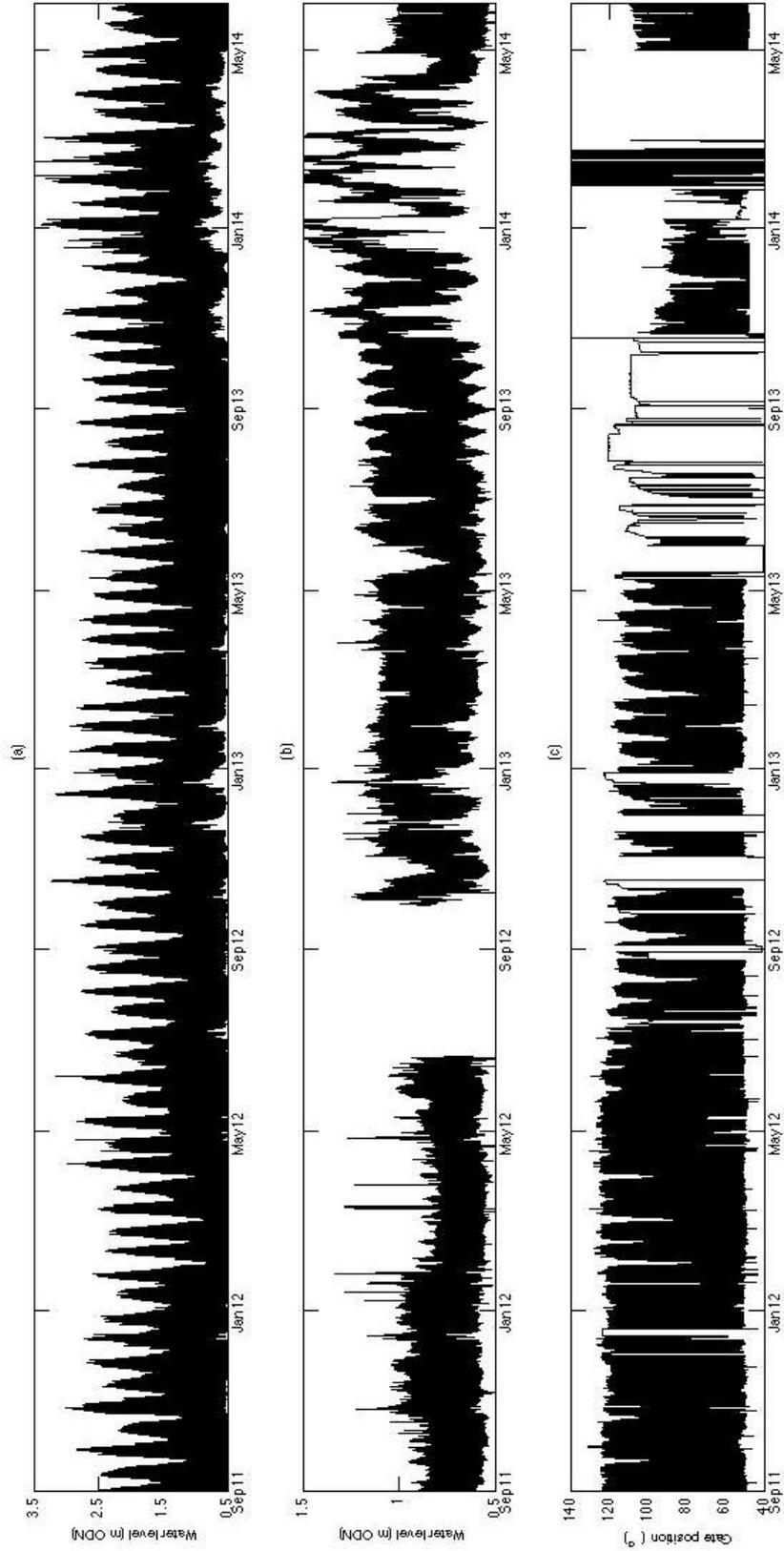


Figure 4.5 – Time series of (a) water levels (m ODN) in the estuary; (b) water levels (m ODN) in South Efford managed realignment site; (c) position of the self regulating tidal gate (SRT; °) from September 2011 to May 2014. Gaps in the data are due to sensor malfunction.

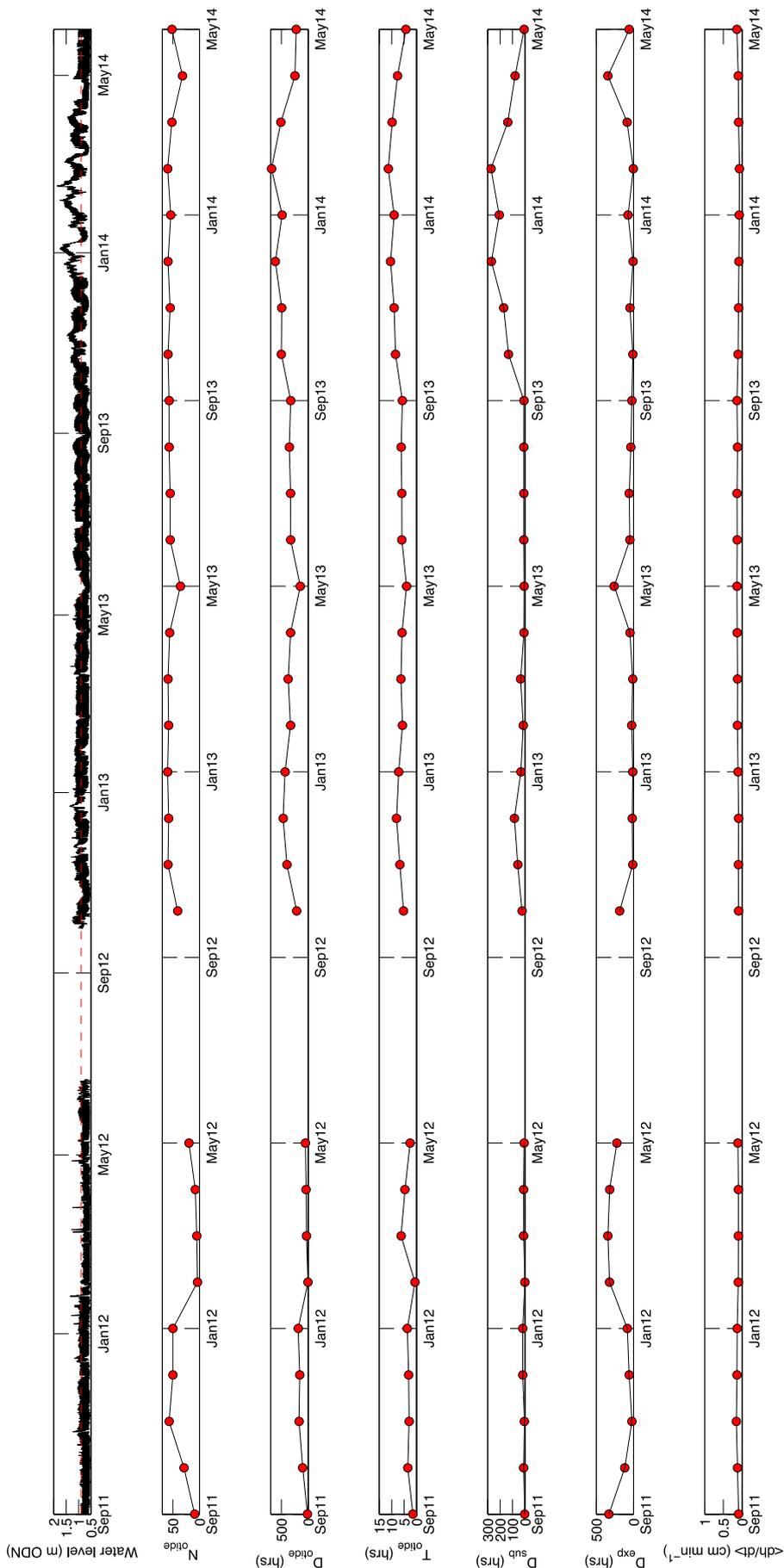


Figure 4.6 – Time series at South Efford restored marsh (a), natural marsh (b) and tidal flat (c), of (i) number of inundations; (ii) inundation duration (hours); (iii) hydroperiod (hrs); (iv) maximum duration of submergence (hours); (v) maximum duration of exposure (hours); (vi) rate of falling tide, per month ($cm\ min^{-1}$). Gaps in the data are due to sensor malfunction.

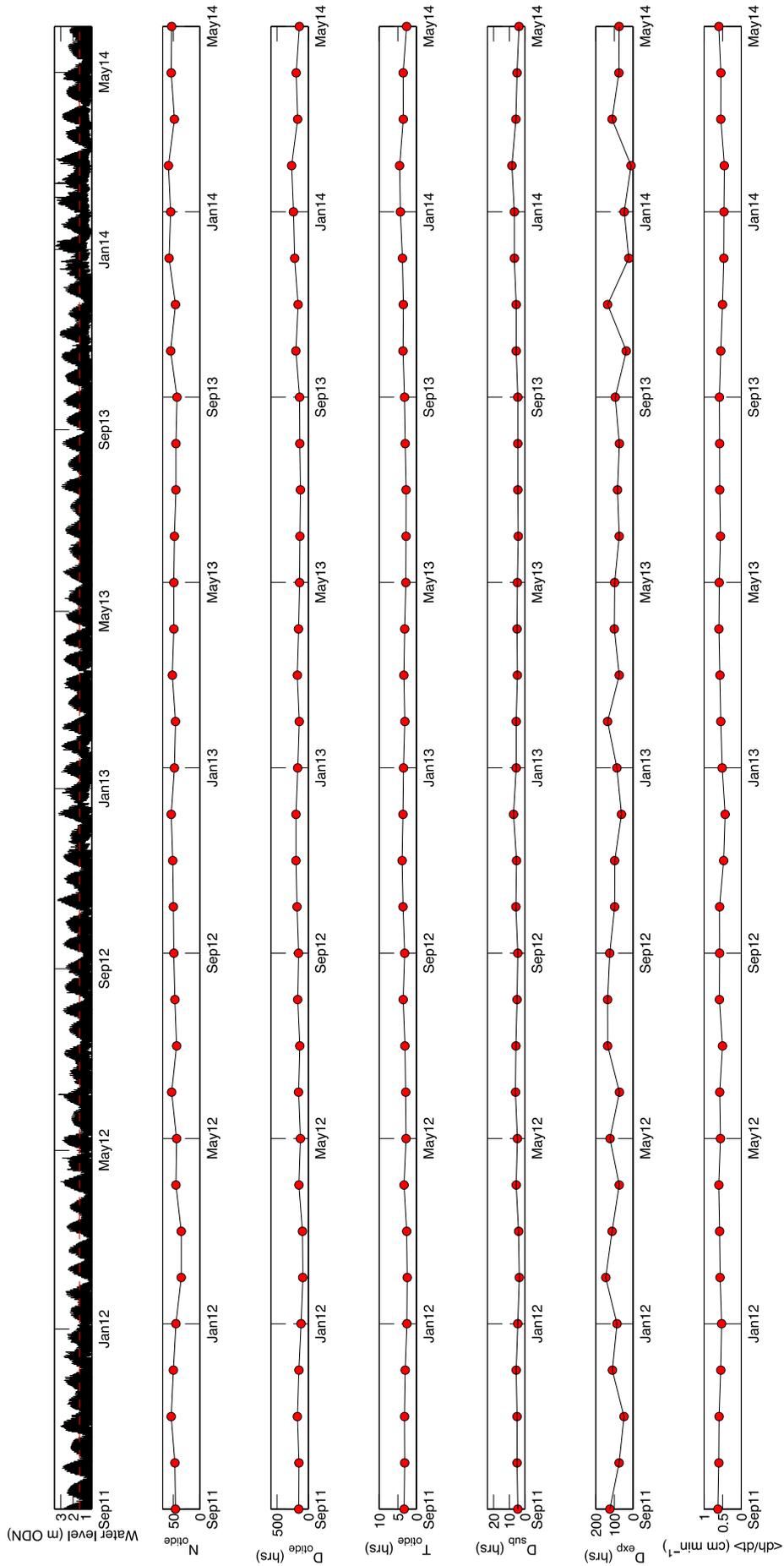


Fig. 4.6 ctd.

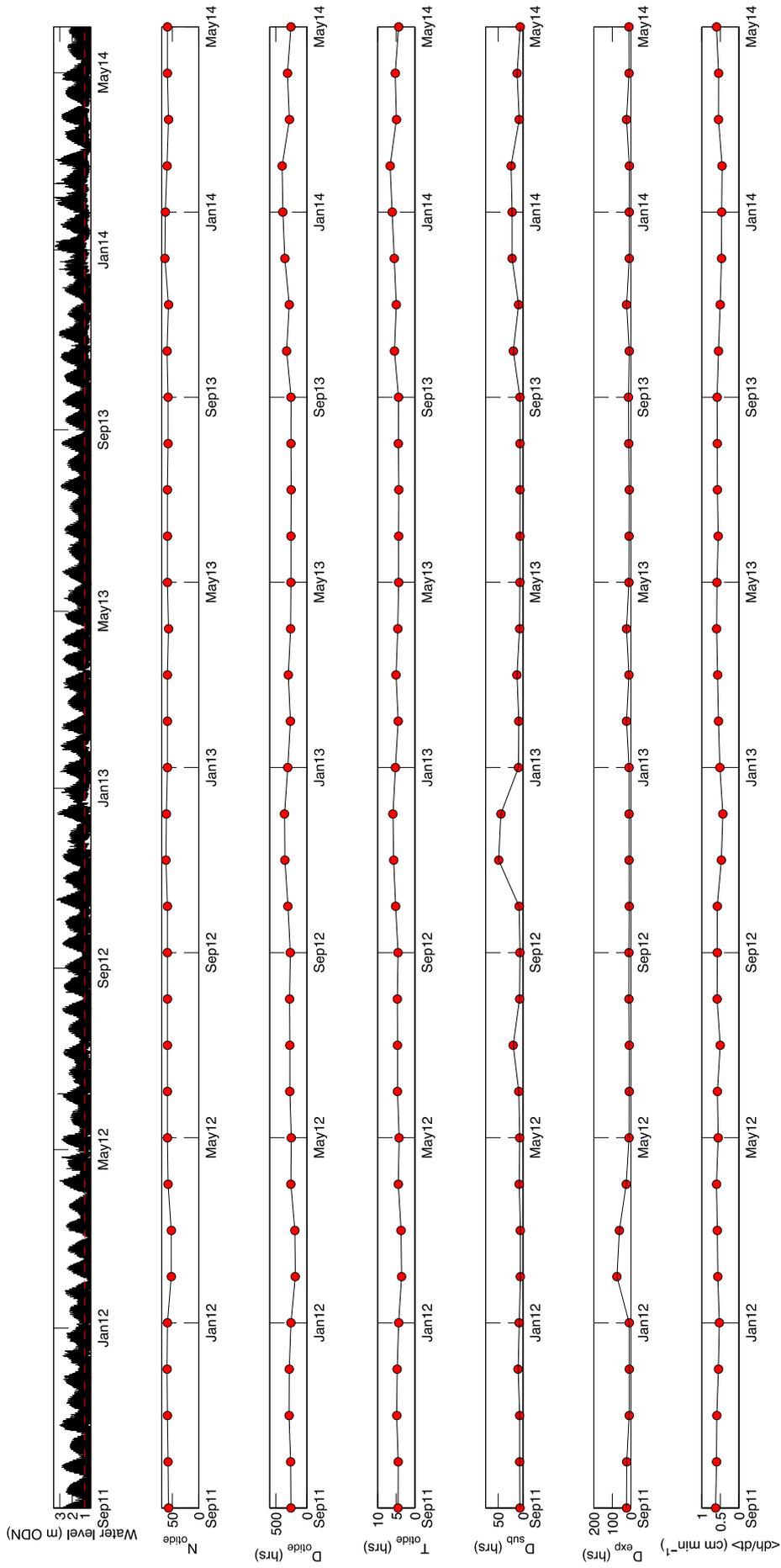


Fig. 4.6 ctd.

Consequently, monthly values of each inundation characteristic were averaged over specific phases, based on similar hydrodynamic conditions: (1) September 2011 – May 2012; (2) October 2012 – May 2013; (3) September 2013 – May 2014. Hydrodynamics differed substantially between these phases. During Phase 1, water levels at high tide generally remained below 1 m ODN (Fig. 4.5b), whilst minor adjustments to the SRT caused an increase in high tide levels to ~1.2 m ODN during Phase 2. A combination of heavy rainfall and SRT malfunction caused further increases in Phase 3.

Phase 1 is characterized by low inundation frequency in the restored site, with a lower average of 25.8 ± 7.3 overmarsh tides per month (N_{otide}), as opposed to 44.1 ± 2.1 on the natural marsh and 57.0 ± 1.0 on the tidal flat (Fig. 4.7a.). A one-way ANOVA followed by Tukey multiple tests of comparison revealed significant differences between the natural and restored sites ($F_{(2,24)} = 12.78$, $P < 0.05$), as well as the restored site and tidal flat ($P < 0.01$). As a result, the restored site had the longest average value of maximum exposure at 234.5 hours, longer than both the natural marsh and tidal flat ($F_{(2,24)} = 11.17$, $P < 0.01$). The restored site was inundated for 82.7 ± 23.9 hours per month, which was significantly lower than the tidal flat at 248.8 ± 11.9 hours per month ($F_{(2,24)} = 26.72$, $P < 0.01$) and marginally lower than the natural salt marsh at 132.3 ± 9.9 hours per month (Fig. 4.7b). Although not shown in Fig. 4.7, the average hydroperiod per month was also significantly different between all groups ($F_{(2,24)} = 23.17$, $P < 0.01$), again the shortest occurring in the restored area at 1.4 ± 0.4 hours and the longest on the tidal flat at 4.1 ± 0.2 hours. Despite this, the restored site had the longest length of maximum submergence per month at 9.6 ± 2.1 hours, more than twice as long as maximum submergence of the natural marsh ($F_{(2,24)} = 4.14$, $P < 0.05$) (Fig. 4.7c). Average depth of inundation was significantly different between all sites ($F_{(2,24)} = 4.14$, $P < 0.01$), with lowest depths occurring on the restored marsh (0.07 ± 0.02 m) and highest depths on the tidal flat (0.6 ± 0.02 m) (Fig. 4.7e). The average rate of falling tide was also slower on

the restored site than both natural marsh and tidal flat ($F_{(2,24)} = 811.1$, $P < 0.01$), falling at just $0.07 \pm 0.004 \text{ cm min}^{-1}$, five times slower than in the natural environment at $0.35 \pm 0.006 \text{ cm min}^{-1}$ (Fig. 4.7f).

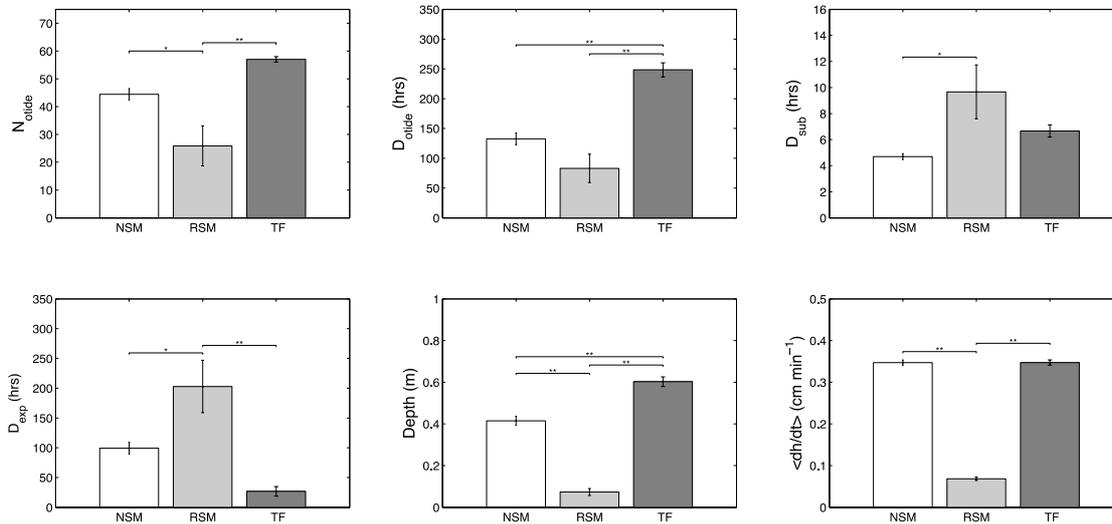


Figure 4.7 – Comparison of the natural marsh (NSM), restored area (RSM) and tidal flat (TF) at South Efford during Phase I (September 2011 – May 2012) in mean (\pm SE) (a) number of inundations; (b) inundation duration (hours); (c) maximum duration of submergence (hours); (d) maximum duration of exposure (hours); (e) depth at high tide (m); (f) rate of falling tide, per month (cm min^{-1}). Asterisks mark significance (* = $P < 0.05$; ** = $P < 0.01$; $N = 9$).

Inundation frequency was greatly increased in the restored area during Phase 2, as 93 % of high tides inundated the marsh surface, increased from 51 % in Phase 1 (Fig. 4.8a). Inundation duration had become longest in the restored site at 334.1 ± 38.9 hours per month ($F_{(2,21)} = 12.93$, $P < 0.01$), longer than inundation of the tidal flat at 300.7 ± 14.3 hours per month ($P < 0.01$) and the natural salt marsh at 169.2 ± 8.0 hours per month ($P < 0.01$) (Fig. 4.8b). Similarly, the average hydroperiod per month at the restored site was 5.7 ± 0.7 hours, almost twice as long as the natural marsh hydroperiod ($F_{(2,21)} = 9.94$, $P < 0.01$) and closely followed by the tidal flat average hydroperiod at 4.9 ± 0.2 hours. Maximum duration of submergence remained longest in the restored area at 34.1 ± 9.7 hours, approximately 30 hours longer than in the natural marsh ($F_{(2,21)} = 4.6$, $P <$

0.05) (Fig. 4.8c). However, although average depth of inundation increased in the restored area to 0.14 ± 0.01 m in Phase 2, it is still significantly lower than in the natural marsh and tidal flat ($F_{(2,21)} = 560.90$, $P < 0.01$) (Fig. 4.8e). Similarly, the average rate of falling tide remained unchanged, significantly lower than that of the natural marsh and tidal flat ($F_{(2,21)} = 179.25$, $P < 0.01$) (Fig. 4.8f).

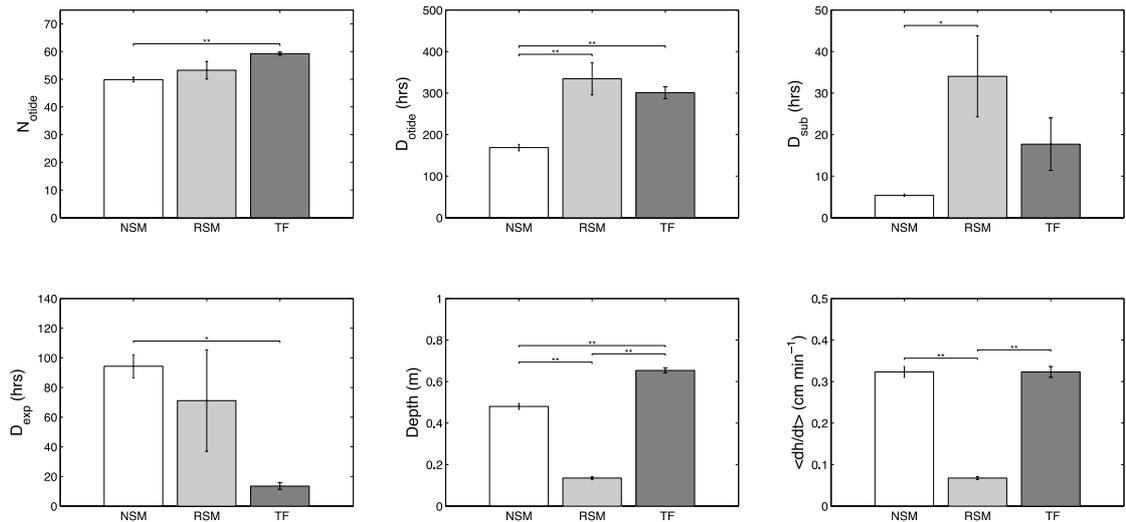


Figure 4.8 – Comparison of the natural marsh (NSM), restored area (RSM) and tidal flat (TF) at South Efford during Phase II (October 2012 – May 2013) in mean (\pm SE) (a) Number of inundations; (b) Inundation duration (hours); (c) maximum duration of submergence (hours); (d) maximum duration of exposure (hours); (e) depth at high tide (m); (f) rate of falling tide, per month ($cm \cdot min^{-1}$). Asterisks mark significance (* = $P < 0.05$; ** = $P < 0.01$; $N = 8$).

During Phase 3, inundation frequency remained high in the restored area, similar to Phase 2 (Fig. 4.9a). However, the site was inundated for significantly longer per month than the tidal flat as well as the natural marsh ($F_{(2,24)} = 15.35$, $P < 0.01$) (Fig. 4.9b) and maximum length of submergence was also significantly longer in the restored marsh than the other sites ($F_{(2,24)} = 15.71$, $P < 0.01$) (Fig. 4.9c), having risen from 34.1 ± 9.7 hours in Phase 2 to 138.1 ± 32.3 in Phase 3. As in Phase 2, maximum lengths of exposure in the restored area were reduced from those in Phase 1 to become similar to the natural marsh (Fig. 4.9d; 71.7 ± 35.5 hours and 69.4 ± 14.3 , respectively) ($F_{(2,24)} =$

2.31, $P > 0.05$). Although average water depths almost doubled in the restored area to 0.14 ± 0.01 m, they remained significantly lower than on the natural marsh and tidal flat ($F_{(2,24)} = 57.38$, $P < 0.01$) (Fig. 4.9e), as did the average rate of falling tide ($F_{(2,24)} = 237.20$, $P < 0.01$) (Fig. 4.9f).

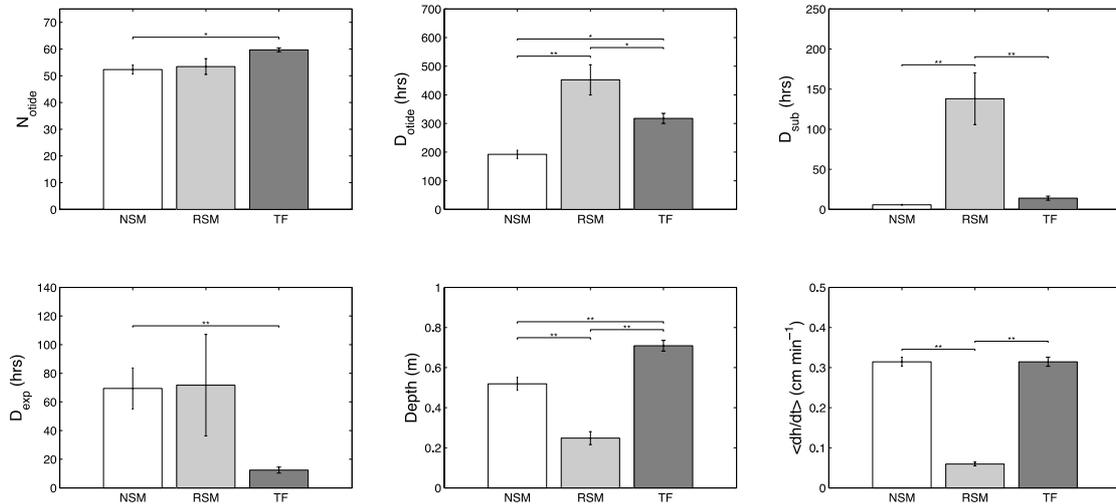


Figure 4.9 – Comparison of the natural marsh (NSM), restored area (RSM) and tidal flat (TF) at South Efford during Phase III (September 2013 – May 2014) in mean (\pm SE) (a) Number of inundations; (b) Inundation duration (hours) ; (c) maximum duration of submergence (hours); (d) maximum duration of exposure (hours); (e) depth at high tide (m); (f) rate of falling tide, per month ($cm\ min^{-1}$). Asterisks mark significance (* = $P < 0.05$; ** = $P < 0.01$; $N = 9$).

Figure 4.10 shows a cumulative frequency of the water level data per week for each phase and in Figure 4.11 the spatial distribution of the inundation characteristics is presented. During Phase 1, water levels were below 0.9 m (average marsh elevation) for approximately 90 % of the average month, which would explain the visibly limited spatial extent of inundation per month in Fig. 4.11a. It would appear that only areas of very low elevation (i.e. less than 0.9 m ODN) were inundated for a longer amount of time, such as the crater at $y = 400m$ which was inundated for up to 500 hours per month. During Phase 2, water levels were much higher, with levels above 0.9 m ODN for almost 50 % of the month (Figure 4.10). This is reflected in Fig. 4.11b, where a large proportion of the marsh surface was inundated between 250 and 350 hours per month.

Water levels were much higher for a larger proportion of the time in Phase 3 (Fig. 4.10) and there was a massive increase from Phase 2 in the spatial extent of flooding (Fig. 4.11c), with some areas at $y = 700\text{m}$ inundated for over 350 hours per month. The same area of marsh surface that was inundated between 250 and 350 hours per month in Phase 2 was inundated in excess of 400 hours per month in Phase 3.

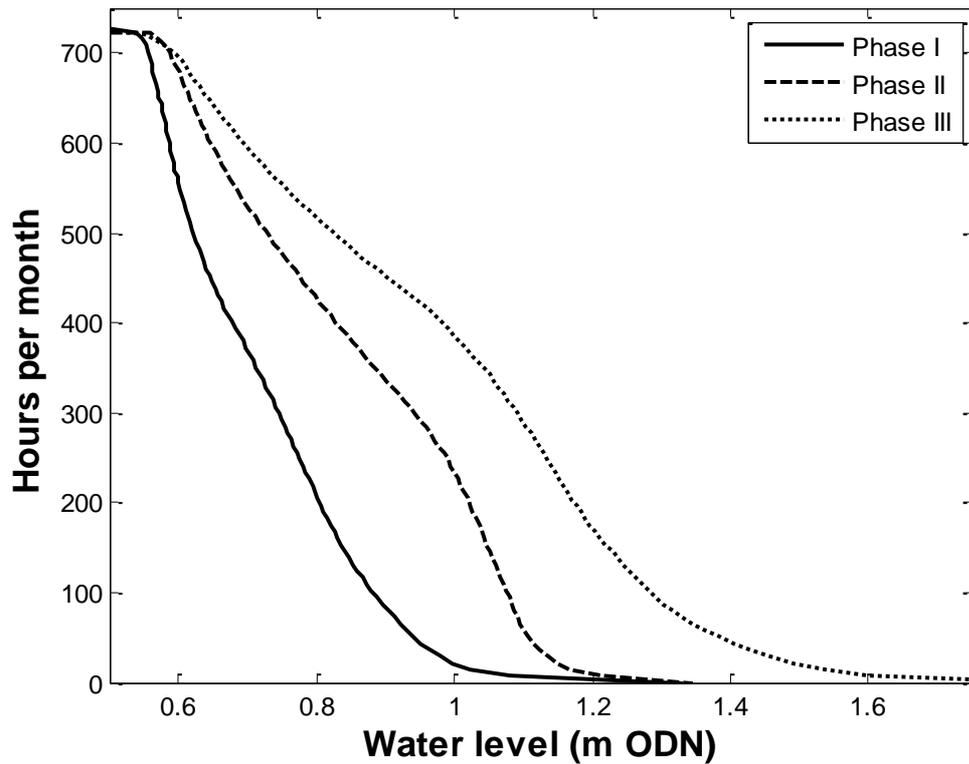


Figure 4.10 – The cumulative temporal distribution of water levels (m ODN) in South Efford managed realignment site in average hours per month during Phase I, II and III.

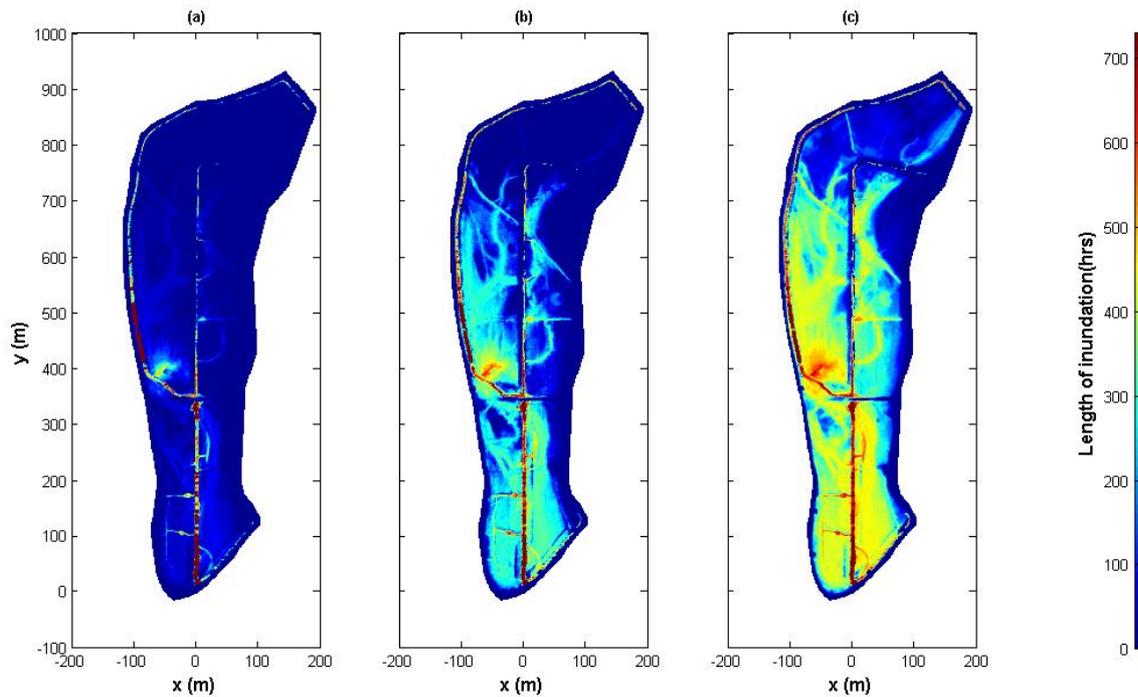


Figure 4.11 – Spatial patterns of tidal inundation in South Efford restored area in average hours per month during (a) Phase I; (b) Phase II and (c) Phase III. The SRT is at the origin of the measurement grid (0) and the x-axis and y-axis represent the width and length axis of the marsh, respectively. LIDAR data courtesy of Channel Coastal Observatory (www.channelcoast.org).

4.3.2 Morphological development

The most obvious morphological change was on the 25 m transect, as widening and deepening occurred on the west side of the channel, causing the channel bank to retreat by ~5 m between 2011 and 2014 (Fig. 4.12a). Deposition occurred in the channel on the eastern side (Fig. 4.13). This effect was fairly localized, as no significant widening of the channel occurred at 50 m (Fig. 4.12b), 100 m (Fig. 4.12c) and 200 m (Fig. 4.12d). New creek formation was not evident on any transect. Significant differences in marsh surface elevation are difficult to identify between surveys due to inaccuracies of the survey method and vegetation growth. However, by 2014, the marsh surface in some areas is higher in elevation than in the 2011 baseline survey. For example, the marsh surface adjacent to the channel on the 25 m transect ($x = -20 - -40$) has risen by <10cm.

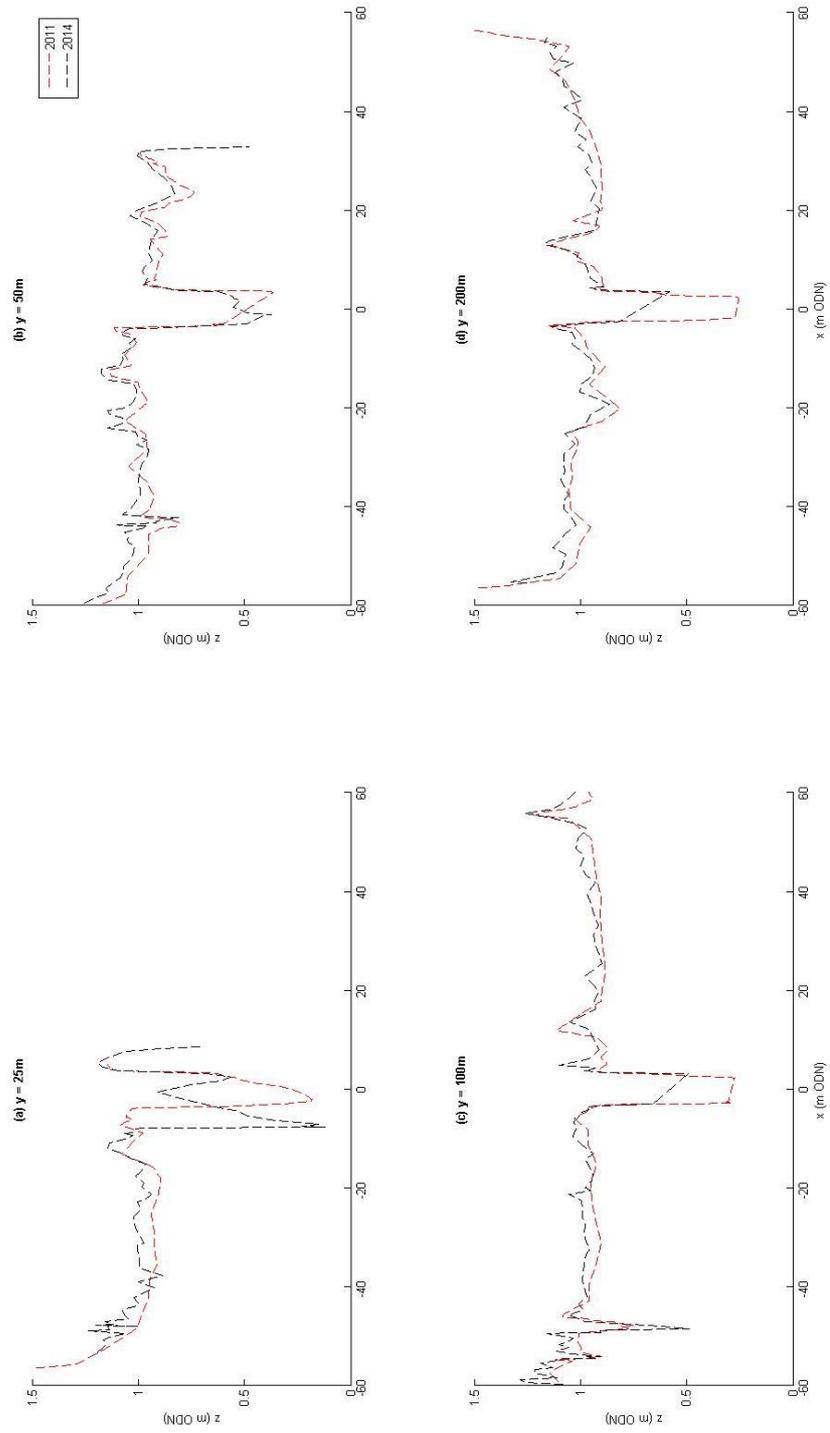


Figure 4.12 – Morphological development in South Efford managed realignment site between 2011 (red-dashed) and 2014 (black-dashed), at (a) 25 m; (b) 50 m; (c) 100 m; (d) 200 m from the SRT. The main central channel, aligned perpendicular to the SRT is at the origin of the x-axis (0).



Figure 4.13 – View of South Efford managed realignment site in May 2014, looking inland (north). Erosion has occurred on the western side of the channel and sediment has been deposited on the eastern side.

4.4 Discussion

The tidal regime of the restored marsh differed considerably from that of the natural marsh during the first three years of realignment. RTE structures are specifically designed to manipulate the tidal signature of a managed realignment site in order to manage flood risk and optimise habitat creation. However, Middleton (2009) states that in order for a restored site to return to its biological natural state, the modified tidal regime must not deviate excessively from hydrological patterns on nearby natural salt marshes.

The rotating plate of the SRT moves with the estuary rising tide and covers the culvert at a predetermined point, therefore ‘cutting off’ the natural high tide maxima in the restored area. Seawater is retained in the site until the SRT reopens on the ebb tide in the estuary, allowing the site to drain. The closure of the SRT during this period causes the restored area to be flooded for longer than the natural reference site, especially on a spring tide. This is similar to the ‘controlled reduced tide’ (CRT) technique employed in the Schelde estuary, Belgium (Cox et al. 2006). Here, a specific design of high infall and low outfall sluices in the polder control the hydrologic regime in the restored area. However, CRT allows more spring-neap variation than most other RTE mechanisms, such as the SRT at South Efford, which greatly reduces spring-neap variability. Spring-neap cycles are extremely important in the facilitation of vegetation growth as variation in wetting and drying drives biogeochemical and nutrient cycles (Nuttall & Hemond 1988).

In the first year of realignment, the SRT was set to close at a low estuary water level, which limited the average tidal prism in the restored area. For most of the time, water levels remained so low that only the main channel filled with water and rarely spilled over the banks (apart from when the SRT malfunctioned). Consequently, the spatial extent of inundation was limited, with only the lowest elevated areas getting covered by a shallow layer of water (Figure 10a) and in comparison with the natural marsh and tidal flat, the frequency and duration of inundation were extremely low. However, when the marsh was inundated by an overmarsh tide, it was inundated for longer than the natural marsh and tidal flat, as reflected in the extended maximum period of submergence.

Such a tidal regime likely placed serious limitations on salt marsh development and general biodiversity (see Chapter 5). Many species present in the relatively biodiverse lowland grassland that existed prior to realignment are intolerant of occasional extended

floodings, as exemplified by the sensitivity of *Trifolium repens* populations to simulated short duration seawater inundation (Chapter 3; White et al. 2014). As hydrochory is the major process responsible for seed dispersal on salt marshes, the infrequency of overmarsh tides would limit the dispersal of salt marsh seeds to the site (see Chapter 6; Lindig-Cisneros & Zedler 2002; Wolters & Bakker 2002; Wolters et al. 2005), thereby hindering the development of a salt marsh vegetation community (Dausse & Bonis 2008).

By the second year of realignment, average water levels were raised in the restored site to match natural marsh inundation frequency. The projected extent of marsh area was therefore regularly inundated and inundation frequency exceeded that of the natural marsh (Figure 10b). Research suggests that seed and sediment input from external sources increases with tidal inundation frequency, therefore accelerating salt marsh development (see Chapter 6; Friedrichs & Perry 2001; Wolters et al. 2005). Many managed realignment sites in the Netherlands, such as Kruikeke–Bazel–Rupelmonde on the Schelde, have an additional difficulty in the design of RTE structures, as a compromise exists between habitat creation and flood risk (Maris et al. 2007). High inundation frequency is required to optimize habitat development, yet as a consequence, the site will accrete more rapidly which reduces the potential volume of water the site can accommodate during a flood event (Cox et al. 2006; Maris et al. 2007).

The managed realignment site was inundated for significantly longer than the natural salt marsh during the second phase and later exceeded inundation durations on the tidal flat as well. As described above, this was mainly due to the retention of water in the restored site during estuary high tide and incomplete drainage as the SRT closes at low tide. Additionally, observations indicated that the problem was accentuated during periods of heavy rainfall, in particular during Winter 2013-2014. Winter 2013-2014 was

the wettest for the UK since 1910, with the UK receiving 165% of the 1981-2010 average rainfall (equating to 545 mm) (Met Office 2014). This was reflected by the consistently high water levels recorded in the restored area during Phase 3. Waterlogging of the site may have serious implications for the soil biogeochemistry and therefore the vegetation community composition of the restored site, as shown in a national-scale study by Mossman et al. (Mossman et al. 2012b). However, successful vegetation development has been observed at a tidal freshwater CRT site on the Schelde at Lippenbroek, despite the lengthened hydroperiod imposed by the CRT device (Jacobs et al. 2009).

The SRT did allow occasional long periods of exposure between inundations on the restored site. During the first year of realignment, the longest period of exposure was excessive due to infrequent overmarsh inundation. However, in the second and third phases, the longest periods of exposure were variable and similar to the natural salt marsh. The potential for successful seedling germination may have increased during these long periods, and seedlings may have been able to establish a root system (Chapman 1960), especially as seed input to the restored site had increased during the latter periods (Chapter 6). However, the further establishment of salt marsh plants may be limited by extreme abiotic conditions induced by prolonged waterlogging (Wolters et al. 2005; Erfanzadeh et al. 2009; Garbutt & Wolters 2008; Mossman et al. 2012b).

Overmarsh depths increased in the restored area as water levels were raised over time. However, relative to the natural habitats, depths and the rate of falling tide remained relatively low in the restored area. These factors may explain the lack of morphological development at SEM. Firstly, deeper flows are able to transport greater loads of suspended sediment to the marsh surface, required for sediment accretion (see Chapter 6). Secondly, the development of a creek network is dependent upon deep flows and

strong ebb currents. Williams (2002) describes the importance of depth in the formation of ‘channel-forming flows’, as the velocity gradient from the marsh surface to the breach increases with depth. Breach design is also key in the generation of ‘channel-forming flows’ as a strong ebbing current is generated according to the drainage efficiency of the site (Friess et al. 2014). It is possible that the narrow culvert of the SRT at SEM limits the speed at which tidal flows can drain from the site, therefore restricting the strength of ebbing current velocities (Pethick 2002).

The channel banks adjacent to the SRT in the restored area have eroded as they accommodate the increasing tidal prism and the high velocity flows through the infall, which are directed into the eroding channel bank. However, this sediment is rapidly re-deposited in the lee of the flow to the east of culvert. Breach erosion has posed difficulties in other RTE sites. For example, excessive scour occurred on the natural side of the SRT during the first few years of realignment at Goosemoor, Exe estuary, UK (Lyons & Ausden 2008). Friess et al. (2014) emphasise the importance of breach design in ensuring a steady, straight flow of water into and out of the realigned site, to prevent the erosion of potential habitat in addition to future technical failure of the SRT.

4.5 Conclusions

Over the first three years of managed realignment, the tidal signature of SEM did not mimic natural tidal patterns. The SRT mechanism cuts off the natural estuary high tide maxima, preventing variation in tidal amplitude between spring and neap tides. Additionally, closure of the SRT at high tide causes the restored site to retain water for long durations. During the first year of realignment, water levels in the restored area were restricted by the SRT, therefore the spatial extent, frequency and duration of overmarsh inundation were limited. However, the SRT was adjusted to allow higher water levels in the second year of realignment. Inundation duration and frequency

exceeded levels on the natural salt marsh and later on increased to exceed levels on the tidal flat as a result of SRT malfunction and heavy rainfall. The potential for sediment and seed transport is likely to have been increased during the later stages of the study (Chapter 6). However, waterlogging of the site due to inefficient drainage may have created unsuitable abiotic conditions for vegetation establishment (Chapter 5). In comparison with the natural salt marsh and tidal flat, the average depths of high tide and rates of the falling tide remained relatively low on the restored site throughout the study. The latter effect was most likely due to slow drainage through the small culvert in the SRT. As both factors are key processes in the development of salt marsh morphology, this may explain why morphological development at SEM was extremely slow.

Chapter 5 – Short-term salt marsh development in a recently implemented managed realignment scheme: Vegetation

5.1 Introduction

Successful habitat restoration is often primarily judged on the development of a diverse, self-sustaining plant community, similar to those in natural habitats (Garbutt & Wolters 2008). Plant species diversity has been shown to improve ecosystem functioning in a range of habitats, as individual species have particular (potentially exclusive) functions (functional groups) (Huston 1999; Zedler et al. 2001; Sullivan et al. 2007). Therefore, communities containing a range of plant species benefit from greater productivity (Naeem et al. 1994; 1995; 1996); maintain soil fertility through nutrient retention (Ewel et al. 1991); and have increased resistance and resilience to disturbance (Tilman 1999). The latter is particularly important in coastal habitats, which are vulnerable to prolonged flooding and high current velocities during storm events (Hoggart et al. 2014).

Following managed realignment, the development of a salt marsh plant community depends on the existence of a seed supply from nearby natural salt marshes and suitable abiotic conditions that promote seedling establishment. Tidal regime has a significant degree of control over both of these processes. Overmarsh tides transport seeds onto the marsh surface (Friedrichs & Perry 2001), a process which will be discussed in more detail in Chapter 6. In this chapter, the indirect influence of the tidal regime on vegetation development through alteration of the abiotic environment will be investigated. In Chapter 3, *Trifolium repens*, a terrestrial species, showed notable salinity stress responses when exposed to simulated seawater flooding in the greenhouse (White et al. 2014). However, in the field, additional factors associated with inundation duration, such as soil redox potential, may determine the dieback of pre-alignment

terrestrial vegetation and the subsequent colonization of halophytes following realignment (e.g. Baldwin & Mendelssohn 1998).

In the first few months of realignment, bare patches within the pre-alignment vegetation should naturally start to occur, as the majority of pre-breach plant species will not cope with regular saline inundation (Erfanzadeh 2010). Pioneer halophytes possess specialised adaptations to salinity and other associated abiotic conditions, but are competitively excluded by glycophytic species when tidal inundation is limited in frequency and extent. The gradual occurrence of unvegetated microsites is therefore essential for the establishment of halophytic colonisers (French 2006). However, problems may also arise if the site lies at an elevation too low in the tidal frame or if drainage is impeded. Longer, deeper and more frequent inundations cause harsh abiotic conditions (Townend et al 2011), as waterlogging lowers soil oxygen concentrations (Silvestri et al. 2005) and plants are exposed to high salinities for longer periods of time. Waterlogging may be a particular problem on managed realignment sites where soils have overconsolidated during years of reclamation, leading to the formation of an aquitard (Townend et al. 2011; Crooks & Pye 2000). This may cause the rapid and widespread death of pre-alignment vegetation, as opposed to the slow emergence of bare patches (French 2006). Consequently, anoxic conditions may develop, preventing the germination and establishment of even the most hardy pioneer halophytes (Portnoy 1999).

Vegetation development is most rapid where halophytes occur in the pre-existing vegetation or in a viable below-ground seedbank (Wolters et al. 2008). However, these situations are rare in managed realignment sites as halophytes are outcompeted by terrestrial species after reclamation and salt marsh plants do not tend to create long-lasting seedbanks (Morzaria-Luna & Zedler 2007). Alternatively, the deliberate planting

of vegetation plugs into newly flooded areas in order to initiate salt marsh development is a recognised management technique (Craft et al. 2002). This method can be especially useful in managed realignment sites where seed dispersal has been proven to be limited (Diggory & Parker 2011) and where observed vegetation development has been slow and/or sediments appear unstable (Reed et al. 1999). Most studies in this field have focused on the use of *Spartina* species as an erosion control, due to its clonal growth form, robust plant morphology and dense root network (Fragoso & Spencer 2008; Yang et al. 2008; Balke et al. 2012). Originating from Southampton Water in the late 1800s, *Spartina anglica* Hubbard (a hybrid of *Spartina maritima* (Curt.) Fernald and *Spartina alterniflora* Loiseleur) is now found extensively in the pioneer zone on salt marshes across the UK. The stiff, tall (<1 m) shoots of *Spartina anglica* attenuate flows very effectively (Bouma et al. 2005; Fragoso & Spencer 2008) and stimulate sediment accretion (Sánchez et al. 2001). Chichester Harbour Conservancy planted a 450 m² plot of *Spartina anglica* at Bosham (West Sussex), which has consequently spread to increase sedimentation and inhibit erosion adjacent to the car park (Adnitt et al. 2007). However, there is concern over the invasive nature of *Spartina* species, as they are very efficient competitors for resources (Yang et al. 2008). Liao et al. (2008) claim that ecophysiological properties, such as a greater leaf area index and epiphytic nitrogen fixation in dead shoots of *Spartina alterniflora*, have given the species a competitive advantage over native species in many Chinese marshes. Therefore, if allowed to spread, *Spartina* species may prevent the establishment of a more diverse array of native species. In future vegetation plantings, it may therefore be useful to plant species that can stimulate an effective compromise of both coastal defence and biodiversity over longer timescales. Langlois et al. (2003) offer *Puccinellia maritima* (Huds) Parl. as a Western European native salt marsh grass that could be planted as an alternative to *Spartina* species. Like *Spartina anglica*, *Puccinellia maritima* is generally found at

lower marsh elevations. *P. maritima* shoots are less stiff and grow closer to the ground than those of *S. anglica*, yet *P. maritima* is able to perturb local hydrodynamics sufficiently to encourage rapid sediment deposition. For example, where this species was present in Mont Saint Michel Bay, the soil level was almost twice that of neighbouring plots of bare ground. The hummocky topography that developed in the marsh as a result of heterogeneous *P. maritima* growth also promoted higher landscape-scale biodiversity, as higher marsh species were able to establish on areas of higher, stable ground (Langlois et al. 2003). However, the technique of vegetation planting has often been used with little consideration of the abiotic pre-requisites necessary for the optimum establishment of individual species (Diggory & Parker 2011), which could negatively impact on plant survival or functioning (Zedler et al. 2001; Spencer & Harvey 2012).

Any mistakes affecting vegetation development in the early stages of managed realignment schemes could ultimately affect linkages within biogeomorphological salt marsh ecosystems and their long-term sustainability (Cooper et al. 2004; Viles et al. 2008). This is a particular risk where natural tidal exchange is significantly altered by engineered structures in managed realignment sites. Such mechanisms are designed to create the optimum tidal signature for salt marsh habitat development, yet very little data exists on the short-term trajectory of vegetation development in regulated tidal exchange (RTE) sites. Consideration of the initial responses of both pre-alignment vegetation and new halophytic colonisers to tidal signatures imposed by RTE structures could allow for both on-site adjustments and alterations to future designs and also indicate potential timescales of salt marsh development in future projects (Spencer & Harvey 2012). Consequently, the social and economic benefits of current and proposed managed realignment schemes would be reduced (Nicholson-Cole & Riordan 2009).

In Chapter 4, the self-regulating tidal gate (SRT) at South Efford managed realignment site (SEM) was shown to impose a highly variable tidal regime, which significantly differed from the tidal signature of the adjacent natural salt marsh in many ways. This chapter will investigate how the plant community at SEM has developed as a result of such hydrological variations.

I will firstly investigate any temporal and spatial patterns in plant species diversity. For example, how does plant diversity change after realignment and are there any variations with distance from the SRT? I will also so examine how glycophytic species present in the pre-realignment vegetation react to seawater inundation over time, with particular attention paid to *Trifolium repens*, the key species in Chapter 3. Subsequently, patterns of halophyte colonization will be investigated. For example, how long did it take species present in the natural salt marsh species pool to colonise the restored site? Which species were present after three years of realignment and where?

The importance of abiotic conditions in the success of transplanting schemes will also be investigated through transplanting two key halophytes with proven records as ecological engineers (*Puccinellia maritima* and *Spartina anglica*) at SEM and in an unmanaged realignment site at Great Orcheton Fields (GOF), on the neighbouring Erme Estuary (see Chapter 2.2 for full field description). The latter site is a useful comparison for SEM, as it is naturally breached rather than RTE; therefore, it is exposed to greater hydrodynamical activity. Despite these high current velocities, halophytic vegetation was fast to establish within the first few years of realignment (Chapter 2.2) and the pioneer species *Salicornia europaea* now covers the majority of the site. In the second part of this chapter, it will be investigated whether there are any differences between both sites and species in plant survival and/or growth. Does *Spartina anglica* have a

higher survival/growth rate than *Puccinellia maritima* when transplanted? And does this differ between sites?

5.2 Methods

5.2.1 Vegetation transition

Before the SRT became operational at SEM (see Chapter 2.1 for full site description), a laser total station was used to establish a measurement grid relative to the location of the SRT (Trimble Total Station 5600). Eleven transects were located to span the width of the area at increasing distances from the SRT, including one on the adjacent natural reference marsh south of the SRT (see Fig. 4.2 (Chapter 4)). On each transect, four 4 m² quadrats were positioned randomly along each transect, ensuring two quadrats lay either side of the central channel (green squares in Fig. 4.2). This design, adapted from the Countryside Survey Protocol (Carey 2008), allowed vegetation across a range of elevations and geomorphological settings to be monitored. Surveys were conducted in October and June 2011 (pre-flooding), 2012, 2013 and 2014 (although June surveys were primarily used in analysis, to eliminate seasonal differences). During surveys, the percentage cover of all vascular plant species and bare ground was recorded in the 4 m² quadrats and very rare species were recorded as covering 0.01 %.

As measures of species richness may not fully encapsulate slight changes in plant community composition (Silvestri et al. 2005), Shannon's entropy was used to measure plant diversity within each 4 m² quadrat. This is a combined measure of the number of species present (species richness) and their density within each quadrat (species evenness), and is thus a fairly accurate indication of gradual vegetation transition (Silvestri et al. 2005). A two-way repeated measures analysis of variance (ANOVA) followed by Tukey's HSD test were used to examine the effect of survey date and distance (fixed factors) from the SRT on plant Shannon entropy. Only data collected

within 300 m of the SRT were used in analysis as this area was most regularly inundated, therefore undergoing the most dynamic change (see Chapter 4). A Mauchly's test showed that the assumption of sphericity had been violated ($\chi^2(5) = 15.56, P < 0.05$); therefore, Greenhouse-Geisser estimates of sphericity were employed to correct the degrees of freedom ($\epsilon = 0.37$). In addition, Kruskal - Wallis non-parametric tests were used to test for changes in the abundance of individual plant species within 300 m of the SRT over the measurement period. The more immediate effect of seawater flooding on *Trifolium repens* was investigated by including data from the October 2011 and subsequent October surveys (2012, 2013), as these effects were expected to be more short-term than the other species of interest (Chapter 3; White et al. 2014). This enabled more comparisons to be drawn between short-term laboratory experiments in Chapter 3. However, changes in the abundance of other species were identified through comparison of June (2011–2014) surveys.

In May 2012, a laser total station survey was conducted on the managed realignment site, as described in Chapter 4. Simultaneous elevation measurements and observations of dominant plant species were recorded as feature codes along transects at 25 m, 50 m, 100 m and 200 m from the SRT. A one-way analysis of variance was performed on plant dominance and elevation data to investigate the development of plant zonation in relation to elevation in the tidal frame.

5.2.2 Vegetation transplants

Spartina anglica and *Puccinellia maritima* were selected as species to transplant in SEM and GOF. Both species are perennial salt marsh grass species, which grow clonally, generally at lower marsh elevations (Langlois et al. 2003; Balke et al. 2012). Both species have recognized ecological engineering attributes (e.g. Langlois et al. 2001;

2003; Bouma et al. 2005; Fragoso & Spencer 2008), although *Spartina anglica* has been most commonly transplanted into restored salt marshes in the USA (Adnitt et al. 2007).

In June 2012, 156 *Puccinellia maritima* turfs and 156 individual ramets of *Spartina anglica* were taken from natural marsh adjacent to South Efford realignment site. Turfs of *P. maritima* were collected using a 5cm length of PVC pipe of 5cm diameter, whilst ramets of *S. anglica* with at least 1cm root either side were extracted with a trowel. Individual ramets of *P. maritima* are much smaller and more fragile than *S. anglica*, hence the decision to transplant small but robust turfs of *P. maritima*.

At SEM, paired 0.5 m x 0.5 m plots (six in total) were located and cleared of vegetation on the established 50 m, 100 m, 150 m and 200 m transects to ensure a range of elevations between paired plots (0.88 – 1.13 m ODN), yet little variation within the paired plots (Fig. 5.1a). An additional paired plot was established and cleared of vegetation on the natural salt marsh as a control. At GOF, two paired plots were located and cleared of vegetation in the first field (closest to the breach), second field and third field (six in total; see Chapter 2.2 for field locations, at approximately 0-100 m, 100-300 m, 300-450 m) from the breach (Fig. 5.1b), ranging in elevation from 0.98 to 2.3 m ODN. The precise location and elevation of each plot was recorded using a Trimble DGPS Real-Time Kinematic base station and rover, with vertical errors <1.3 cm (Network Adjustment Reports, Trimble Business Centre).

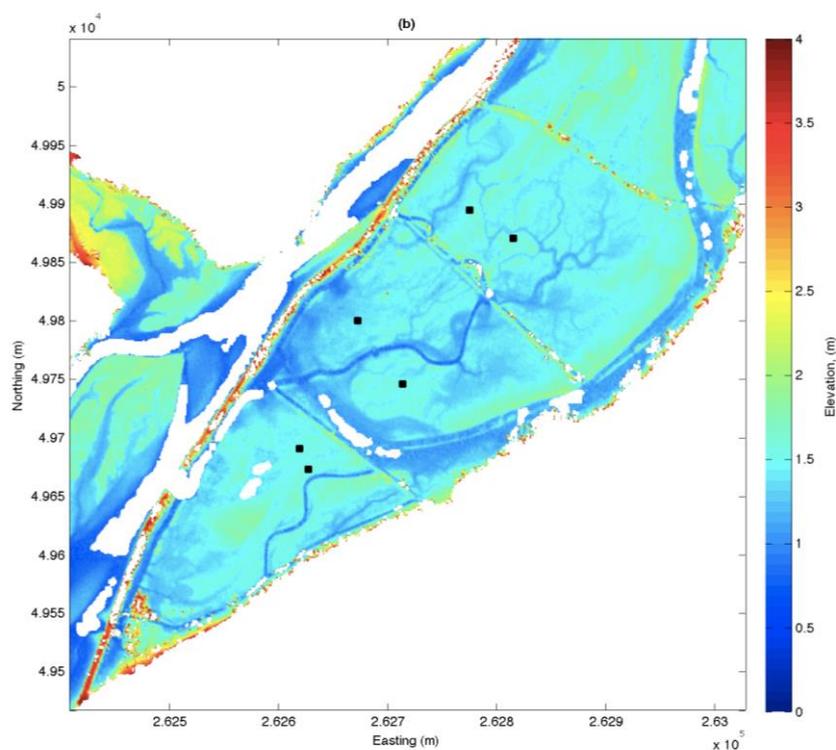
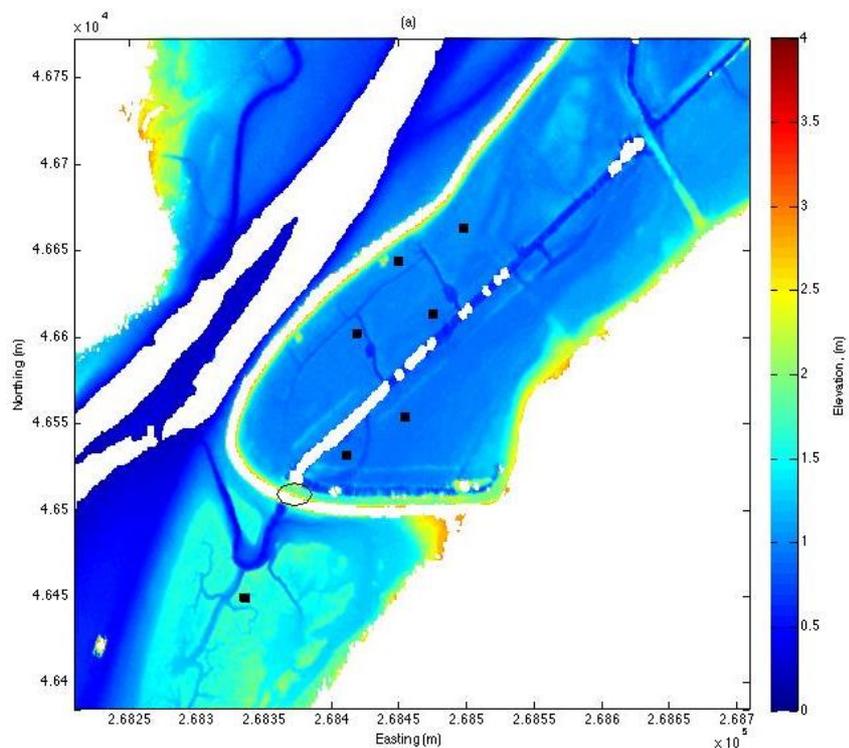


Figure 5.1 – Locations of paired transplant plots at (a) South Efford (SEM/SEN) and (b) Great Orcheton Fields (GOF), indicated by black squares. Breaches are marked by hollow ellipses (black outline). LIDAR data courtesy of Channel Coastal Observatory (www.channelcoast.org).

At both sites, the collected *P. maritima* turfs were planted into the soil in one of each of the paired plots, whilst the harvested *S. anglica* ramets were planted in the adjacent plot. This arrangement was randomly assigned for each paired plot. In each corner of a square plot, three turfs or ramets were transplanted, giving a total of 12 transplants per plot (Fig. 5.2, 5.3). Each corner was marked with a wooden cane to aid exact relocation of transplants.

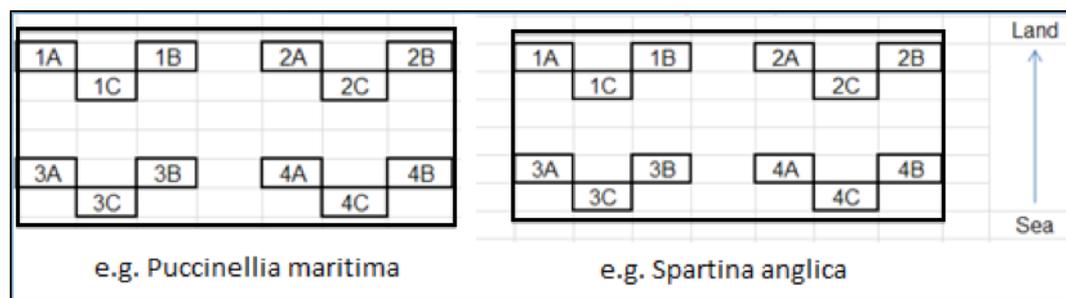


Figure 5.2 - Layout of transplants in paired plots at South Efford and Great Orcheston Fields. Of each pair, one plot was planted with twelve turfs of *Puccinellia maritima* and the other with ramets of *Spartina anglica*. Replicates of separate species (*P.maritima* and *S. anglica*) are labelled 1A-C; 2A-C; 3A-C; 4A-C.

Once planted, some initial measurements were taken. For *P. maritima*, these consisted of the number of shoots and the length of the longest shoot in each individual piece of turf. The central spike length and number of leaves on each individual ramet of *S. anglica* were recorded.

In early November 2012, the plants were re-located and mortalities recorded at both sites. Above-ground measurements of all surviving plants were taken again. As in Langlois et al. (2001), the comparison of secondary above-ground measurements with those on initial transplantation allows growth and therefore the relative establishment of each plant to be calculated. Wilcoxon signed-rank tests were performed to compare the growth parameters of surviving plants with initial measurements.

All data were analysed using SPSS 21.0 (SPSS Inc, Chicago, IL, USA) and MATLAB 2011a (The Mathworks, Inc., Massachusetts, United States).

5.3 Results

5.3.1 Vegetation transition

Survey date significantly influenced plant diversity ($F_{(1,12,3.35)} = 24.36, P < 0.05$) and post-hoc tests indicated that significant variation existed between June 2011 and 2012 surveys ($P < 0.01$), when diversity decreased from 2.1 ± 0.1 in June 2011 to 0.7 ± 0.1 in June 2012 (Fig. 5.3). Relative to pre-inundation, diversity remained low in June 2013 ($P < 0.01$) and June 2014 ($P < 0.01$). Natural salt marsh diversity did not differ between years ($F_{(2,6)} = 1.116, P > 0.05$), at 2.1 ± 0.1 in 2011, 1.8 ± 0.1 in 2012, 1.9 ± 0.2 in 2013 and 1.6 ± 0.2 in 2014. Distance from the SRT did not influence diversity ($F_{(1,8,5.39)} = 1.61, P > 0.05$) and there was no interaction between survey date and distance ($F_{(2,39,7.18)} = 4.16, P > 0.05$). However, in the pre-inundation (June 2011) survey, diversity in quadrats 25m from the SRT was marginally lower in comparison to all other transects (Fig. 5.4).

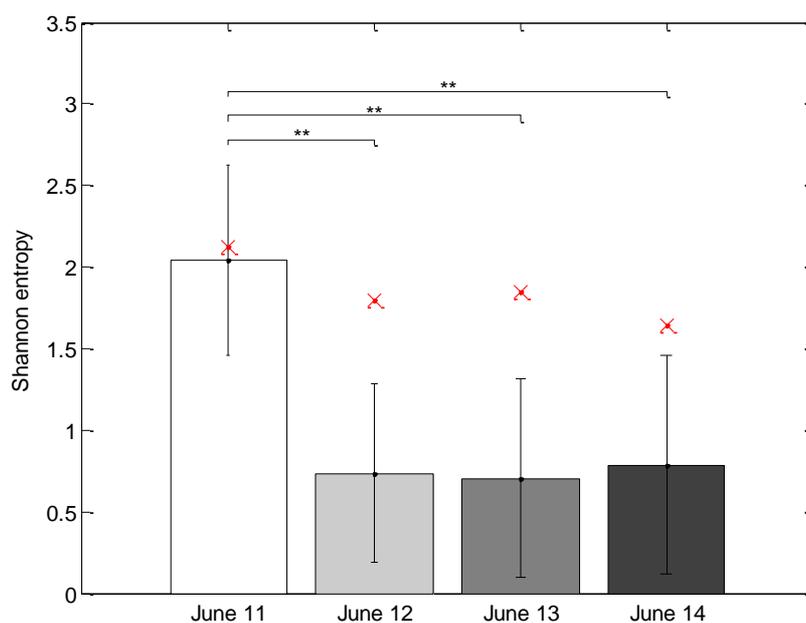


Figure 5.3 – Mean (\pm SE) Shannon entropy of quadrats within 300 m of the SRT ($n = 24$) in June 2011, 2012, 2013 and 2014. Red crosses mark average natural marsh Shannon entropy ($n = 4$) and significance by asterisks ($P < 0.01$)

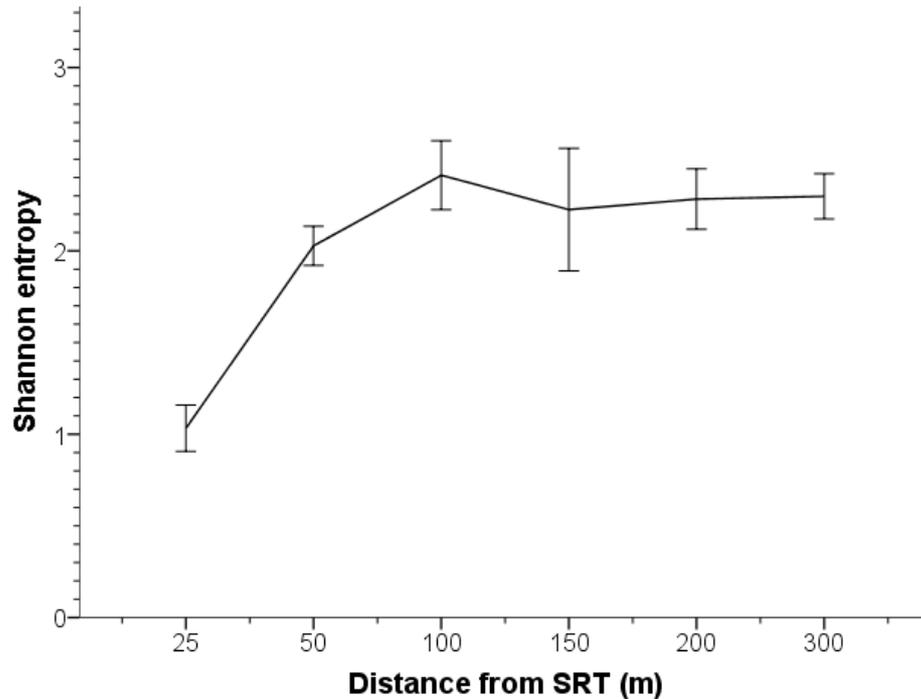


Figure 5.4 – Pre-realignment (June 2011) mean (\pm SE) Shannon entropy of quadrats on transects increasing in distance from the embankment (25-300 m) ($n=4$).

In June 2012, the number of glycophytic species within 300 m of the SRT was reduced by 35 % compared with pre-inundation and by 2013, glycophyte species richness was reduced by a further 34 %, as only 7 glycophyte species remained (Fig. 5.5). Mean percentage cover of *Trifolium repens* significantly differed between survey dates ($\chi^2_{(6)} = 125.6, P < 0.01$). *Trifolium repens* cover was relatively high in the pre-inundation survey in June 2011 at 11.7 ± 1.6 and was reduced to 1.7 ± 0.5 by October 2011. Percentage cover in consequent surveys remained extremely low and in June 2013, *Trifolium repens* was not recorded in any quadrat within 300 m of the SRT (Table 5.1).

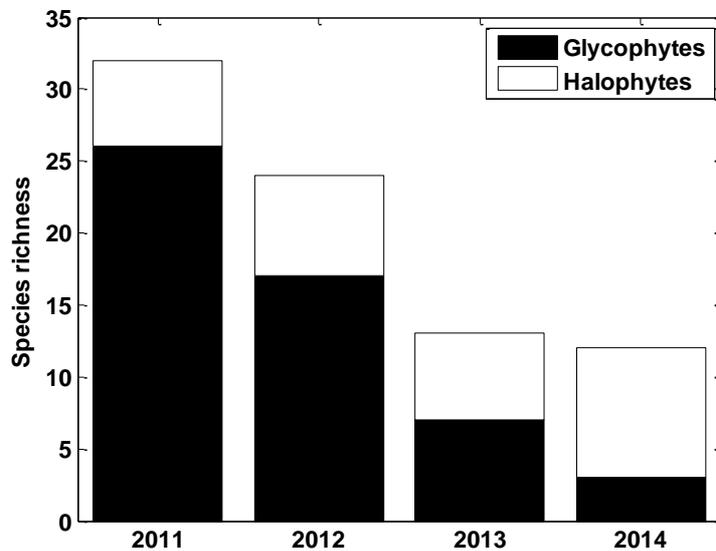


Figure 5.5 – Number of halophyte and glycophyte species recorded in quadrats within 300 m of the SRT in June 2011, 2012, 2013 and 2014.

By 2012, *Juncus gerardii* and *Agrostis stolonifera* (and bare ground) had the highest cover in the restored area (Table 5.1), but dominated at significantly different elevations ($F_{(2,466)} = 68.12, P < 0.01$). Bare ground was most prevalent at low elevations (0.92 ± 0.004 m ODN), *Juncus gerardii* dominated at 0.9 ± 0.007 m ODN and *Agrostis stolonifera* dominated at high elevations of 1.0 ± 0.006 m OD (Fig. 5.6). *Juncus gerardii* cover did not differ between surveys ($\chi^2_{(3)} = 2.59, P > 0.05$), whilst *Agrostis stolonifera* decreased in frequency and percentage cover over time ($\chi^2_{(3)} = 52.52, P < 0.01$), occurring in only 16.67 % quadrats in 2014, with mean cover of 2.42 ± 1.88 %. In contrast, percentage cover of bare ground in quadrats increased over time ($\chi^2_{(3)} = 66.49, P < 0.01$), attaining mean cover of 86.3 ± 4.3 % by June 2014 (Table 5.1).

Plants	Jun-11		Jun-12		Jun-13		Jun-14	
	Frequency	Mean cover (%)	Frequency	Mean cover (%)	Frequency	Mean cover (%)	Frequency	Mean cover (%)
<i>Agrostis stolonifera</i>	100	42.7 (± 5.3)	95.8	46.3 (± 6.1)	62.5	13.1 (± 3.7)	16.7	2.4 (± 1.9)
<i>Alopecurus geniculatus</i>	41.7	0.9 (± 0.3)	25	0.3 (± 0.2)	20.8	1.3 (± 0.6)		
<i>Anthoxanthum odoratum</i>	4.2	0.04 (± 0.04)						
<i>Arrhenatherum elatius</i>	4.2	0.00 (± 0.00)						
<i>Cynosurus cristatus</i>	70.8	4.3 (± 1.5)						
<i>Elytrigia repens</i>	54.2	1.8 (± 0.9)						
<i>Festuca pratensis</i>	16.7	0.4 (± 0.4)						
<i>Holcus lanatus</i>	87.5	5.1 (± 1.0)						
<i>Lolium perenne</i>			8.3	0.01 (± 0.01)	4.2	0.4 (± 0.4)		
<i>Poa annua</i>	4.2	0.2 (± 0.2)						
<i>Poa pratensis</i>	4.2	0.04 (± 0.04)						
<i>Poa trivialis</i>	8.3	0.1 (± 0.04)						

<i>Puccinellia maritima</i> *	4.1	0.2 (± 0.2)			16.7	0.5 (± 0.3)	25.0	1.0 (± 0.6)
Sedges/Rushes								
<i>Bolboschoenus maritimus</i> *			8.3	0.1 (± 0.1)	4.2	0.1 (± 0.1)	12.5	0.2 (± 0.1)
<i>Carex (divisia)</i>	54.2	2.4 (± 1.1)						
<i>Carex otrubae</i>	41.7	0.8 (± 0.3)	25.0	0.8 (± 0.5)	8.3	0.3 (± 0.2)		
<i>Eleocharis palustris</i>	25.0	7.4 (± 3.3)	16.7	3.0 (± 2.0)	4.2	0.2 (± 0.2)		
<i>Juncus articulatus</i>	8.3	0.1 (± 0.1)	4.2	0.04 (± 0.04)				
<i>Juncus bufonius</i>			4.2	0 (± 0)				
<i>Juncus compressus</i>			4.2	0.1 (± 0.1)				
<i>Juncus effusus</i>	45.8	9.8 (± 3.2)	29.2	0.6 (± 0.3)	16.7	0.5 (± 0.3)	4.2	0.2 (± 0.2)
<i>Juncus conglomeratus</i>			8.3	1.0 (± 0.7)				
<i>Juncus gerardii</i> *	33.3	6.0 (± 2.7)	50.0	14.5 (± 4.5)	41.7	10.5 (± 3.8)	33.3	8.4 (± 3.6)
Forbs/Woody Sp								
<i>Aster tripolium</i> *			4.2	0 (± 0)			50	1.0 (± 0.4)

<i>Atriplex prostrata</i> *	8.3	0.1 (± 0.1)					29.2	0.9 (± 0.4)
<i>Cardamine pratensis</i>	8.3	0.01 (± 0.01)						
<i>Cerastium fontanum</i>	29.2	0.2 (± 0.1)	4.2	0 (± 0)				
<i>Glaux maritima</i> *	4.2	0.2 (± 0.2)	4.2	0.6 (± 0.6)	4.2	0.1 (± 0.1)		
<i>Leontodon autumnalis</i>	4.2	0.04 (± 0.04)						
<i>Leontodon hispidus</i>	8.3	0.1 (± 0.1)						
<i>Plantago major</i>	4.2	0.04 (± 0.04)						
<i>Plantago media</i>			4.2	0 (± 0)				
<i>Prunella vulgaris</i>			4.2	0 (± 0)				
<i>Ranunculus acris</i>	4.2	0.04 (± 0.04)						
<i>Ranunculus repens</i>	83.3	10.0 (± 1.7)	12.5	0.01 (± 0.01)				
<i>Rumex conglomeratus</i>	8.3	0.1 (± 0.04)						
<i>Rumex crispus</i>	4.2	0 (± 0)						
<i>Rumex obtusifolius</i>			16.7	0.02 (± 0.01)				

<i>Salicornia europaea</i> *			12.5	0.01 (± 0.01)			62.5	0.7 (± 0.3)
<i>Spartina anglica</i> *							12.5	0.1 (± 0.04)
<i>Spergularia media</i> *	8.3	0.1 (± 0.1)	37.5	1.0 (± 0.6)	12.5	0.3 (± 0.2)	20.8	0.1 (± 0.1)
<i>Taraxacum officinale</i>	12.5	0.01 (± 0.01)	16.7	0.1 (± 0.1)	4.2	0.04 (± 0.04)	4.2	0 (± 0)
<i>Trifolium dubium</i>	4.2	0 (± 0)						
<i>Trifolium repens</i>	100.0	14.0 (± 2.1)	4.2	0.04 (± 0.04)				
<i>Triglochin maritimum</i> *	4.2	0.2 (± 0.2)	4.2	0.2 (± 0.2)	4.2	0.6 (± 0.6)	4.2	0.04 (± 0.04)
Bare ground	8.3	0.3 (± 0.2)	95.8	28.3 (± 5.6)	91.7	72.6 (± 6.8)	100.0	86.3 (± 4.3)

Table 5.1 – Percentage cover and frequency (percentage of quadrats where the species were recorded) of plant species found in the vegetation quadrats within 300 m of the SRT at South Efford managed realignment site ($N = 24$), including functional group, during June 2011 (pre-realignment), June 2012, June 2013 and June 2014. Species marked with * are considered typical of salt marshes (Stace 1997).

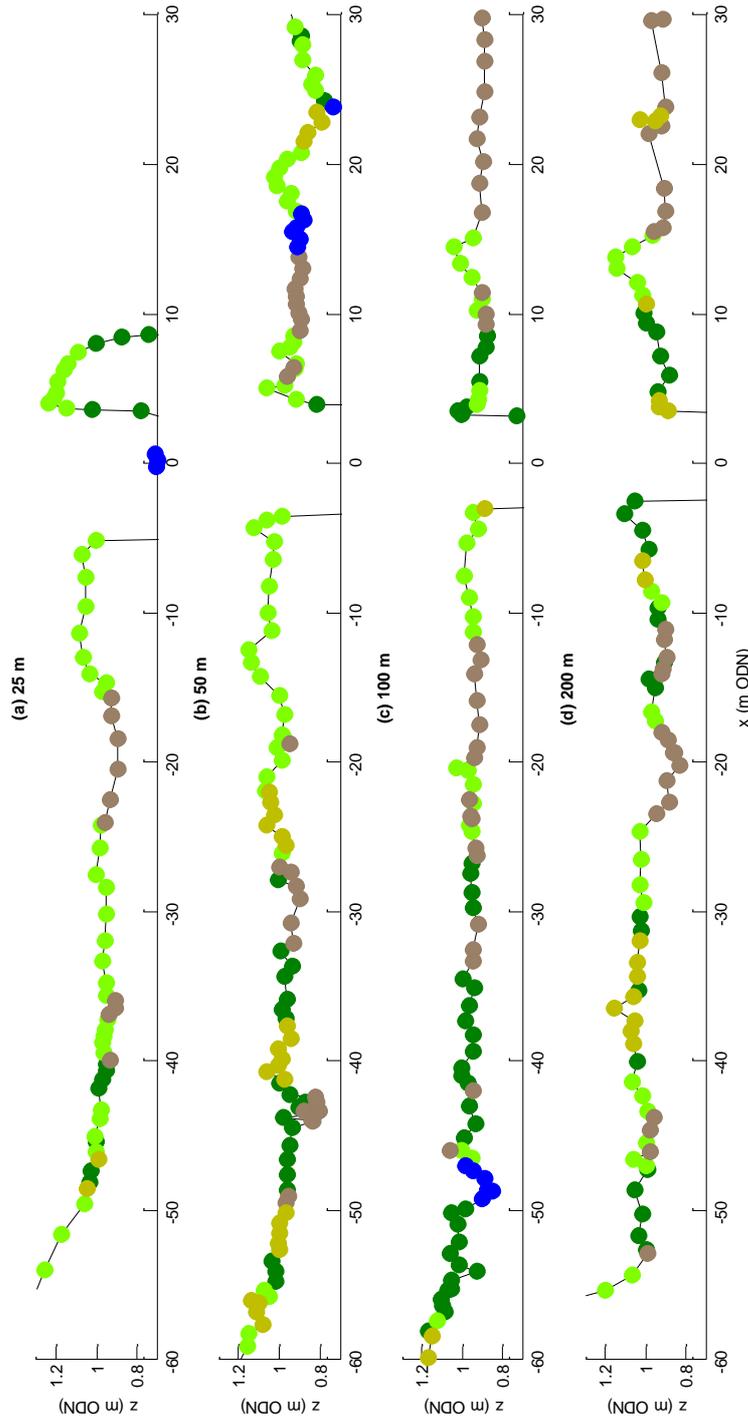
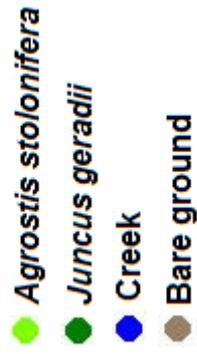


Figure 5.6 – Total station survey cross-sections of marsh elevation and dominant vegetation at (a) 25 m; (b) 50 m; (c) 100 m; (d) 200 m from the SRT in May 2012. The SRT is at the origin of the measurement grid and the x-axis represents the width axis of the marsh, respectively. Generally, the central channel and areas of open water (blue) and bare ground (brown) exist at the lowest elevations; *Juncus gerardii* (dark green) dominates at mid-elevations and *Agrostis stolonifera* (light green) dominates the highest elevations.

Four halophyte species from the natural salt marsh ‘pool’ were already present in the restored area in the pre-inundation survey: *Puccinellia maritima*, *Atriplex prostrata*, *Glaux maritima*, *Spergularia media* (Table 5.2), albeit in very low abundance (Table 5.1) and only recorded along the 25–50 m transects. In June 2012, *Aster tripolium* was recorded in 3 individual quadrats, 50 m, 100 m and 200 m from the SRT, and *Salicornia europaea* was also recorded in 4 quadrats; two on the 25 m transect, one at 50 m and one at 100 m from the SRT. In 2013, these colonisers were not recorded in any quadrat. However, by 2014, *Aster tripolium* was recorded in 50 % of all quadrats within 300 m of the SRT and *Salicornia europaea* occurred in 62.5 % of these quadrats (Table 5.1). In 2014, *Spartina anglica* had colonised four quadrats (Table 5.1). The latter three species were not recorded in June 2011 quadrats, nor in County Wildlife Site surveys conducted in 1992 and 2010 (Environment Agency 2010). By 2014, the only species present in the natural salt marsh ‘pool’, but with no sightings in the restored area were *Atriplex portulacoides* and *Plantago maritima* (Table 5.2). However, although halophyte frequency had risen by 2014, *Puccinellia maritima* had the highest percentage cover (of those present in the natural pool) within 300 m of the SRT, at just 1 ± 0.6 %.

Observations outside the surveyed quadrats during 2013 and 2014 indicate that halophyte colonization, mainly by *Salicornia europaea* and *Aster tripolium*, was more likely to occur along the channel banks (Fig. 5.7a) or areas slightly higher in elevation (Fig. 5.7b).

Plants	2011		2012		2013		2014	
	SEN	SEM	SEN	SEM	SEN	SEM	SEN	SEM
<i>Spartina anglica</i>	x		x		x		x	x
<i>Atriplex portulacoides</i>	x		x		x		x	
<i>Plantago maritima</i>	x		x		x		x	
<i>Puccinellia maritima</i>	x	x	x		x	x	x	x
<i>Atriplex prostrata</i>	x	x	x		x			x
<i>Salicornia europaea</i>	x		x	x	x		x	x
<i>Aster tripolium</i>	x		x	x	x		x	x
<i>Spergularia media</i>	x	x	x	x		x	x	x
<i>Glaux maritima</i>		x	x	x	x	x	x	

Table 5.2 – Presence of plant species considered typical of salt marshes (Stace 1997) in the vegetation quadrats within 300 m of the SRT at SEM (N = 24) and adjacent SEN (N = 4) during June 2011, June 2012, June 2013 and June 2014. The sampling occasion on which the species were recorded is denoted by X.

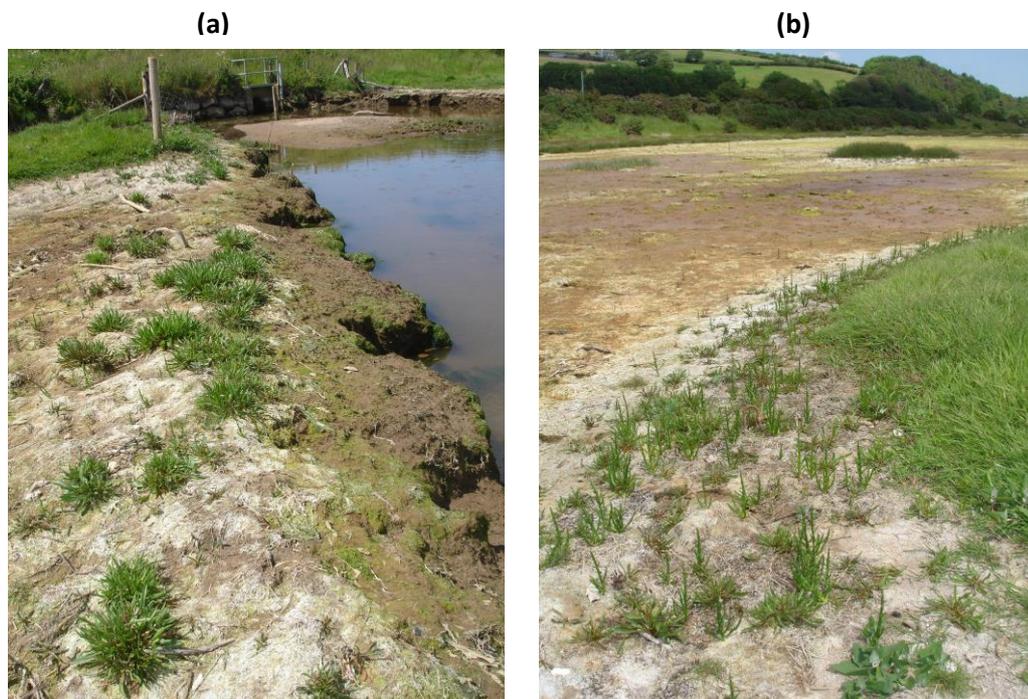


Figure 5.7 – Colonisation of (a) *Aster tripolium* on SEM channel banks in June 2013, looking towards the SRT (south); (b) *Salicornia europaea* on higher elevated ground (just below a dense sward of *Agrostis stolonifera*) in June 2014, looking inland.

5.3.2 Vegetation transplants

At both SEM and GOF, there was a very low recovery of transplanted plugs. The transplants in the control plot on SEN were unidentifiable, as they had been overgrown by rapidly growing salt marsh vegetation. The recovery of transplanted plugs was particularly low at SEM. 8.3 % (i.e. six) transplanted *Puccinellia maritima* plugs had remained *in-situ* and only two (33.3 %) of the recovered individuals were alive (Fig. 5.8a). All remaining plants were found in a single plot on the 50 m transect, which lies at the lowest elevation in the tidal frame. Four (5.6 %) of the total transplanted *Spartina anglica* plugs were recovered, but only one (i.e. 25 %) of the recovered individuals survived (Fig. 5.8a). All remaining plugs were found in single plot on the 150 m transect, which was the second highest in elevation.

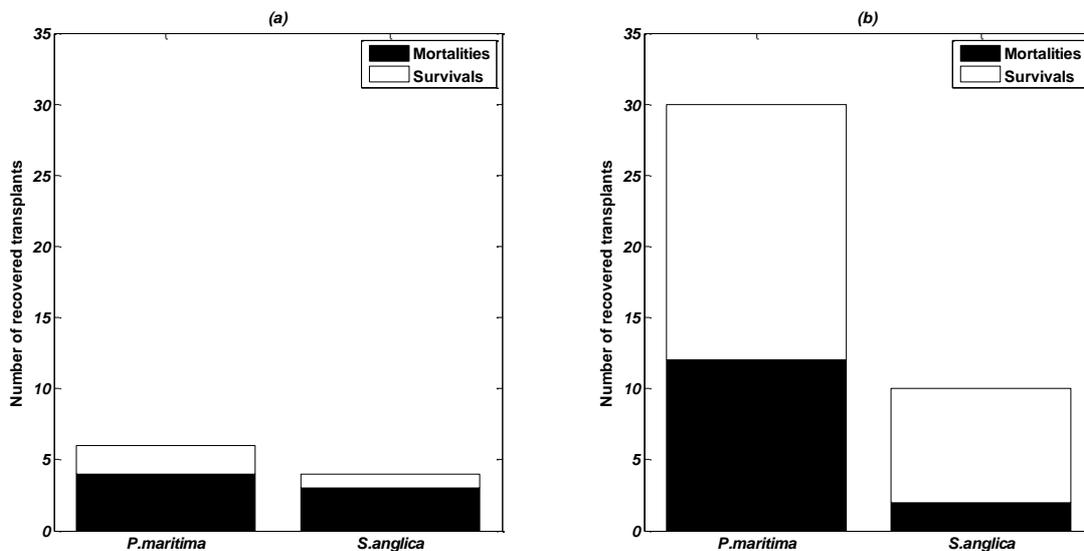


Figure 5.8 – Number of recovered transplanted *Puccinellia maritima* and *Spartina anglica* plugs at (a) SEM and (b) GOF unmanaged realignment site. Mortalities (shaded) are indicated.

The experiment had a much higher recovery and survival rate at GOF. No plants were recovered within 100 m of the breach (i.e. two plots of each species). Overall, 41.7 % (i.e. 30) of the original number of *P. maritima* plugs was recovered in 3 of the 4

remaining plots, of which 60 % (i.e. 18) remained alive (Fig. 5.8b). *S. maritima* mortality was higher, as only 13.9 % (i.e. 10) of plugs were found. However, 80 % (i.e. 8) of those recovered had survived (Fig. 5.8b). The number of leaves on the surviving *Spartina anglica* transplants significantly increased over time ($Z = -2.54$, $n = 8$, $P < 0.05$) (Fig. 5.9), whilst length of the inflorescence spike did not increase ($Z = -0.840$, $n = 8$, $P > 0.05$). There were no significant differences in the number of leaves ($Z = -0.65$, $n = 18$, $P > 0.05$) and the maximum leaf length ($Z = -0.46$, $n = 18$, $P > 0.05$) for *Puccinellia maritima* transplants.

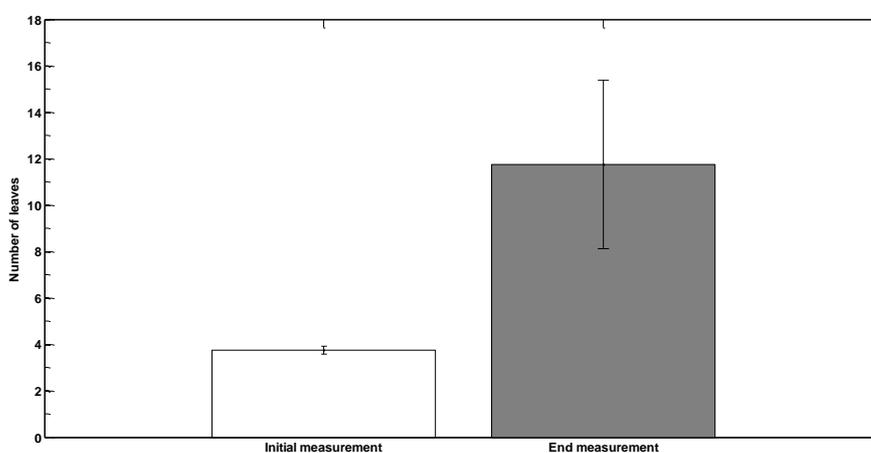


Figure 5.9 – Number of leaves on surviving *Spartina anglica* transplants at GOF, on initial planting ('Initial measurement') and at the end of the experiment ('End measurement'). $N = 8$.

5.4 Discussion

5.4.1 Vegetation transition

Before the tidal regime was re-introduced at SEM in 2011, plant species diversity was lower in transects closer to the embankment (where the SRT was later installed). This likely reflects the fact that soils closer to the embankment were more saline (Chapter 3; White et al. 2014). It is reasonable to assume that saline soils closer to the embankment were the main cause of lower plant diversity (particularly grasses), as few glycophytic species possess the specialized adaptations that enable them to tolerate raised salinities.

Results from Chapter 3 also indicate that *Trifolium repens* ecotypes closer to the embankment were more resilient to higher soil salinities than clovers occurring further inland (White et al. 2014). Similarly, more halophytes were able to persist closer to the embankment post-reclamation. Halophytes are able to grow in saline environments due to specialised external adaptations such as succulent leaves, in addition to internal adaptations, including the ability to compartmentalise Na⁺, K⁺ and Cl⁻ ions (and other detoxification mechanisms) (Flowers & Colmer 2008). Such species also thrive in the absence of glycophytic competition (Crain et al. 2004). In many other studies monitoring post-reclamation vegetation community composition, glycophytic species quickly outcompeted remnant halophytes, with all halophytes disappearing within 10 years when the site is not grazed (Beeftink 1979). However, Bonis et al. (2005) revealed that halophytic species still persist in 800–1000 year old polders on the west Atlantic coast in France, but only in areas of higher soil salinity and lower competition, where the site has been grazed. Indeed, *P. maritima* and *S. media* still existed in very saline areas in a grazed recent polder after 20 years of reclamation. The latter species were sporadically recorded in pre-inundation vegetation at SEM, but only at 25 – 50 m from the embankment where salinities were highest and competition was therefore reduced.

One year post-inundation, species diversity had plummeted. Some glycophytic individuals may survive short-duration seawater immersion. For example, in Chapter 3 (White et al. 2014) it was shown that *Trifolium repens* ecotypes that are more resilient to short-duration seawater immersion may occur in areas previously exposed to salinity. However, saline inundation of just the roots for 24 hours was enough to cause mortalities of *Trifolium repens* and significantly compromise plant ecophysiology. Although the maximum period of submergence was on average 9.6 ± 2.1 hours per month during September 2011 – May 2012 (Chapter 4), the cumulative effect of repeated inundations (at 82.7 ± 23.9 hours of inundation per month), would likely

exceed the tolerance of *Trifolium repens* (and other glycophytes of similar ecophysiology), leading to significant mortalities just one month post-realignment and reduced diversity after one year. Indeed, in the first and second years of realignment, plant diversity was most reduced at lower elevations, which were inundated for longer. This indicates the great control inundation duration has over abiotic conditions associated with the growth of both glycophytic and halophytic vegetation.

Stochastic gaps within pre-existing vegetation are critical in the early stages of many types of habitat restoration, as new species are able to colonise and initiate early succession (Erfanzadeh 2010). Halophytes are light-demanding but have a very slow rate of growth (Ellenberg 1978); therefore, will benefit from reduced competition on bare ground. In a transplanting experiment on salt and freshwater marshes, Crain et al. (2004) indicated that the colonisation of salt marsh vegetation is primarily controlled by biotic rather than abiotic factors, as salt marsh plants actually grew in freshwater as well as saltwater environments, providing all neighbouring freshwater vegetation was removed. Unvegetated patches had started to appear at low elevations (where most frequently inundated) at SEM by June 2012 and species from the adjacent natural marsh, *Aster tripolium* and *Salicornia europaea*, were recorded. However, cover of these species (and other halophytes) in the pre-existing vegetation remained low. Salt marsh restoration is a slow process and should not be expected to occur just one year after realignment (Andrews et al. 2006), yet it is likely that the limited frequency and extent of inundation during this period (Chapter 4) further slowed the transition. Firstly, waterborne seed transport onto the marsh surface will have been limited (Chapter 6). Secondly, the widespread domination of opportunistic species *Agrostis stolonifera* and *Juncus gerardii*, usually typical of the upper marsh/terrestrial fringes, may have caused competitive exclusion of halophytic seedlings. Both species are very good competitors, as they are clonal and quickly form relatively high swards (Herben & Hara 1997; Bonis

2005). *Juncus gerardii* is a sub-halophyte, tolerant of high salinities and reasonably high soil moisture, but not as high as halophytes such as *Puccinellia maritima* (Rozema & Blom 1977). This was reflected by the dominance of the species at low elevations in 2012, but not the lowest, most frequently inundated areas. Bonis et al. (2005) describe *A. stolonifera* as ‘ubiquist-competitive’, therefore it can tolerate slightly saline/wet environments where other terrestrial vegetation dies, but does not grow well under high salinities (Rozema & Blom 1977), as demonstrated by its restriction to higher elevations in 2012 and gradual constriction in spatial extent in 2013 and 2014.

By June 2013, the spatial extent and frequency of inundation was increased and the restored area was inundated for significantly longer than the natural salt marsh (Chapter 4) and the vast majority of the marsh was left unvegetated. *Agrostis stolonifera* was reduced by the high salinities associated with increased inundation duration, yet halophyte richness and abundance decreased rather than increased in the absence of glycophytic competition. Species that had colonised during the first year of realignment (*Aster tripolium* and *Salicornia europaea*) were not recorded in any quadrats and halophytes already present in the pre-existing vegetation (e.g. *Spergularia media*) were reduced in frequency. During this period, the restored area was experiencing similar lengths of tidal inundation to the adjacent tidal flat, which caused widespread waterlogging and reduced soils in the restored area due to its relative drainage inefficiency (Chapter 5). Soil seedling germination is very sensitive to waterlogging (Spencer & Harvey 2012), therefore it is highly likely that harsh abiotic conditions at South Efford managed realignment site prevented the germination of many seeds deposited on the marsh surface. Similarly, the expansion of many species present in the pre-inundation survey may have been restricted in the second year of realignment by altered soil biogeochemistry.

Waterlogging has been a problem at other managed realignment sites. For example, saturated soils at Tollesbury managed realignment site (Essex, UK) initiated the growth of algal mats, thought to hinder establishment of *Salicornia europaea* (Crooks et al. 2002). Similarly, soils at Orplands managed realignment site (Essex, UK) were very reduced after realignment, indicating a similar hydrologic regime to the estuarine mudflats (Macleod et al. 1999). Indeed, reduced soils are thought to be the main cause of differences in vegetation community composition between restored and natural sites (Mossman et al. 2012b). Altered abundances of certain species in managed realignment sites may affect the functioning of these salt marshes (Zedler et al. 2001; Sullivan et al. 2007), yet research is lacking on how such ecosystems may function in the long term (Spencer & Harvey 2012). On managed realignment sites with a simple breach(es), the major cause of waterlogging is likely to be edaphic (Townend et al. 2011; Crooks & Pye 2000) or due to homogenous topography (Zedler 2005; Zedler & Callaway 1999). These are likely to be major problems on RTE sites too, yet results from this study indicate that insufficient drainage through the RTE mechanism itself may further hinder vegetation development. This emphasises the need for managers to carefully consider the design of engineered structures regulating tidal exchange on managed realignment sites, as aspects of the natural tidal signature that are key to the development of a sustainable salt marsh community may be significantly altered.

Salt marsh development started to look more promising at SEM after three years of realignment, as *Salicornia europaea* and *Aster tripolium* were recorded in many quadrats and *Spartina anglica* was sighted for the first time, although all were very low in abundance. Slightly reduced water levels following a winter of prolonged flooding (Chapter 4) may have allowed sufficient exposure time for some seedlings to germinate (Chapman 1960). However, greater coverage of these species was observed outside the quadrats on areas of slightly higher elevation or the channel banks, where soils were

better drained (Ursino et al. 2004; Chapter 7). It is therefore likely that the colonisation of halophytes will be yet again impeded if water levels are raised, whether intentionally or through technical malfunction.

5.4.2 Transplanting salt marsh vegetation

Mortality rates of transplanted *Spartina anglica* and *Puccinellia maritima* plugs at SEM were very high. As the survival rate of both species at GOF was much higher and the natural establishment of halophytes at SEM was limited during this period, it can be assumed that environmental conditions were not adequate for the establishment of *S. anglica* or *P. maritima*. Garbutt et al. (2006) also experienced high mortalities in a transplanting experiment at Tollesbury managed realignment site, which was suggested to be due to waterlogging occurring in the depressions where the plugs were planted as well as tidal action washing away many of the transplants. This may have been the case at lower elevations at SEM and the transplants closest to the breach at GOF were most definitely washed away by high-energy flows (Chapter 6). However, at higher elevations at SEM, where inundation frequency and duration will have been limited, it is likely that the transplanted halophytes were outcompeted by *Agrostis stolonifera* and *Juncus gerardii* (Bonis et al. 2005).

Salt marsh development was far more advanced at GOF (see Chapter 2.2), indicating preferable environmental conditions for the establishment of halophytes. *P. maritima* had a higher survival rate than *S. anglica* at GOF, despite the frequent use of the latter species as an erosion control. This potentially indicates that at this particular location, *P. maritima* may function as a more effective ecosystem engineer than *S. anglica*. The use of *P. maritima* instead of or as well as *S. anglica* in transplanting schemes in the pioneer zone could incur greater biodiversity benefits and prevent the establishment of a monospecific sward of *Spartina* spp. (Langlois et al. 2001; 2003). Surviving *S. anglica*

individuals did, however, show signs of growth, whilst *P. maritima* plugs did not. This may indicate that the energetic cost of survival after transplantation compromises the growth of *P. maritima* plugs.

Transplantations of *Spartina* species have been successful in some schemes in the US (e.g. Craft et al. 1999; Santín et al. 2009) and *Spartina anglica* has successfully established on many salt marshes in the UK, where it was planted to stabilise rapidly eroding soils (Adnitt et al. 2007). *P. maritima* grows close to the ground and individuals are rapid to establish through the growth of vegetative propagules on the stolons (Gray & Scott 1977; Langlois et al. 2001). In contrast, although the tall, stiff shoots of *Spartina* species may be more efficient at attenuating current velocities (T. Bouma et al. 2005; Neumeier & Amos 2006), individual plants may be more likely to be washed away by tidal action before sufficient root networks has develop (O'Brien & Zedler 2006). For example, O'Brien and Zedler (2006) found that planting *Spartina foliosa* seedlings in tightly spaced groups on Friendship Marsh, Tijuana Estuary, San Diego County, California increased survival of plants by 18%. There are many different ways of transplanting *Spartina anglica* and other ecosystem engineers, therefore an understanding of how species function when planted in various locations and formations would be extremely beneficial in management plans.

5.5 Conclusions

Many factors in this chapter indicate that abiotic conditions linked to the hydroperiod are the major limiting factor on vegetation development at SEM. Firstly, limited inundation in the first year of realignment prompted the domination of *Agrostis stolonifera* and *Juncus gerardii*, which easily outcompeted halophytes from both expanding in abundance. Secondly, prolonged inundation duration in the following years likely challenged the establishment of halophyte seedlings transported into the site.

However, by June 2014, all species from the natural salt marsh had colonised the realignment site, with the exception of *Atriplex portulacoides* and *Plantago maritima*. Low recovery rates and high mortality in a transplanting experiment also reflect how challenging conditions at SEM were for halophyte establishment, in comparison with a nearby unmanaged realignment site (GOF), where a greater number of plugs were recovered with a higher survival rate. More *Puccinellia maritima* plugs were recovered than *Spartina anglica*, but surviving *S. anglica* plugs showed signs of growth. This pilot experiment highlighted the necessity of carefully planning the design of planting schemes at a variety of scales. Certain species may therefore be more suitable to transplant into specific environments, due to the varied tolerances of abiotic and biotic conditions that halophytes possess, whilst species susceptible to tidal action may be better planted in turfs or multiple formations of plugs. Consideration and experimentation with such ‘informed’ transplantings would be more economically and ecologically efficient. However, transplanting vegetation on managed realignment sites should still be considered as a ‘last resort’, as if a natural salt marsh is situated nearby and the correct tidal signature is re-instated, then desired salt marsh communities should develop over time.

Chapter 6 - A comparison of two coastal realignments: patterns of sediment and seed deposition

6.1 Introduction

Patterns of halophyte colonization and establishment are highly dependent on the (relative) elevation of the salt marsh surface within the tidal frame. As discussed in Chapter 4, elevation is closely linked to inundation; i.e. low relative-elevation sites experience relatively more frequent, deeper and longer inundation than sites higher in the tidal frame. Harsher abiotic conditions therefore exist at lower elevations, limiting the type and extent of salt marsh plant species to those which can tolerate such extreme environments (e.g. *Salicornia europaea*) while topographic variation strongly influences the distribution and overall diversity of salt marsh plants (Chapter 7).

Both allochthonous (from an external source) and autochthonous (produced *in-situ*) sedimentation are responsible for changes in salt marsh surface elevation, their relative importance depending on geomorphological setting (Adame et al. 2010). The balance of inorganic and organic matter, inherent to the structure of the marsh soil, also differs according whether the marsh is minerogenic or organogenic (Nyman et al. 1990). Minerogenic salt marshes, composed mainly of sands and silts, are the typical marsh type in Britain, whilst organogenic marshes (composed of organic matter) tend to be the dominant marsh type in the US (Alghamdi 2012). Organic matter, composed of plant detritus and other decomposing living material, mainly accumulates in situ, whilst it may also form a component of allochthonous sediment input if transported from a nearby marsh in suspension. The majority of mineral sediment at many sites tends to be allochthonous; therefore, an adequate supply or external 'source' of suspended sediment in the estuary is critical for the morphological development of many salt marshes (Stoddart & Reed 1989; Friedrichs & Perry 2001). Often, this sediment is eroded from

nearby tidal flats and salt marshes (Rotman et al. 2008; Coulombier et al. 2012). However, autochthonous mineral sedimentation may also occur where new creek networks are being eroded, or where existing channels are widening as a result of increased water levels (D'Alpaos et al. 2007).

Despite the dependence of morphological and therefore potential future vegetation development on sedimentation rates, temporal and spatial patterns in sediment deposition are often neglected in the planning and design of managed realignment sites. Excessive sedimentation at Orplands managed realignment site on the Blackwater Estuary (Essex, UK) for example, caused the rapid decay of buried pre-alignment vegetation and the development of soil anoxia, which slowed vegetation establishment (Macleod et al. 1999). Similarly, high concentrations of suspended sediment in the Humber estuary (south Yorkshire, UK) have led to rapid elevation gain and the expansion of salt marsh in managed realignment schemes originally aiming to compensate for the loss of tidal flat habitat in the estuary (Mazik et al. 2010). In contrast, Reed et al. (1997) raised concerns over the use of engineered structures to control tidal exchange in various restoration schemes on the coast of Louisiana, as sediment deposition was reduced in restored areas in comparison with sites with no engineered management.

The composition of deposited sediment may also influence the distribution of salt marsh vegetation (Yang et al. 2008; Cott et al. 2013). In a study by Cott et al. (2013), the diversity of plant species was higher on peat-based substrate (i.e. high in organic matter) than on non-peat substrate on salt marshes on the south-west coast of Ireland. Concentrations of ammonium ions, which can be directly absorbed by plant roots for growth, were higher in the peat substrate and soil conductivity was also lower, allowing a greater diversity of plants to establish. However, soils with high organic content have

low porosity and are therefore more saturated and prone to water-logging (Boelter 1969). The establishment of certain plant species which are sensitive to soil aeration may be inhibited in these areas, such as *Atriplex portulacoides* (Armstrong et al. 1985; Cott et al. 2013). Soil porosity increases with particle size; so although ammonium levels may be lower in coarser textured, sandy substrates (Hazelden & Boorman 2001), conditions may be more preferable for the establishment of species sensitive to waterlogging. Additionally, the root development of certain salt marsh species, such as *Spartina* spp., may be hindered by compacted substrate (Bertness 1988; Huckle et al. 2000) on formerly reclaimed land that was intensively farmed. Waterlogging may also occur as drainage is impeded (Crooks et al. 2002). The deposition of a thin layer of coarser sediment following managed realignment site may therefore initiate the colonisation of certain species, as root networks are able to expand more easily and soil aeration is increased.

If relying on natural colonization, seed dispersal through hydrochory is an essential process in the restoration of salt marsh vegetation. Salt marsh seed banks are relatively short-lived, as the seeds of most salt marsh plants have a short lifespan once deposited (Morzaria-Luna & Zedler 2007), despite retaining viability following flotation times of up to several months (Koutstaal et al. 1987). It is only possible to understand and predict vegetation development at a site if it is known what species are entering the site via hydrochory, where such species are deposited, and when the seeds of specific species are more abundant (Morzaria-Luna & Zedler 2007). Additionally, there has been little research on the transport and deposition of seeds in relation to sedimentation patterns in salt marshes, even though close links between sediment and seed deposition are known from riparian settings (Goodson et al. 2003). Of particular importance may be whether seed supply varies with the amount of deposited sediment to a site (Goodson et al. 2003). Such information would provide a valuable insight into the mechanisms of

vegetation development in managed realignment sites.

The aim of this chapter is to investigate the main controls on sediment and seed deposition in a managed realignment site where tidal exchange is regulated by an engineered structure. Temporal and spatial patterns will be analysed in conjunction with hydrodynamic data and compared with a storm-breached site where natural tidal exchange has been reinstated. Associations between sediment and seed deposition will be analysed and the impact of tidal regulation on such processes will be discussed. Key questions include: What are the main hydrodynamic influences on temporal and spatial sediment and seed deposition in realignment sites, and does this differ between sites? How and why does the quantity and composition of deposited sediment and seeds differ between sites?

6.2 Materials and Methods

6.2.1 Study sites

Field work was primarily conducted at two study sites in south Devon, UK: South Efford managed realignment site (SEM), on the Avon estuary and Great Orchard Fields unmanaged realignment site (GOF), on the Erme estuary. Full field descriptions of both sites can be viewed in Chapter 2.1 and 2.2, respectively. The mouths of the Avon and Erme estuaries are separated by only ~5.5 km on the south Devon coastline and their rivers drain from Dartmoor along similar lengths (37 km and 24 km, respectively (Devon AONB)). Both sites therefore occupy similar geomorphological settings. Estuary hydrodynamics, such as tidal levels, currents and salinity are also expected to be comparable at both locations, as the sites are ‘estuary-fringing marshes’ (Allen 2000; Chapter 2), located in the uppermost reaches of the estuary and differing in dimension by only 5 ha. Additionally, GOF and SEM have similar histories of former

agricultural land-use as grazing pasture. However, since realignment in 2011, the tidal regime at SEM has been restricted by a self-regulating tidal gate, whilst tides have been flowing through a simple breach at GOF since the wall was damaged in a storm in late 2007. The development of salt marsh vegetation was rapid at GOF (Chapter 2.2), whilst salt marsh species are low in abundance at SEM (Chapter 5). Therefore GOF has great value as an unmanaged reference site, which can be compared with deliberate realignment at SEM. Some reference measurements will also be taken from the natural salt marsh at South Efford (SEN).

6.2.2 Sampling methods

At SEM, two adjacent squares of Astroturf mat (21 cm x 21 cm) with 1.5 cm plastic tufts (Lambert & Walling 1987) were deployed on the southwestern corner of every 4 m² quadrat on 25 m, 50 m, 100 m, 150 m, 200 m and 300 m transects at increasing distances from the SRT (24 stations; Chapter 4: Fig. 4.2). Astroturfs were also deployed on the -60 m transect on SEN (4 stations; Chapter 4: Fig. 4.2). At GOF, two adjacent mats were deployed at four stations on transects 50 m, 100 m, 200 m, 250 m, 400 m and 550 m from the breach (24 stations; Fig. 6.1). Mats were secured to the ground surface with a 30 cm steel peg in each corner. The elevation (m ODN) of each sample station was recorded using a Trimble DGPS Real-Time Kinematic base station and rover, with vertical errors <1.3 cm (Network Adjustment Reports, Trimble Business Centre). Fieldwork at both sites was concentrated on the lower marsh area, due to its greater dynamicity and sensitivity to hydrodynamic variation (Coulombier et al. 2012).

Mats were collected and new ones deployed at the same stations for ‘trials’ of 141-203 days between 21/09/11 and 19/02/14 at SEM and SEN (Trials 1-5) and between 13/09/12 and 13/02/14 (Trials 3-5) at GOF. Table 6.1 displays deployment dates of each trial and the number of mats available for separate seed and sediment analyses further

described below (N). Mats were occasionally lost due to tidal/animal activity, as indicated by lower ‘N’ in Table 6.1. All mats were lost on SEN during Trials 2 and 3.

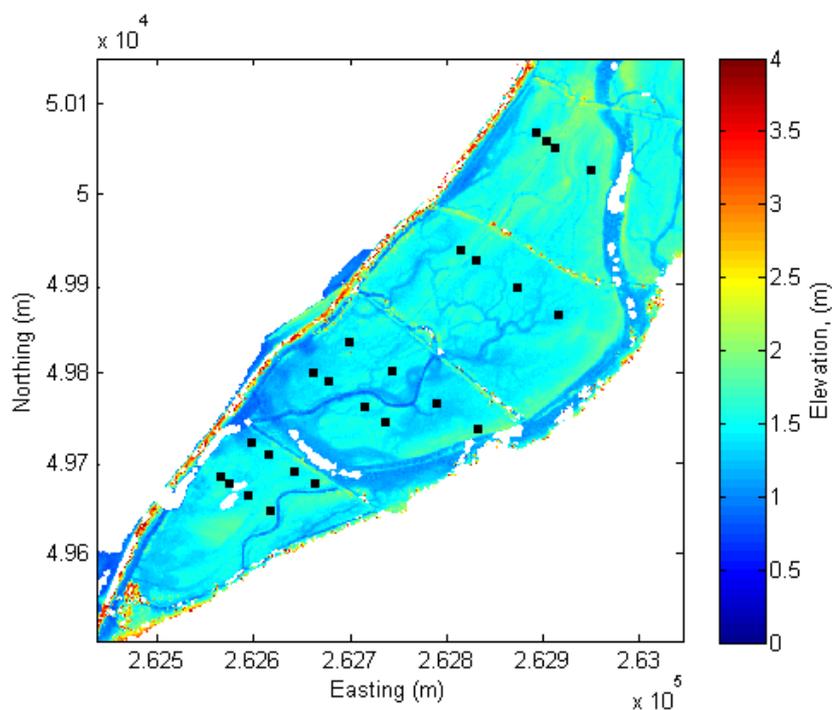


Figure 6.1 – Locations of Astroturf mat pairs (black squares) at Great Orcheton Fields. Four stations were placed on each transect, located at 50 m, 100 m, 200 m, 250 m, 400 m and 550 m from the breach (refer to Chapter 2.2 for breach location). LIDAR data courtesy of Channel Coastal Observatory (www.channelcoast.org).

	SEM			SEN	GOF		
	Deployed	Collected	N	N	Deployed	Collected	N
Trial 1	21/09/2011	16/02/2012	22	4	N/A	N/A	N/A
Trial 2	16/02/2012	08/08/2012	24	0	N/A	N/A	N/A
Trial 3	08/08/2012	27/02/2013	24	0	13/9/12	06/03/2013	24
Trial 4	27/02/2013	18/09/2013	24	4	06/03/2013	25/09/2013	22
Trial 5	18/09/2013	19/02/2014	24	3	25/09/2013	13/02/2014	22

Table 6.1 – Deployment dates for Astro turf trials at South Efford managed and natural sites (SEM, SEN, respectively; Trials 1-5) and Great Orcheston Fields (GOF; Trials 3-5). Number of astro turf mat pairs collected after each trial is indicated by N.

Once collected and transported for analysis in separate, sealed plastic bags, one mat from each pair was used to determine dry weight, mean particle size and the percentage of sand, silt, clay and organic content of the deposited sediment. The other mat was placed in a naturally lit greenhouse at a regulated temperature and used for germination trials to determine the number and species of deposited viable seeds (Goodson et al. 2003).

For sediment analyses, each mat was weighed prior to deployment. On collection, mats were dried for 48 hours at 55 °C and weighed again once cooled. The total weight of deposited sediment during that trial was then calculated by subtracting the pre-deployment mat weight from post-deployment weight. Due to slight variation in the lengths of deployment trials, the weight of deposited sediment on each Astro turf mat was standardized by expressing as $\text{g/m}^2/\text{d}^{-1}$ for the length each trial ('Sediment weight'; Reed et al. 1997).

Sediments were removed from Astro turf mats using a stiff paintbrush. Loss-on-ignition in a muffle furnace determined organic matter content (percentage 'Organic content') where over 10 g of sediment was deposited. This involved heating a known weight of sediment to 550 °C for 4 hours and subtracting the post-ignition weight to calculate weight loss as a percentage (Emery & Fulweiler 2014). The remainder of the non-combusted sediment was used in particle size analysis. The >4 mm, >2 mm and >1 mm fractions were separated by dry-sieving. Following the removal of organic material using Sodium hypochlorite (pH 9.5) (Lavkulich & Wiens 1970), the <1 mm fraction was analysed from five replicates per sample using a Malvern Mastersizer 2000.

GRADISTAT software (Blott & Pye 2001) was used to analyse the replicates, to give the median grain size ('D50', measured in phi (the negative logarithm to the base 2 of the particle size measured in mm)); the percentage sand and coarser grains ('% sand'; <4 phi); the percentage silt ('% silt'; 4–9 phi) and the percentage clay ('% clay'; >9 phi) for each sample.

Germination trials were conducted in a naturally lit and heated greenhouse in Plymouth. Mats were kept in seedling trays filled with compost and were punctured to allow them to drain easily when watered twice a day. A thin layer of vermiculite was put on each mat to prevent drought under higher temperatures. On germination, seedlings were identified and removed, over 10-week periods (Goodson et al. 2003).

Due to the temporal variability of the tidal regime at SEM (Chapter 4), water levels were measured throughout the whole study period, using an Impress S12C pressure transducer, which logged data at 15 min intervals. At GOF, a pressure transducer (INW Smart Sensor, PT2X) was deployed adjacent to the breach between September and December 2012, programmed to take measurements every 10 minutes for 92 days (collecting a total of 13,500 measurements). Pressure measured during low tide was assumed to be atmospheric pressure. Therefore the atmospheric data was subtracted from the full pressure on rising/high tides and the resultant pressure dataset was converted to equivalent water levels, on the assumption that 1 psi = 0.703 m ODN water depth. The water level data were then corrected for the elevation of the pressure transducer (measured by RTK GPS) in order to give actual water levels (m ODN).

6.2.3 Data analysis

Tidal statistics were calculated for each sample station as in Chapter 4, but by using the measured elevations (m ODN) of each sample station in conjunction with water level data. At GOF, tidal statistics were calculated as a monthly average from the 3 month

dataset. At SEM, monthly averages were calculated from the water levels measured during each trial. The following statistics were calculated for each sample station: average inundation duration per month ('inundation duration'); average frequency of over-marsh inundations per month, given as a percentage of the natural high tides ('inundation frequency'); average depth of over-marsh high tides per month ('depth'). Additionally, 'inundation frequency' was combined with 'depth' to give the cumulative amount of water covering each mat per month ('cumulative depth').

Following log 10 transformation where necessary, the mean weight of sediment ($\text{g/m}^2/\text{d}^{-1}$) deposited at SEM was compared between deployment trials with a one-way repeated measures analysis of variance (ANOVA) followed by Tukey's post-hoc tests ($N = 21$; samples only used where data available for all trials). Mauchly's test showed that the assumption of sphericity had been violated ($\chi^2_{(9)} = 115.13$, $P < 0.01$); therefore, Greenhouse-Geisser estimates of sphericity were employed to correct the degrees of freedom ($\epsilon = 0.32$).

The organic content of sediment deposited at South Efford managed realignment site during Trials 1, 3 and 4 was also compared using a one-way repeated measures ANOVA for 15 samples (samples only used where data available for all trials), followed by Tukey's tests. The assumption of sphericity had been violated ($\chi^2_{(2)} = 6.15$, $P < 0.05$) and the degrees of freedom were corrected by using Greenhouse-Geisser estimates of sphericity ($\epsilon = 0.726$).

Independent samples t -tests were used to test whether there were any differences in 'sediment weight' collected on each Astroturf mat ($\text{g/m}^2/\text{d}^{-1}$), 'organic content', 'D50' and '% silt' between SEM and GOF during Trials 3 and 4.

Principle components analyses (PCA) were used to further examine and visualise the relationships between hydrological and sediment variables at during Trials 3 and 4 at

SEM and GOF. Samples were only included in the analyses where a full dataset of sediment characteristics were available. Explanatory variables were: Distance from the breach/SRT ('distance'), 'inundation duration' and 'cumulative depth'. Dependent variables were: 'sediment weight', 'organic content', 'D50', '% sand', '% silt' and '% clay'. All variables were standardised and analysed in separate PCAs for each site, using PAST 3.02 (Hammer et al. 2001).

Numbers of viable seeds deposited per square metre were compared between all trials (1-5) at SEM and between Trials 3-5 at GOF using Kruskal–Wallis non-parametric tests. Numbers of seeds were compared between sites for Trials 3-5 using Mann-Whitney U tests.

Sørensen's similarity index (Jongman et al. 1995) was employed to compare the species composition of seeds deposited during autumn trials with plant species recorded in vegetation surveys in neighbouring quadrats during the following summer at SEM and SEN (as in Chapter 5). At both sites, Sørensen's indices were calculated to compare deposited seeds from Trial 1 with the June 2012 vegetation survey and seeds from Trial 5 were compared with the June 2014 vegetation survey. Seed data from Trial 3 were compared with the June 2013 vegetation survey on the restored site only.

Pearson's correlation was used to test whether the number of deposited seeds correlated with 'sediment weight' at each site, using data from Trial 5 only, due to the relatively large amount of sediment deposited at both sites during this period. All data were analysed using MATLAB (The Mathworks, Inc., Massachusetts, United States), SPSS 21.0 (SPSS Inc, Chicago, IL, USA) or PAST 3.02 (Hammer et al. 2001).

6.3 Results

6.3.1 Hydrodynamic comparisons

Inherent differences in tidal regimes between SEM, GOF and SEN are evidenced by significant differences in hydrodynamics (Table 6.2). In Chapter 5, data showed how water levels in SEM increased over time, mainly as a result of adjustments/malfunctions with the SRT. This is reflected by increases in ‘inundation frequency’, ‘inundation duration’, ‘depth’ and ‘cumulative depth’ (Table 6.2). The SEN tidal statistics remained relatively similar between trials and it can be assumed that hydrodynamics at GOF would also remain relatively similar, as the tidal regime is not regulated. Inundation characteristics at the naturally-breached GOF site are extremely similar to those at SEN. Despite sampling locations being approximately 0.5 m lower in elevation at SEM in comparison with SEN and GOF, ‘inundation frequency’ was extremely low at the restored site during the first two trials. During Trial 3, ‘inundation duration’ suddenly became almost double that of the natural salt marsh and 53.7 % longer than at GOF, at 285.9 ± 21.4 hours. ‘Inundation duration’ continued to increase throughout the remaining trials. Even though ‘inundation duration’ and ‘inundation frequency’ was highest at SEM during Trial 3-5, ‘depth’ and therefore ‘cumulative depth’ remained lower than at SEN and GOF. For example, ‘depth’ was only 0.1 ± 0.01 m in the restored area in Trials 3 and 4, 0.26m lower than at GOF and 0.3 - 0.35 m lower than SEN. Therefore, despite high ‘inundation frequency’ in SEM, ‘cumulative depth’ was only 25.8 % and 30.8 % of that at SEM and 33 % and 46.2 % of that at GOF in Trials 3 and 4, respectively. Therefore, SEM was inundated by regular, but relatively shallow tidal flows in later trials (see also Chapter 4).

	GOF	Trial 1		Trial 2		Trial 3		Trial 4		Trial 5	
		SEM	SEN	SEM	SEN	SEM	SEN	SEM	SEN	SEM	SEN
Elevation (m)	1.52 (±0.03)	0.97 (±0.02)	1.6 (±0.05)	0.97 (±0.02)	1.6 (±0.05)	0.97 (±0.02)	1.6 (±0.05)	0.97 (±0.02)	1.6 (±0.05)	0.97 (±0.02)	1.6 (±0.05)
Inundation duration (hrs)	153.62 (±7.86)	73.69 (±13.25)	126.96 (±9.37)	21.9 (±4.82)	96.36 (±7.37)	285.9 (±21.39)	152.75 (±9.82)	245.76 (±17.97)	124.45 (±9.01)	496.19 (±16.60)	186.03 (±11.15)
Inundation frequency	75.94 (±2.07)	37.8 (±5.77)	73.06 (±2.97)	10.78 (±2.81)	60.93 (±2.88)	75.53 (±4.23)	73.01 (±2.87)	81.61 (±4.02)	73.01 (±3.25)	75.99 (±0.91)	71.03 (±2.01)
Depth (m)	0.37 (±0.01)	0.07 (±0.00)	0.39 (±0.02)	0.1 (±0.00)	0.39 (±0.02)	0.11 (±0.01)	0.46 (±0.02)	0.11 (±0.01)	0.41 (±0.02)	0.25 (±0.01)	0.51 (±0.02)
Cumulative depth (m)	16.57 (±0.73)	1.64 (±0.30)	17.16 (±1.35)	0.47 (±0.10)	10.97 (±0.95)	5.46 (±0.56)	21.2 (±1.52)	7.65 (±0.78)	24.88 (±1.97)	11.03 (±0.67)	21.21 (±1.20)

Table 6.2 - Mean (\pm SE) values for elevation (m ODN), hours of inundation per month ('inundation duration'); frequency of overmarsh inundations per month, given as a percentage of the natural high tides ('inundation frequency'); depth of overmarsh high tides per month ('depth') and cumulative depth per month ('cumulative depth'), of all sampling locations on South Efford managed realignment site (SEM; N = 23) and South Efford natural marsh (SEN; N = 4) during Trials 1-5, and Great Orcheston Fields (GOF; N = 23) during a separate deployment period.

6.3.2 Sediment analysis

At both SEM and GOF, the largest amount of sediment was deposited on mats closest to the SRT/breach. At SEM, 35.5 ± 8.7 % of the total amount of deposited sediment during each trial was collected on a mat on the 25 m transect adjacent to the SRT. Likewise, 33.9 ± 14.7 % of sediment deposited at GOF during each trial was collected on the 50 m transect, directly opposite the breach (see Fig. 6.1). These mats were consequently excluded from further sediment analysis.

There was a significant difference in the amount of sediment deposited between trials at SEM ($F_{(1.26, 25.27)} = 57.27$, $P < 0.01$), with Tukey's post-hoc tests revealing significant differences between all trials. In Figure 6.2, it is clear that immediately following the reintroduction of the tidal regime, sedimentation rates were extremely low, at below $2 \text{ g/m}^2/\text{d}$ for the first two trials. In fact, sedimentation rates were at their lowest during trial two, at only $0.26 \pm 0.05 \text{ g/m}^2/\text{d}$. The amount of deposited sediment significantly increased (alongside tidal inundation) over the following three trials, with $9.92 \pm 1.36 \text{ g/m}^2/\text{d}$ sediment deposited in Trial 5, $5.39 \text{ g/m}^2/\text{d}$ more than in Trial 4. There was also a reduction in percentage organic content between Trials 1, 3 and 4 at SEM ($F_{(1.45, 20.34)} = 8.171$, $P < 0.01$).

For each of Trials 1, 4 and 5 (astroturf mats on the reference natural marsh could not be located for Trial 2 or 3), more sediment was deposited on the natural marsh than on the restored site (Fig. 6.2.). Sedimentation rates do, however, vary between trials on the natural marsh and are almost as low as the restored marsh during Trial 4, at $6.45 \pm 1.49 \text{ g/m}^2/\text{d}$. This amount was tripled during Trial 5, when $21.43 \pm 4.59 \text{ g/m}^2/\text{d}$ was deposited on the natural salt marsh. Sediment deposited on SEN was lower in organic content than on SEM, when measured in Trials 1 and 4. Mean organic content of the

natural sediment was 17.3 ± 0.7 % in Trial 3 and 18.5 ± 1.0 % in Trial 4, less than half of the organic matter in deposited sediment in the restored area, at 40.3 ± 4.0 % and 39.9 ± 0.1 % in Trials 3 and 4, respectively.

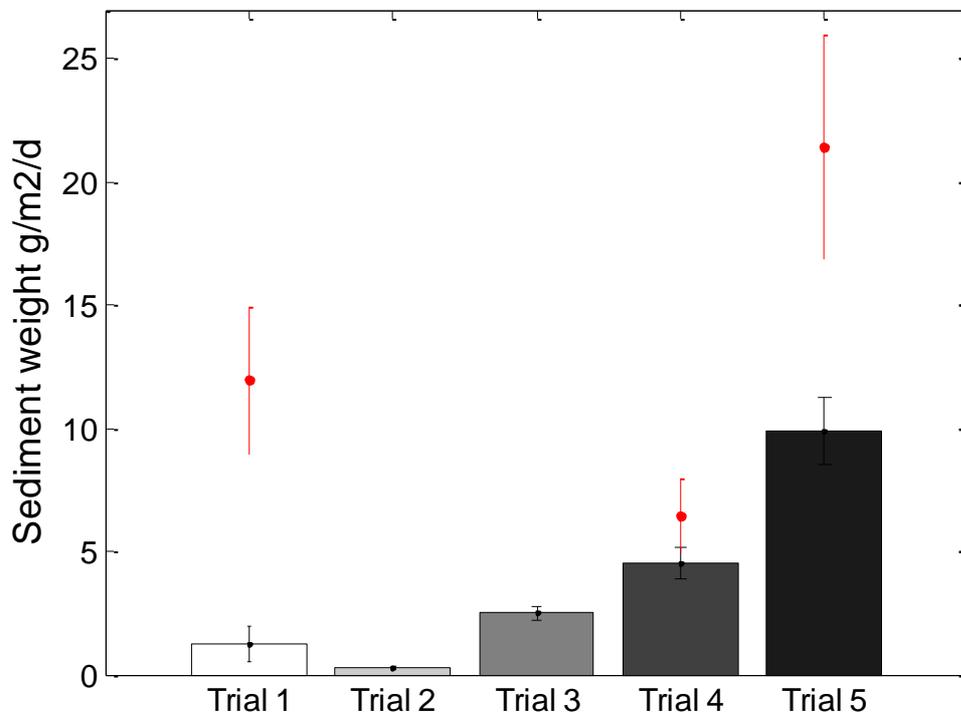


Figure 6.2 - Mean weight (\pm SE) sediment ($\text{g}/\text{m}^2/\text{d}$) deposited at South Efford managed realignment site during Trials 1-5 ($N = 21$). Significant differences exist between all trials ($P < 0.01$). Red error bars indicate mean weight (\pm SE) sediment ($\text{g}/\text{m}^2/\text{d}$) deposited on the natural salt marsh at South Efford during Trial 1 ($N = 4$), Trial 4 ($N = 4$) and Trial 5 ($N = 3$).

More sediment was deposited at GOF than at SEM during Trial 3 ($t_{(41)} = -6.29$, $P < 0.01$), Trial 4 ($t_{(39)} = -4.70$, $P < 0.01$) and Trial 5 ($t_{(42)} = -5.63$, $P < 0.01$) (Results for Trial 3 and 4 shown in Fig. 6.3a). Mean sediment organic content was also significantly higher at SEM in comparison with GOF, during Trial 3 ($t_{(41)} = 11.02$, $P < 0.01$) and Trial 4 ($t_{(39)} = 9.78$, $P < 0.01$) (Fig. 6.3b). During Trial 3, sediment deposited at SEM contained 29.7 % more organic matter than sediment deposited at GOF and 21.7 % more during Trial 4.

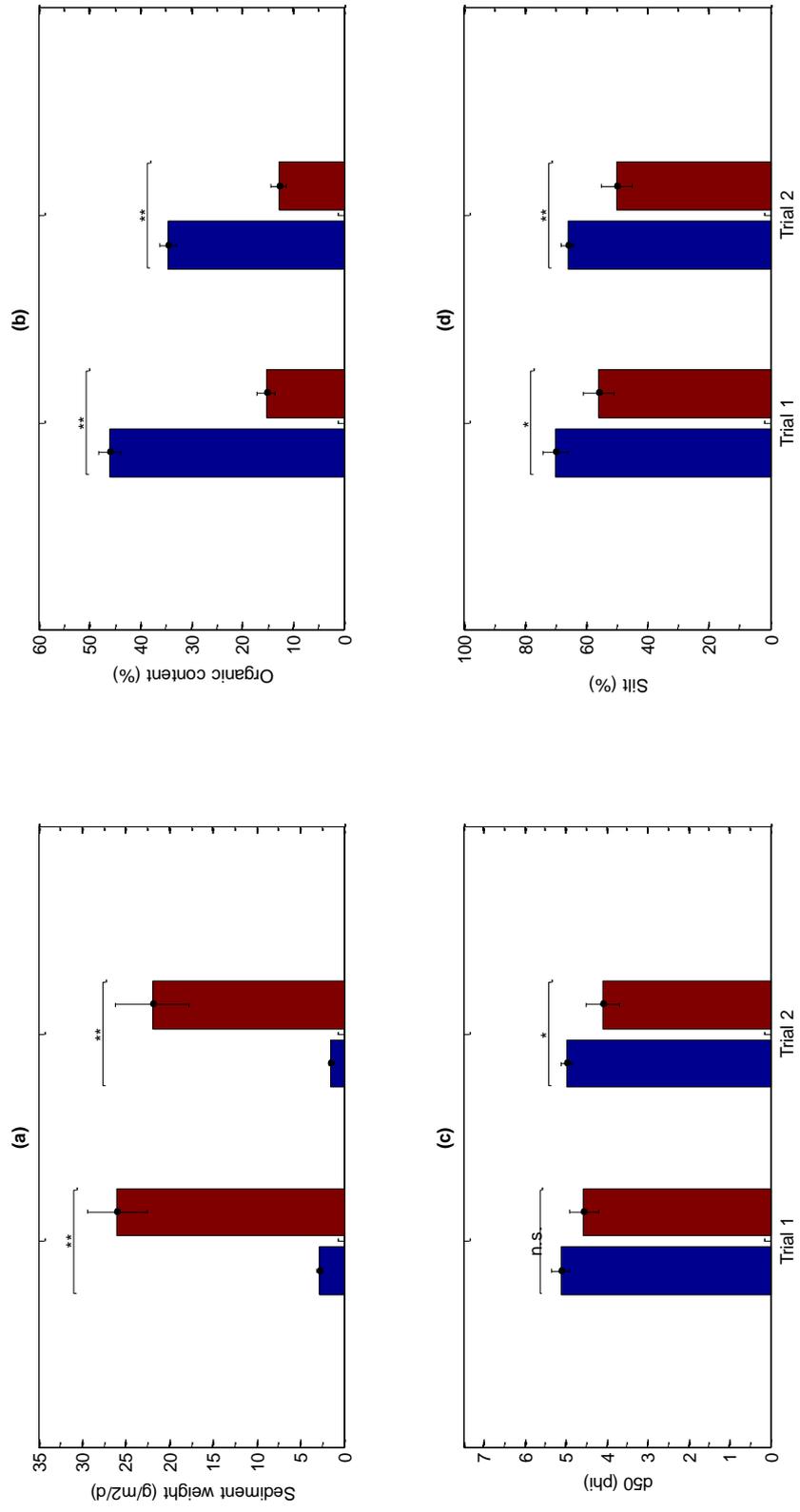


Figure 6.3 – (a) ‘Sediment weight’; (b) ‘Organic content’; (c) ‘d50’ and (d) ‘% Silt’ of sediment deposited at South Efford managed realignment site (blue bars) and Great Orcheton Fields (red bars) during Trials 3 and 4. N = 20, 21 (South Efford managed realignment: Trials 3 and 4 respectively); N = 23, 20 (Great Orcheton Fields: Trials 3 and 4 respectively).

Although there was little variation in the elevations of sampling stations at GOF (Table 6.2), ‘D50’ and ‘% silt’ varied greatly between sampling stations, as did ‘Sediment weight’ (Fig. 4.3c, 4.3d, 4.3a). ‘d50’ was significantly lower at GOF than at SEM in Trial 4 ($t_{(39)} = 2.14$, $P < 0.05$), indicating larger mean particle size at GOF (Fig. 4.3c). The particle size of sediment deposited on SEN also appeared slightly larger than at SEM at 4.63 ± 0.33 phi (N = 4). Deposited sediment at SEM was relatively high in silt content in comparison with GOF in Trial 3 ($t_{(41)} = 2.23$, $P < 0.05$) and at 66.2 ± 9.2 %, was significantly higher than GOF in Trial 4 ($t_{(39)} = 2.87$, $P < 0.01$), at 50.3 ± 23.7 % (Fig. 4.3d). Deposited sediment at SEN at 59.0 ± 5.2 % (N = 4) during Trial 4 was marginally higher in silt content than GOF, but lower than at SEM.

Forty one sediment mats from SEM during Trials 3 and 4 were used in the PCA analysis. The first four components cumulatively explained 92.3 % variance within the dataset, with 74.9 % explained by the first two components (Table 6.3). The first and second components are visualised in Fig. 6.4a.

The first component predominantly reflects variation in sediment characteristics, with loadings of at least 0.45 (Table 6.3). As would be expected, ‘D50’ (measured in phi) negatively correlates with ‘% sand’, whilst it positively correlates with finer silt and clay content (Fig. 6.4a). However, no other variables appear to be associated with the particle size of deposited sediment and the distribution of samples from both trials are fairly well dispersed; therefore there are no obvious controls on sediment composition at South Efford MR site.

A relatively high amount of variance (31.47 %) is explained by Component 2 (Table 6.3). This is mainly due to the high loadings of ‘inundation duration’, ‘cumulative depth’ and ‘sediment weight’ on this axis (>0.49), which are all positively associated. All of these variables are negatively associated with ‘distance’ and ‘organic content’,

indicating that the site slopes upward in elevation inland (Fig. 6.4a). ‘Distance’ may have a slightly independent positive association with ‘organic content’, reflected by high loadings (0.42 and 0.78, respectively) on Component 3. However, this effect is slight, as only 10.02 % variance is explained by Component 3 (Table 6.3).

	PC 1	PC 2	PC 3	PC 4
Eigenvalues	3.91	2.83	0.90	0.67
% variance	43.39	31.47	10.02	7.39
Distance	-0.16	-0.32	0.42	0.81
% Organic content	0.06	-0.30	0.78	-0.49
D50	0.49	-0.10	-0.10	0.06
% Sand	-0.49	0.12	0.05	-0.07
% Silt	0.49	-0.12	-0.05	0.07
% Clay	0.45	-0.12	0.05	0.06
Sediment weight	0.14	0.49	0.37	0.02
Cumulative depth	0.13	0.49	0.17	0.29
Inundation duration	0.11	0.52	0.17	-0.02

Table 6.3 - Environmental variables included in a PCA analysis of South Efford managed realignment data from Trials 3 and 4, with their loadings on the four components of the PCA, eigenvalues and the percentage variance explained by each axis.

A PCA was also conducted using data from GOF, including 43 mats from Trials 3 and 4. 96.18 % variance in the dataset was explained by the first four components and 87.55 % of the stated variance was explained by the first two components (Table 6.4). The greatest amount of variance in the dataset is explained by Component 1 (Table 6.4). Component 1 is mainly composed of sediment characteristics, as ‘organic content’, ‘D50’, ‘% sand’, ‘%silt’ and ‘clay’ all have loadings of at least 0.31. The loadings indicate that organic content increases with distance from the breach and particle size

decreases simultaneously, reflected by increasing ‘D50’ (phi), ‘% silt’ and ‘% clay’. In contrast, ‘% sand’ decreases with distance from the breach. ‘Sediment weight’ also appears to be negatively associated with ‘distance’ on Component 1 in Fig. 6.4b and Table 6.4 additionally shows that this association is particularly strong on Component 3, yet this component only explains 5.7 % variance.

	PC 1	PC 2	PC 3	PC 4
Eigenvalues	6.15	1.73	0.51	0.26
% variance	68.33	19.22	5.70	2.92
Distance	0.31	0.18	0.70	-0.58
% Organic content	0.36	0.05	0.14	0.54
D50	0.39	0.13	-0.17	0.06
% Sand	-0.39	-0.16	0.07	-0.15
% Silt	0.39	0.14	-0.08	0.08
% Clay	0.38	0.14	0.02	0.08
Sediment weight	-0.32	0.16	0.63	0.55
Cumulative depth	-0.20	0.64	-0.15	0.04
Inundation duration	-0.17	0.67	-0.15	-0.14

Table 6.4 - Environmental variables included in a PCA analysis of Great Orcheton Fields data from Trials 3 and 4, with their loadings on the four components of the PCA, eigenvalues and the percentage variance explained by each axis.

‘Inundation duration’ and ‘cumulative depth’ have high loadings on the Component 2 (Table 6.4; Fig. 6.4b), at 0.67 and 0.64, respectively. However, sediment characteristics do not appear to be strongly associated with these hydrological variables on this, or any other axis.

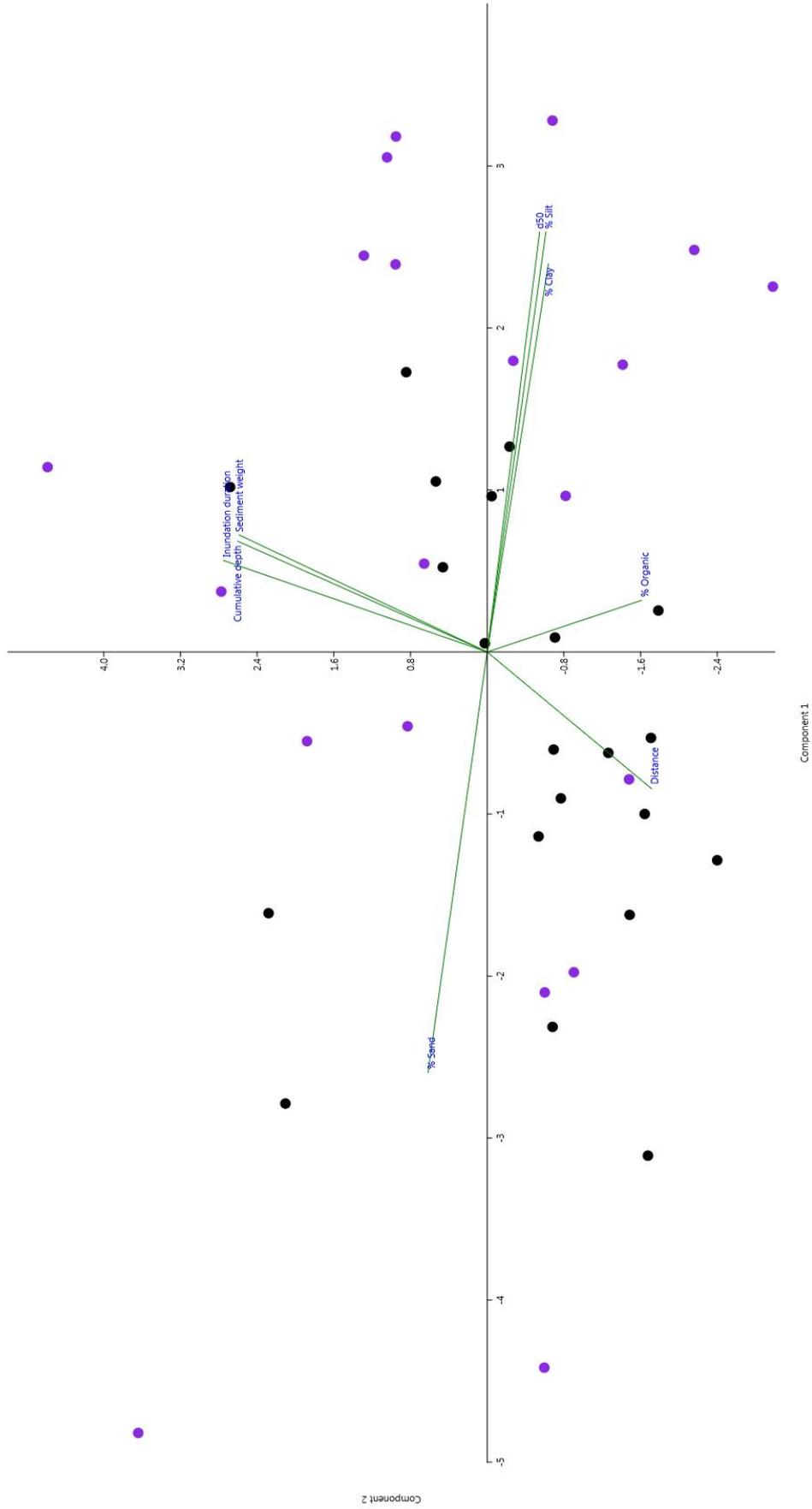


Figure 6.4 - Relationships between the hydrological and sediment variables and distribution of the sampling stations on the first and second components of PCA analyses using data from (a) South Efford managed realignment site (Purple; N = 41) and (b) Great Orcheton Fields (Black) during Trials 3 and 4 (N = 43). Continued overleaf.

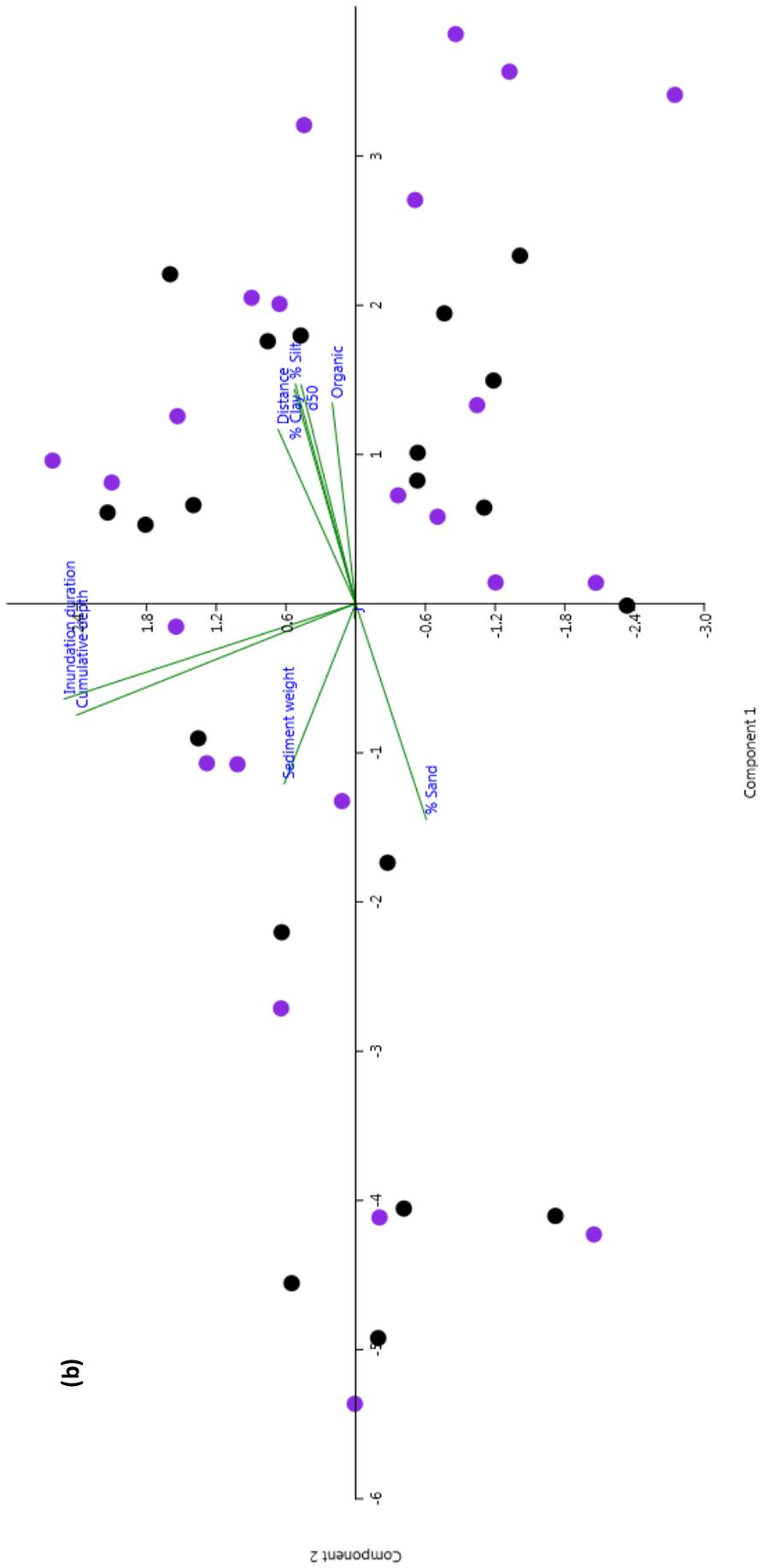


Fig. 6.4 ctd.

6.3.3 Seed analysis

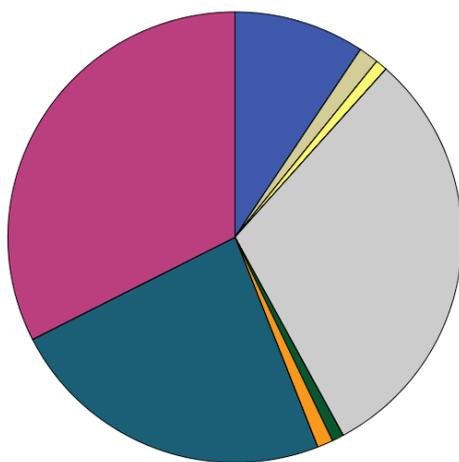
Twenty species were recorded during Trials 1-5 on mats from SEM, but only 8 of these were salt marsh species. 1390 individual seedlings were recorded in total (equivalent to 262.66 viable seeds m⁻²). 18 % of seedlings were identified as salt marsh species. *Triglochin maritima* and *Juncus gerardii* were the most frequent salt marsh species to germinate on the Astroturf mats, at 33 % and 31 %, respectively. 9 % salt marsh seedlings were *Aster tripolium* (Fig. 6.5a).

Nine salt marsh species were recorded on SEN, with three glycophytes also recorded. Fewer individual seedlings were counted overall, due to the reduced sample size and additional loss of samples during some trials on the natural marsh, but 1028.51 viable seeds were deposited m⁻², 765.85 m⁻² more than on the restored site. Additionally, 97 % of the total recorded seedlings were salt marsh species. *Aster tripolium* was the most abundant salt marsh species to germinate on the mats, at 86 %. However, only 0.2 % salt marsh seedlings were recorded as *Triglochin maritima* and *Atriplex portulacoides* (Fig. 6.5b).

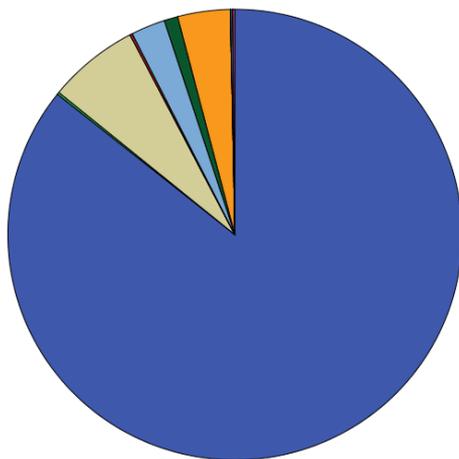
At GOF, 13 salt marsh species were recorded from a total of 34 species. Although data were only collected during Trials 3-5, 4,366 individuals were counted, (1,455.92 viable seeds m⁻²). 97 % of all seedlings were salt marsh species. 79 % of salt marsh seedlings to germinate on Astroturf mats were *Salicornia europaea* (Fig. 6.5c).

The number of seeds deposited at SEM significantly differed between trials ($H(4) = 49.89$, $P < 0.01$). On examination of the means (Fig. 6.6), seed deposition increased, although Trials 1 and 4 were significantly lower than in Trials 2, 3 and 5 and the number of viable seeds deposited in Trial 5 was marginally higher than in previous trials.

(a) South Efford managed realignment



(b) South Efford natural



(c) Great Orcheton Fields

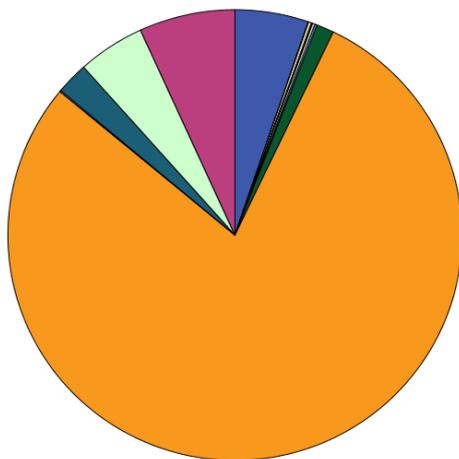


Figure 6.5 – Relative percentage of salt marsh seedlings that germinated on Astroturf mats from (a) South Efford managed realignment site (Trials 1-5); (b) South Efford natural marsh (Trials 1, 4 and 5); (c) Great Orcheton Fields (Trials 3-5). 246, 616 and 4239 salt marsh seedlings germinated at each site, respectively.

Seed deposition follows the same pattern at GOF (Fig. 6.6), in that fewer seeds were deposited during Trial 4 ($H(2) = 38.57, P < 0.01$). Consequently, seed deposition at GOF and SEM did not significantly differ during Trial 4 ($U = 190, N = 24,22, P > 0.05$), whilst seed deposition at GOF was significantly higher than the restored site during both Trial 3 ($U = 150, N = 24, P < 0.01$) and Trial 5 ($U = 83.5, N = 24,22, P < 0.01$). No correlation was found between the numbers of deposited seeds and ‘sediment weight’ at SEM ($r = 0.149, N = 23, P > 0.05$) nor GOF ($r = -0.391, N = 21, P > 0.05$).

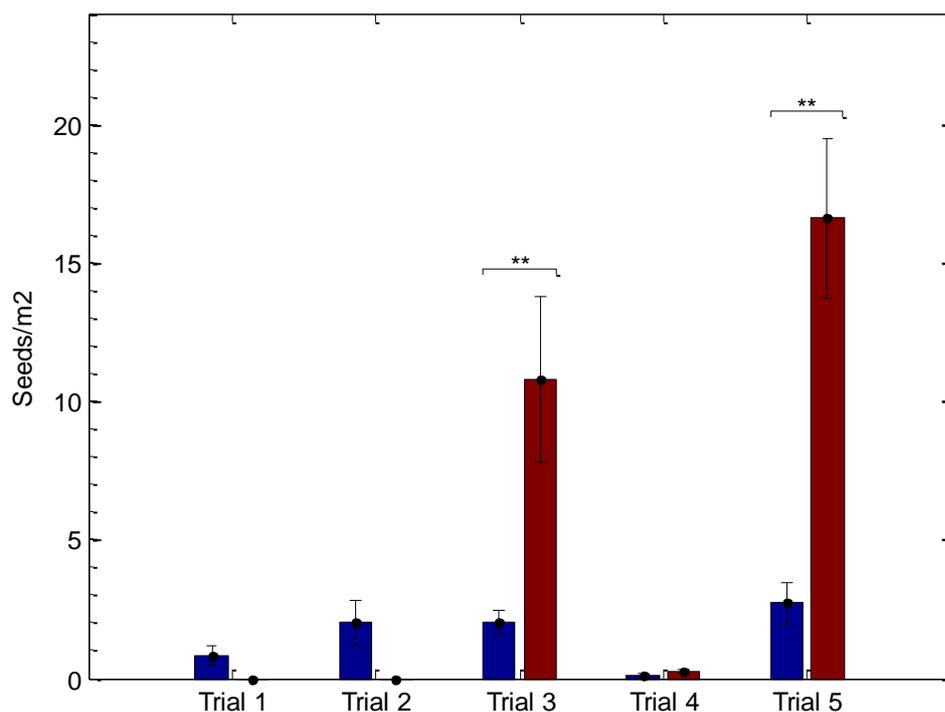


Figure 6.6 - Numbers of viable seeds deposited per unit area (m^2) during Trials 1-5 at South Efford managed realignment site and between Trials 3-5 at Great Orcheton Fields. Asterisks reflect significant differences between the two sites (** = $P < 0.01$).

The species composition of standing vegetation and deposited seeds at SEM became more similar over time (Table 6.5). Sørensen's index for Trial 1/June 2012 was 0.44,

indicating low-intermediate similarity. All deposited seeds were found in the standing vegetation, but only two of these species (*Spergularia media* and *Atriplex prostrata*) were salt marsh species. A large number of species (18) were found in the standing vegetation but not in the deposited seeds, mostly terrestrial species, but some halophytes, such as *Aster tripolium*, *Glaux maritima*, *Salicornia europaea* and *Triglochin maritimus*. In Trial 3/June 2013, Sørensen's index had increased slightly to 0.55, mostly due to the reduction in species richness of the standing vegetation. However, many halophytes had also disappeared from the standing vegetation and were still not present in the deposited seeds. By Trial 5/June 2014, Sørensen's index had almost doubled in comparison to the first trial, to 0.84. Nine of the eleven species in the standing vegetation were halophytic and all of these were recorded in the deposited seeds, except for *Spartina anglica*.

Sørensen's index was also relatively high on SEN during Trial 1/June 2012, at 0.71, whilst in Trial 5/June 2014 it was only 0.4 (Table 6.6). *Agrostis stolonifera* was deposited on both occasions, but was not found in the standing vegetation. In contrast, *Spartina anglica* and *Glaux maritima* were recorded in the standing vegetation in both trials, but were not found amongst germinated seedlings on the Astroturf mats. Sørensen's index was particularly low in Trial 5/June 2014, perhaps due to the presence (albeit low in frequency) of *Cochlearia anglica* and *Triglochin maritima* in the deposited seeds but not in the standing vegetation, whilst *Atriplex portulacoides* was highly abundant in the standing vegetation (Chapter 5), yet was not recorded in the deposited seeds.

	Trial 1 / June 2012		Trial 3 / June 2013		Trial 5 / June 2014	
	Veg.	Dep.	Veg.	Dep.	Veg.	Dep.
<i>Agrostis stolonifera</i>	X	X	X	X	X	X
<i>Alopecurus geniculatus</i>	X		X			
<i>Aster tripolium</i>	X				X	X
<i>Atriplex prostrata</i>	X	X			X	X
<i>Bolboschoenus maritimus</i>	X		X		X	X
<i>Carex otrubae</i>	X	X	X	X		
<i>Cerastium fontanum</i>	X					
<i>Eleocharis palustris</i>	X		X			
<i>Glaux maritima</i>	X		X			
<i>Juncus articulatus</i>	X		X	X		
<i>Juncus bufonius</i>	X					
<i>Juncus compressus</i>	X					
<i>Juncus conglomeratus</i>	X					
<i>Juncus effusus</i>	X	X	X	X		
<i>Juncus gerardii</i>	X		X	X	X	X
<i>Lolium perenne</i>	X		X			
<i>Plantago media</i>	X					
<i>Prunella vulgare</i>	X					
<i>Puccinellia maritima</i>			X		X	X
<i>Ranunculus repens</i>	X	X				
<i>Rumex obtusifolia</i>	X	X		X		
<i>Salicornia europaea</i>	X				X	X
<i>Spartina anglica</i>					X	
<i>Spergularia media</i>	X	X	X	X	X	X
<i>Taraxacum officinale</i>	X		X		X	

<i>Trifolium repens</i>	X					
<i>Triglochin maritima</i>	X		X		X	X
<i>Urtica urens</i>				X		
Total number of species	25	7	14	8	11	9
Sørensen's index	0.44		0.55		0.82	

Table 6.5 – Species present in standing vegetation recorded in surveys at South Efford managed realignment site in June 2012, 2013 and 2014 (Veg.) alongside the viable seeds in deposited sediments on *Astroturf* mats during Trials 1, 3 and 5 (Dep.). Presence indicated by X.

	Trial 1 / June 2012		Trial 5 / June 2014	
	Veg.	Dep.	Veg.	Dep.
<i>Agrostis stolonifera</i>		X		X
<i>Betula pubescens</i>		X		
<i>Spartina anglica</i>	X		X	
<i>Plantago maritima</i>	X	X	X	
<i>Puccinellia maritima</i>	X		X	X
<i>Atriplex prostrata</i>	X	X		X
<i>Atriplex portulacoides</i>	X	X	X	
<i>Salicornia europaea</i>	X	X	X	X
<i>Aster tripolium</i>	X	X	X	X
<i>Spergularia media</i>	X	X	X	
<i>Glaux maritima</i>	X		X	
<i>Cochlearia anglica</i>				X
<i>Triglochin maritima</i>				X
Total number of species	9	8	8	7
Sørensen's index	0.71		0.4	

Table 6.6 – Species present in standing vegetation recorded in surveys at South Efford natural salt marsh in June 2012 and 2014 (Veg.) alongside the viable seeds in deposited sediments on

6.4 Discussion

6.4.1 Sedimentation patterns

The weight of sediment deposited at SEM increased with ‘inundation duration’ and ‘cumulative depth’. Similarly, Temmerman et al. (2003) found that on a salt marsh on the Scheldt Estuary (near Antwerp), suspended sediment concentrations at high tide increased linearly with inundation height and exponentially with inundation duration. At high elevations in the tidal frame, the rate of sedimentation may be limited by infrequent inundation of the marsh surface, shallow depths and a shorter hydroperiod (Friedrichs & Perry 2001). As the elevation of the marsh surface in the tidal frame decreases, more allochthonous and autochthonous sediment is delivered to the marsh surface by more frequent inundations and an elongated hydroperiod allows time for sediment to fall out of suspension onto the marsh surface. However, sedimentation rates will plateau as inundation frequency approaches its maximum relative to the natural tidal regime. Similarly, if inundation duration exceeds the length of time it takes for sediment to fall out of suspension, sedimentation rates will no longer increase with extended inundation duration. At this point, sedimentation rates will only increase with increased water depths, as a larger amount of sediment will be suspended in the heightened water column (Temmerman et al. 2003).

As average water levels during the first two years of realignment at SEM were extremely low, gradual increases in inundation frequency and duration at SEM as a result of adjustments to the SRT can be assumed to be the explanation for increases in sediment deposition over time. However, sedimentation rates at the restored site remained lower than the natural salt marsh and GOF following Trial 3, despite ‘inundation frequency’ and ‘inundation duration’ becoming significantly higher at SEM in relation to the other sites. The average depth of inundation and therefore ‘cumulative

depth' was still significantly lower at the restored site during Trials 3-5; therefore, it can be assumed that shallow flows were limiting the amount of suspended sediment available for deposition. In addition, shallow flows limit the current strength of over-marsh flows, reducing the capacity for sediment entrainment (Reed et al. 1999). The consideration of 'cumulative depth' instead of inundation frequency alone is therefore crucial in the planning and implementation of RTE schemes, as like at SEM, increased inundation frequency may increase sedimentation to a point, but further adjustments to the tidal prism may be required in order to achieve inundation depths that encourage rates of sedimentation sufficient to keep up with sea level rise (Reed et al. 1999).

At GOF, spatial patterns of sediment deposition were more dependent on distance from the breach, corroborating studies conducted on natural salt marshes where sedimentation rates decrease with distance from the source of suspended sediment (Friedrichs & Perry 2001). For example, on open coastal salt marshes such as in the Danish Wadden Sea, wave action causes large amounts of sediment to be deposited on the marsh fringe but decrease with distance inland as wave energy dissipates (Pedersen & Bartholdy 2007). On mature, high marsh platforms where water is delivered to the marsh surface via dendritic creeks, higher rates of sedimentation may also occur with proximity to tidal channels (Reed et al. 1999; Culberson et al. 2004; Temmerman et al. 2005). On younger salt marshes positioned at low elevations in the tidal frame (such as GOF), tidal water may flow onto the marsh surface as sheet-flow from the marsh edge rather than through the under-developed channel network (Temmerman et al. 2005). Therefore, more sediment may be deposited close to the marsh edge or breach as water velocities decrease when contact is made with the marsh surface, causing flocculating sediment to fall out of suspension (Christiansen et al. 2000). Marsh vegetation may further attenuate waves and reduce tidal velocities inland, which contribute to this negative gradient of sediment deposition (Leonard & Luther 1995). At GOF, sediment

is transported in suspension at high velocities through the open breach and perhaps eroded from the embankment itself, as at Tollesbury (Essex, UK) (Garbutt et al. 2006). A large amount of sediment is deposited directly adjacent to the breach and as velocities decrease, the sediment is gradually deposited onto the marsh surface with distance inland (Reed et al. 1999; Christiansen et al. 2000). In contrast, at SEM, velocities are high adjacent to the SRT where water flows through the narrow culvert and local erosion is occurring (Chapter 4; Fig. 4.12). However, as water depths are limited, the majority of sediment carried in suspension (both allochthonous and autochthonous, from channel erosion) is re-deposited in the channel, in the lee of velocities produced by the SRT (Chapter 4: Fig. 4.12, 4.13); therefore, no decreasing gradient in sediment weight occurs into the marsh interior.

Low amounts of deposited sediment on the restored marsh surface at SEM could also indicate that the SRT design prevents sufficient sediment entering the restored site; a similar situation is reported in restored sites on the coast of Louisiana (Reed 1992; 1997). Additionally, 'Controlled Reduced Tide' systems have been employed on various sites in the Scheldt Estuary as they regulate tidal exchange whilst restricting sedimentation rates in restored areas. These 'flood-control' areas act as accommodation space for tidal waters in areas of high flood risk. High sedimentation rates would raise the elevation of the sites and therefore decrease their value as flood defences (Cox et al. 2006; Maris et al. 2007; Vandenbruwaene et al. 2011a). However, at SEM, further investigation is needed into the possible impact of the SRT structure on sedimentation rates, as the development of a diverse vegetation community is reliant upon elevation variation (Zedler et al. 1999) and is critical for the future sustainability of the restored habitat.

In contrast to general sedimentation patterns, the organic content of deposited sediment

at SEM increased with decreased 'inundation duration' and 'cumulative depth', likely linked to increased mineral sedimentation at locations lower in the tidal frame (Yang 1998). However, increased vegetation cover at higher elevations due to the relaxation of flooding stress could also contribute to higher accretion of plant detritus in situ (Nyman et al. 1993). This would also explain the general reduction in organic content throughout time at the restored site. In Chapter 5, pre-alignment vegetation cover decreased over time in response to increased inundation duration, which would reduce the contribution of plant detritus to organic accumulation.

Although organic content decreased over time at SEM, it remained higher than both the natural marsh (SEN) and GOF in Trials 3 and 4. As overall sedimentation rates at the restored site are low, this is an additional indicator that the majority of sediment deposited at SEM is autochthonous organic sediment rather than allochthonous mineral sediment. This is the likely explanation for limited morphological change observed in Chapter 4, as many studies have shown that an allochthonous mineral sediment supply is vital in the geomorphological (and future ecological) sustainability of salt marsh ecosystems (Cahoon et al. 1995; Leonard & Luther 1995; Friedrichs & Perry 2001). However, Culbertson et al. (2004) similarly demonstrated that allochthonous mineral sedimentation was very low on two marshes in the San Francisco Bay Estuary, yet marsh elevations kept pace with sea-level rise through the accumulation of local organic matter. Therefore, if future allochthonous mineral sedimentation does not increase and rates of organic accumulation at SEM continue to decrease, the site may be at risk of subsidence (Reed et al. 1997).

The organic content of deposited sediment at GOF was predominantly determined by distance from the breach. This is likely due to the greater relative influence of distance on overall sediment deposition, as exogenous mineral content of the sediment decreases,

the relative percentage of organic matter increases (Friedrichs & Perry 2001). Indeed, French et al. (1995) found that at Salicornia Marsh on Scolt Head Island (Norfolk, UK), organic matter was transported in suspension for longer than mineral sediment, therefore could be transported further into the marsh interior.

Sediment deposited at GOF was composed of a lower percentage of silt than SEM, an additional indicator of the higher velocities on the former which are correspondingly able to entrain larger sediment particles. The average particle size of deposited sediment decreased with distance from the breach at GOF, corroborating Yang et al. (2008) who found a landward reduction in grain size on two salt marshes in the Yangtze delta, due to inward attenuation of tidal hydrodynamics. It is also possible that higher rates of erosion are occurring within the storm-breached site or at a nearby site, providing a greater supply of coarse material. Sediment deposited at SEM was generally smaller in particle size than at GOF and SEN. Similarly, Crowther (2007) reports how sediment at Nigg Bay (NE Scotland) managed realignment site was finer than sediment deposited on nearby natural salt marshes and was high in silt content after four years of realignment, a pattern attributed to the sheltered, low velocity environment of the embanked salt marsh and long hydroperiod, during which fine sediment could fall out of suspension. Both of these factors could apply to SEM, but low-velocity, shallow flows may additionally prevent the entrainment of larger particles, which are mostly deposited in the channel adjacent to the SRT on arrival into the site (Chapter 4). No measured variables explained variation in particle size at SEM. French and Stoddart (1992) describe the local entrainment of sand from eroded channel sediments as infrequent and event-based, dependent on greater depths and higher water velocities. As hydraulic conductivity is greater in marshes with sandier substrate (Crooks et al. 2002), drainage may be impeded at SEM, where soils are likely to be composed of fine particles and high amounts of organic matter.

6.4.2 Seed deposition

Seed deposition generally increased over time at SEM site suggesting that the potential for seed transport via hydrochory was increased as the tidal prism was raised. However, seed input remained limited at the restored site in comparison with the natural reference and GOF, with fewer individual seedlings and fewer salt marsh species recorded overall. Seed dispersal is a potentially limiting factor on vegetation development in other restoration sites; for example, low numbers of halophyte seedlings were recorded in deposited material at two restored sites in the Tijuana Estuary, California and as a result, accumulation of the seed bank was very slow (Morzaria-Luna & Zedler 2007).

Triglochin maritima and *Juncus gerardii* were the most abundant halophyte seeds deposited at SEM; both species existed in pre-alignment vegetation and were recorded in every vegetation survey following realignment (Chapter 5) thus seeds were available for local dispersal. On SEN, *Triglochin maritima* and *Juncus gerardii* were not abundant in the vegetation surveys nor deposited seeds, yet *Aster tripolium* was abundant in both measures. These differences reflect the primary influence of local dispersal in restored sites rather than longer distance dispersal (Morzaria-Luna & Zedler 2007; Wolters et al. 2005). Similarly, *Salicornia europaea* dominated at GOF in both standing vegetation (pers. obs.) and seed counts.

The species composition of deposited seeds at SEM became more similar to the standing vegetation over time. A variety of terrestrial and salt marsh plants persisted in the first post-realignment summer vegetation survey in June 2012, yet many of these species were not present in the deposited seeds during the previous winter. Although some terrestrial species persisted post-realignment, they were less abundant (Chapter 5); therefore, the total seed production of individual species would have been reduced. Additionally, the reproductive potential of the remaining pre-alignment plant species

may have been compromised by seawater inundation (Chapter 3). In the final trial, there was an obvious increase in the importance of seed transport from the natural salt marsh, as many seeds present in the seed counts in the winter were not present or were of low abundance in the previous summer vegetation survey (June 2013; Chapter 5), but were present in the natural 'seed pool'. Additionally, standing vegetation in the June 2014 survey was similar to the deposited seed count, potentially indicating that abiotic conditions for the colonization of halophytic plants were improving (Rand 2000).

In comparison with the composition of standing vegetation, certain species were missing or lower in abundance in the deposited seeds than would be expected, notably on the natural salt marsh. *Spartina anglica* and *Atriplex portulacoides* were very abundant on the natural marsh, but absent and scarce (respectively) in terms of total number of seeds deposited. This may be due to the high buoyancy of their seeds, which would cause their net export from the marsh surface (Huiskes et al. 1985). However, both species have been less abundant than expected in other studies investigating seed deposition with Astroturf mats (Wolters et al. 2005; Dausse & Bonis 2008) and it has been suggested that greenhouse conditions are unfavourable for the germination of *Spartina anglica* and *Atriplex portulacoides* seeds (Koutstaal et al. 1987; Wolters et al. 2004; Dausse & Bonis 2008). It could be suggested that the seeds of such species require a stratification period, as described in Wolters et al. (2004). However, germination rates have been limited in other studies that simulated stratification periods; therefore, the seeds may have long dormancy periods during germination trials (Wolters et al. 2004).

The quantity of seeds captured on mats did not vary with the weight of sediment deposited at SEM and GOF. This suggests that other processes besides hydrochory are influencing seed deposition at both sites. Huiskes et al. (2012) found that seed transport

was mainly controlled by tidal currents rather than the height of high tide in a salt marsh in the Netherlands. Other studies have suggested that wind dispersal may influence spatial patterns of seed dispersal, especially where non-halophyte species are present (Wolters et al. 2005). *Agrostis stolonifera* seeds have high potential for anemochory (Westhoff 1947) and as the species was fairly abundant at SEM, it is likely that high numbers of *A. stolonifera* seedlings in the germination trials were due to wind-dispersal. Additionally, there is a strong seasonal effect on the number of seedlings deposited at SEM and GOF, as during Trial 3 (March-September 2013), very few seeds were deposited in comparison with winter trials. Similar patterns in seed deposition have been recorded in other studies, as most native halophytic plants seed during September-December (Morzaria-Luna & Zedler 2007; Wolters et al. 2008). It may therefore be beneficial for new managed realignment sites to be opened to tidal inundation in the beginning of autumn, whilst peak seed dispersal is occurring at adjacent salt marshes in the estuary.

6.5 Conclusions

Mineral sedimentation at SEM increased since realignment, but was still much lower than the natural salt marsh at SEN and the unmanaged realignment at GOF after three years. This was despite regular and elongated tidal inundation of the restored marsh surface. Therefore, deeper tidal flows would be needed to increase sedimentation rates at SEM. As the tidal prism is independent of the elevation of RTE sites (Vandenbruwaene et al. 2011a), the SRT at SEM would need to be adjusted order to allow greater volumes of water into the area. However, this would at the same time increase waterlogging of the site (see Chapters 4 and 5). If sedimentation rates remained low following appropriate alterations of the tidal prism, the effect of culvert size on sedimentation rates would need to be investigated. The culvert at SEM is relatively

small in diameter in comparison to a natural breach; therefore large quantities of sediment (of larger grain size in particular) may be restricted from entering the site. If mineral sedimentation rates remain as they are at SEM, morphological development of the site would remain very slow and soil biogeochemistry could be altered by differences in soil composition. Consequently, the establishment of a salt marsh plant community similar to natural salt marshes would remain unlikely.

External seed input to the restored site increased over time, but remained low in comparison with the natural salt marsh and GOF. Although seed input to the site did appear to increase with increased sedimentation rates over time, within-site seed deposition did not correlate with amounts of deposited sediment. Therefore, other processes besides site hydrodynamics are likely to have an influence on seed deposition, such as wind-dispersal.

The species composition of seeds also differed between sites, indicating that site-scale dispersal has a major influence on seed composition. However, after three years of realignment, the species composition of the standing vegetation and deposited seeds were very similar at SEM. As more seeds were deposited on all sites during autumn/winter trials, early autumn breaches may ensure a greater supply of seeds to new managed realignment sites

Chapter 7 – The influence of tidal channels on drainage and vegetation community composition

7.1 Introduction

Tidal creek networks are fundamental to the biogeomorphological and biogeochemical functioning of salt marsh ecosystems (Spencer & Harvey 2012). Dissecting the marsh platform with sinuous and dendritic networks; creeks transport water, sediment and seeds far into the marsh interior (Reed et al. 1999). Tidal channels are also responsible for the export of tidal water and therefore have an important role in the drainage and dewatering of salt marsh soils (Crooks et al. 2002); both critical processes in the development and evolution of salt marsh vegetation (Mossman et al. 2012b).

Tidal creek morphology is largely dependent on the size of the tidal prism and the topography of the marsh surface (Temmerman et al. 2007). Water draining from the marsh surface during an ebb tide tends to flow into slight dips and depressions, which causes the further erosion of these areas and development of new channels (Fagherazzi & Furbish 2001; D'Alpaos, Lanzoni, Marani & Rinaldo 2007). The formation of fluvial channels is similar in this respect (Rinaldo et al. 1995) and the morphology of both landforms can be highly variable (Temmerman et al. 2005). However, variability in fluvial channel morphology, such as channel width, can be reasonably accurately predicted in models (Rinaldo et al. 1995), whilst bidirectional flows and the influence of vegetation cause complications in predictions of salt marsh creek morphology (Marani et al. 2006; Mason et al. 2006; D'Alpaos et al. 2012). Additionally, peak discharge in salt marsh creeks is of relatively short duration, which (in conjunction with the tendency of channel bed sediments to auto-consolidate) causes channels to be highly variable in width but not in depth (Cahoon et al. 1995). As a result, salt marsh creeks are generally

shallow and wide, but become progressively wider with proximity to the seaward edge, as they enlarge to accommodate the tidal prism (Redfield 1972).

Various studies have been conducted on the effects that tidal creek networks have on local drainage. Ursino et al. (2004) for example found that whilst only vertical flows of subsurface water were present in the marsh interior, both vertical and horizontal flows occur on channel edges, enabling the persistence of an unsaturated, aerated layer of soil directly adjacent to the channel. Even channels of the smallest order have an associated catchment, nested within larger catchments associated with progressively larger channels (Lawrence et al. 2004). On an ebb tide, an hydraulic gradient occurs within such catchments, where water pooled at higher elevations flows into more 'hydraulically efficient' creeks at lower elevations (Friess et al. 2014). Velocities of such flows are increased by a greater tidal prism and therefore increased surface water depths (Friess et al. 2014), which cause heightened erosion and formation of new creeks (Williams et al. 2002).

Where drainage is inefficient and salt marsh soils are saturated for prolonged periods, oxygen levels are reduced by excessive microbial activity (Baldwin & Mendelsohn 1998) and toxic amounts of sulphides, reduced iron and manganese build in the soil causing low redox potential (Ingold & Havill 1984). Biogeochemical changes to the soil composition can inhibit the growth and development of certain plant species that cannot tolerate such extreme abiotic conditions. For example, Armstrong et al. (1985) found that although *Spartina anglica* was well adapted to waterlogging in a natural salt marsh in the Humber estuary, species such as *Atriplex portulacoides* were restricted to aerated soils, such as on creek banks. Additionally, other studies on natural salt marshes have found that although elevation is generally the main driver of abiotic and biotic variability (see Chapter 5); vegetation may vary horizontally as well as vertically in

proximity to tidal channels, with higher species richness on creek banks in comparison with the marsh interior (Hopkins & Parker 1984; Zedler et al. 1999; Sanderson et al. 2000; Morzaria- Luna et al. 2004).

Waterlogging is prevalent on many restored salt marshes (Zedler & Callaway 1999; Crooks et al. 2002; Mossman et al. 2012b). On the majority of sites, the development of natural tidal creek networks has been limited, as hydraulically efficient creek networks are naturally slow to form on salt marshes (Bowron et al. 2011; Friess et al. 2014). Additionally, it has been suggested that if managed realignment sites are not hydrodynamically equivalent to natural salt marshes, tidal velocities may not be sufficient to instigate the erosion of new creeks (see Chapter 4). This has led to suggestions in recent literature that managed realignment sites may not attain equivalent ecosystem functioning to natural salt marshes if they are not as topographically heterogeneous as a natural system (Zedler et al. 1999; Mossman, Davy, et al. 2012; Spencer & Harvey 2012). Creek excavation is sometimes incorporated into the design of managed realignment sites in order to act as a catalyst for further rapid morphological and ecological development. In some cases, as in the Sieperda polder (Scheldt Estuary, near Antwerp), the construction of new creeks has appeared to improve marsh hydrology and stimulate vegetation development (Eertman & Kornman 2002). However, creek networks are often excavated with no regard for the effect that channel morphology, such as width and order may have on physical and biological salt marsh functioning at that particular site. For example, Haltiner et al. (1996) suggested that wide, first order channels with sloping sides are generally excavated on restoration sites, which caused differences in the composition of fish assemblages between natural and restored sites.

Ecosystem functioning can be investigated at a range of different scales and the disregard for scale in field investigations can lead to the misinterpretation of results (Larkin et al. 2006). In this chapter, I will begin by analysing broad-scale variation in salt marsh functioning through the comparison of multiple sites, using several managed realignment sites paired with nearby natural salt marshes. Multiple study sites facilitate investigation of the relative importance of physical processes responsible for variation in vegetation community composition within- and between-sites. This section will therefore aim to elucidate differences in key hydrodynamics, soil drainage and vegetation diversity/community composition between managed realignment sites and natural salt marshes. Although the effects of salt marsh creeks on drainage and vegetation composition have been examined (e.g. Armstrong et al. 1985; Sanderson et al. 2000), physical and ecological parameters have often been assessed independently within a sole study site. Therefore, I will also investigate how tidal channels may introduce differences in topography, hydrodynamics, soil drainage and vegetation diversity/community composition on each of the study sites. Finally, I undertake a smaller-scale study, investigating how such processes vary on the channel bank according to tidal channel morphology (Strahler order and channel width). The combined results of this chapter should contribute to a better understanding of the role of tidal channels in restored and natural salt marsh functioning and how creek morphology may be incorporated in the design of future managed realignment sites.

7.2 Materials and Methods

7.2.1 Study sites

Three managed realignment sites in South West England were selected as field sites for a multi-site investigation (see Chapter 2 for full site descriptions). The embankment surrounding Bleadon Levels managed realignment site (BM), on the Axe estuary,

Somerset (Chapter 2.4) was deliberately breached in winter 1999/2000, in order to create 13ha of salt marsh over the following years. Two herringbone creek networks were cut into the marsh prior to seawater inundation (Ellen McDouall (Wessex Water), pers. comm.).

The remaining two managed realignment sites have regulated tidal exchange: South Efford managed realignment (SEM) is a 7ha site on the Avon estuary, south Devon (Chapter 2.1) and is the most recently implemented site, flooded for the first time in July 2011, whilst an 8.1ha managed realignment site at Goosemoor (GM), Exe estuary, Devon (Chapter 2.3) was opened to the tide in November 2004. An existing network of drainage ditches was enlarged by some profiling prior to inundation at GM (Lyons and Ausden 2008). Although no re-profiling occurred at South Efford, drainage ditches from agricultural use and remnants of the old pre-reclamation creek network remained.

For each managed realignment site, the nearest natural salt marsh in the same estuary was located and sampled both as a reference site and a representation of a natural, established system. The natural reference marshes for GM (GN; Chapter 2.3) and SEM (SEN; Chapter 2.1) were located directly adjacent to the managed realignment sites, separated only by an embankment and the RTE structures. The natural reference marsh for BM is approximately 2km downstream from the managed realignment site, at the foot of the promontory Brean Down (BN; Chapter 2.4). The ages of the reference sites are unknown. SEN was also used as a field site in a more detailed single-site investigation into the effects of channel width on multiple environmental variables and resulting species composition.

7.2.2 Sampling methods

In the multi-site investigation, all sites were sampled between June and September 2013. Prior to field sampling, creek networks at each site were extracted on ArcMap and

channel order was assigned to each channel length between confluences in the network according to Strahler (1964). A representative selection of channels from each order was chosen at each site (see Table 7.1). As in Sanderson et al. (2000), sampling locations were randomly located along channels (stratified by channel order) and measurements were taken on opposite sides of the channel at each sampling location. 78 measurements were taken at SEM, 81 at SEN, 53 at GM, 68 at GN, 60 at BM and 53 at BN.

	First order	Second order	Third order	Fourth order
GM	1	2	1	0
GN	3	1	1	0
SEM	0	3	2	1
SEN	0	2	2	2
BM	3	2	0	0
BN	1	2	0	0

Table 7.1 - Number of channels of each stream order surveyed at each site. GM = Goosemoor managed realignment; GN = Goosemoor natural marsh; SEM = South Efford managed realignment; SEN = South Efford natural marsh; BM = Bleadon Levels managed realignment; BN = Brean Down natural marsh.

On both sides of the channel at each sampling location, 1 m² quadrats were placed directly on the channel bank and 5 m perpendicular to the channel, where measurements of vegetation, elevation and soil redox potential were taken. Percentage cover of all vascular plant species and bare ground was recorded in the quadrat and very rare species recorded as covering 0.01 %. Shannon entropy was later calculated in order to measure plant diversity within each quadrat. This is a combined measure of the number of species present (species richness) and their density within each quadrat (species evenness) (see Chapter 5). Soil redox potential was utilised as a proxy for soil drainage efficiency, as reduced soils are indicative of low oxygen concentrations as a result of

waterlogging (Mossman et al. 2012b). Soil redox potential was measured at low tide, in the downstream corner of the quadrat closest to the channel, at 5 cm depth (as in (Mossman et al. 2012a; 2012b). A Paleo Terra™ (Amsterdam, the Netherlands) customised platinum redox electrode with an Ag/AgCl reference (Vorenhout et al. 2011) was used with a Mettler Toledo SevenGo pro™ pH meter and the probe was left in situ until the reading stabilised. The elevation on each plot (m ODN) was recorded in the same location as redox potential, using a Trimble DGPS Real-Time Kinematic base station and rover, with vertical errors <1.3 cm (Network Adjustment Reports, Trimble Business Centre) (Fig. 7.1).

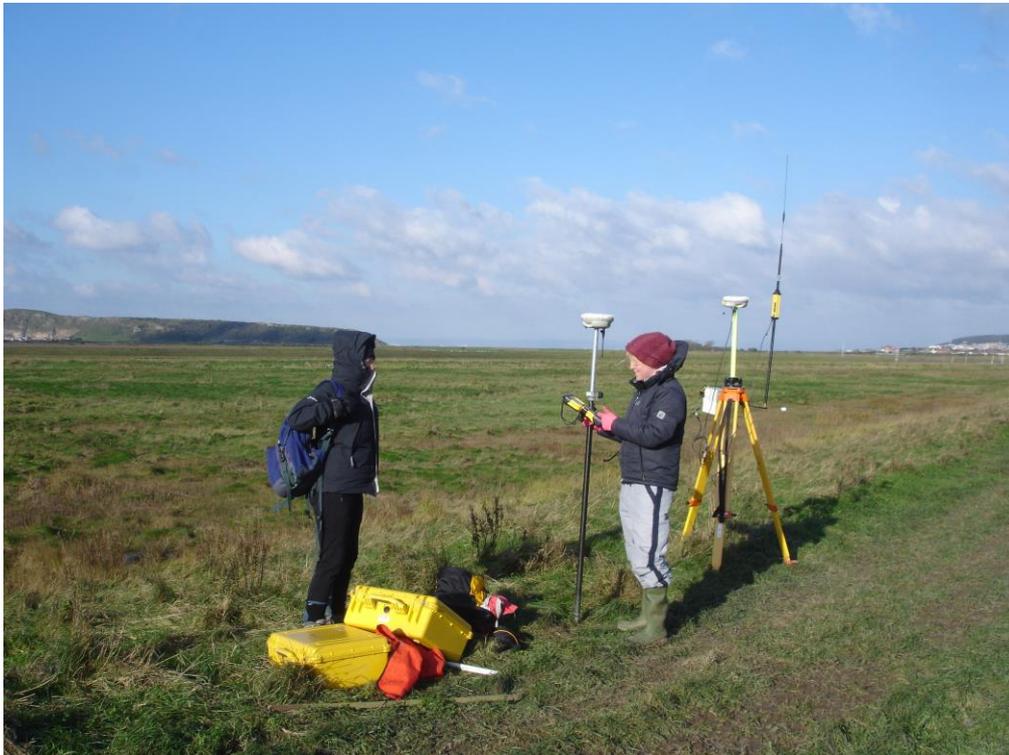


Figure 7.1 – Background (right): Trimble DGPS RTK base station and antenna; foreground (left) Trimble Rover GPS at Bleadon Levels managed realignment (BM).

The channel width investigation at SEN took place during September 2013. Random sampling locations were selected using a 7 m x 7 m grid overlay, with numbered

columns and rows. A random number generator was used to determine two random columns on every row to be sampled. At each sampling location, vegetation, elevation and soil redox potential measurements were taken on the channel bank. Additionally, channel width was measured, using a tape measure pulled taut from opposite sides of the channel bank. Two sediment cores of 10 cm depth and 6 cm diameter (Goodson et al. 2002) were also collected from the mid-point of the quadrat (after vegetation had been quantified) stored in watertight bags during transportation to the laboratory at Plymouth University. Sediment samples were stored at 4 °C for laboratory analysis.

At a later date, a 10g subsample of each core was mixed with distilled water at a 1:5 ratio (British Standards Institution 1997) in order to determine the electrical conductivity and pH of the soil, using Oakton TDSTestr and 4Mettler Toledo FFE20 meters (respectively). The second core from each location was weighed before drying in the oven at 50 °C for 72 hours (Mateos-Naranjo et al. 2008). Once cooled, cores were weighed again and the moisture content of the soil was calculated as a percentage. Soils were then homogenised and combustion for organic content (%) and particle size analysis were conducted following protocol in Chapter 6.

7.2.3 Site hydrodynamics

In order to make hydrological comparisons between sites, pressure transducers (INW Smart Sensor, PT2X) at each site were programmed to take measurements every 10 minutes for 92 days (collecting a total of 13500 measurements). Due to a combination of technical failure and limited availability of pressure transducers, deployments occurred at various 3-monthly periods between July 2013 and May 2014. At GM and GR, pressure transducers were deployed between July and October 2013. At BM, deployments spanned February – May 2014 and at BR, November 2013 – February 2014. At the South Efford sites, pressure transducers were not deployed, as water level

sensors were already in situ (see Chapter 4). Data was extracted for the equivalent number of measurements spanning the 92-day time period, during June - September 2013. Inundation frequency per month (mean overmarsh tides per month as a percentage of mean high tides per month in the estuary) and duration (length of time a specific elevation is inundated per month) were calculated for each sampling location within each site (see Chapter 6 for detailed analysis).

7.2.4 Data analysis

A multivariate analysis of variance (MANOVA) was performed on the multi-site dataset to investigate the effects of 'Site' and 'Channel proximity' on (a) Elevation (m ODN); (b) Inundation frequency per month (%); (c) Inundation duration per month (hrs); (d) Soil redox potential (mV); (e) Shannon entropy and (f) percentage cover bare ground (%). Post-hoc Tukey tests were used to reveal which specific sites differed. Tests for a 'Site' x 'Channel proximity' interaction were also included in the MANOVA and followed up with independent *t*-tests, in order to examine any evidence for site-specific variation in response to channel proximity.

The species composition of samples in relation to environmental variables was investigated using CANOCO v4 (ter Braak & Smilauer 1998). Indirect gradient analyses (detrended correspondence analyses, DCA, (Hill & Gauch 1980)) were used on species data alone, to identify any patterns in species composition. DCA showed that there were no single evident gradients in any of the datasets (all gradients > 2.5); therefore, unimodal, direct gradient analyses (canonical correspondence analysis (CCA)) were used to identify any variability related to the environmental variables. CCA were applied to the combined species and environmental datasets, followed by a Monte-Carlo test of significance (499 permutations). Infrequent and rare species were excluded from individual analyses to prevent overrepresentation of single species.

Firstly, three CCA ordinations were performed, using data from (a) GM and GN (N = 121); (b) SEM and SEN (N = 159); (c) BM and BN (N = 113). Elevation, inundation frequency and duration and soil redox potential were included as environmental variables, whilst channel proximity was represented by symbols.

CCA were also performed using only channel bank samples for each individual site, using the same environmental variables, so that the effects of Strahler channel order on environmental and species variables could be assessed. Different symbols represented channel orders at each site, so that clustering of samples could be easily identified. A CCA was lastly applied to the channel width dataset collected at SEN in order to evaluate the relative influence of the measured environmental variables on plant species composition.

7.3 Results

7.3.1 Site characteristics and the influence of tidal channels

In a multivariate analysis of variance (MANOVA), the investigated variables differed between sites (Wilks' $\lambda = 0$, $F_{(30,1506)} = 295.92$, $P < 0.01$). Further univariate testing revealed variations in: (a) elevation ($F_{(5,381)} = 16073.14$, $P < 0.01$); (b) inundation frequency ($F_{(5,381)} = 158.03$, $P < 0.01$); (c) inundation duration ($F_{(5,381)} = 119.02$, $P < 0.01$); (d) Redox potential ($F_{(5,381)} = 126.52$, $P < 0.01$); (e) Shannon entropy ($F_{(5,381)} = 17.75$, $P < 0.01$); (f) percentage cover bare ground ($F_{(5,381)} = 71.38$, $P < 0.01$) between sites. Elevation differed between all sites ($P < 0.01$), with 5.0 m difference between the highest (BM) and lowest (SEM) site. However, inundation frequency and duration was highest at SEN, closely followed by SEM and GM (Fig. 7.2). The two RTE sites (SEM and GM) were inundated by a similar number of high tides per month (57.0 ± 1.7 % and 56.4 ± 2.1 % respectively) and for a similar duration (105.7 ± 6.1 % and 128.1 ± 5.1 %). Soils at both of these managed realignment sites had lower redox potential than their

reference natural counterparts ($P < 0.01$) and all other sites ($P < 0.01$), with SEM averaging at an extremely low value of -195.7 ± 11.1 mV. Bleadon managed realignment site had the highest average soil redox potential of 172.0 ± 12.7 mV, significantly higher than its natural counterpart at Brean ($P < 0.05$). There was no variation in mean redox potential between the three natural salt marshes ($P > 0.05$).

The three natural marshes (GN, SEN, BN) also had similar Shannon entropy values ($P > 0.05$). GM and BM were the most diverse (1.01 ± 0.06 and 1.04 ± 0.06 respectively) and were more floristically diverse than their natural counterparts ($P < 0.05$). In contrast, SEM was the least diverse with Shannon entropy of 0.42 ± 0.05 ; significantly lower in diversity than SEN ($P < 0.01$). This is reflected in the large average percentage cover of bare ground at SEM (63.5 ± 2.8 %), almost double that recorded at SEN. However, SEN had a relatively large coverage of bare ground in comparison with the remaining sites ($P < 0.01$), with 13.0 ± 3.4 % at GM and under 3.1 % at the remaining sites.

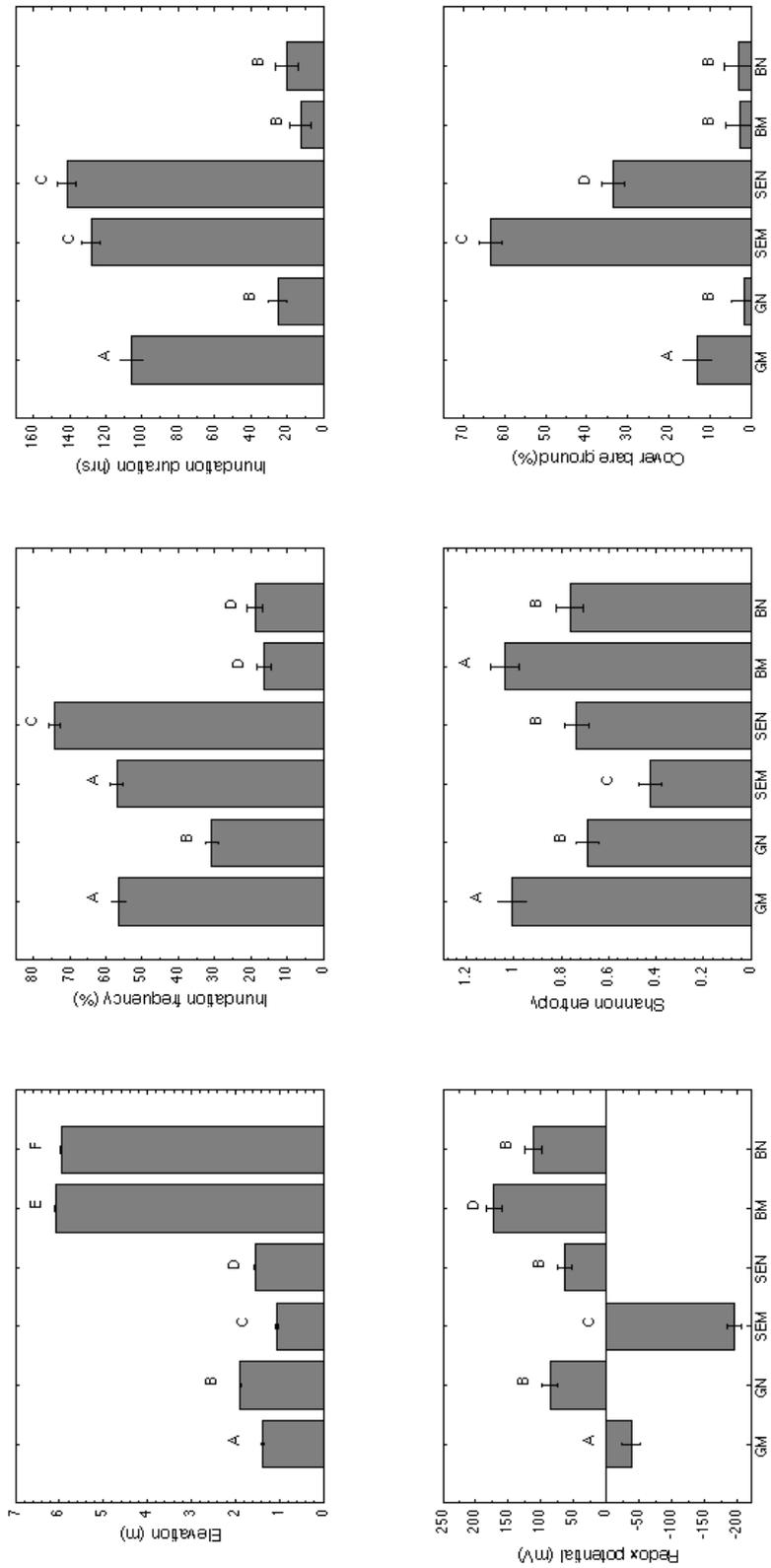


Figure 7.2 - Variations between sites in (a) Elevation; (b) Inundation frequency; (c) Inundation duration; (d) Redox potential; (e) Shannon entropy and (f) Percentage cover bare ground. Significant differences between site means ($P < 0.05$) are marked by different letters.

Using pooled data collected on the channel bank and 5 m from the channel edge from all sites, channel proximity was also revealed to have a significant main effect on abiotic/biotic variability in the MANOVA analysis (Wilks $\lambda = 0.81$, $F_{(6,376)} = 14.39$, $P < 0.01$). Further univariate testing showed that although elevation was significantly lower on the channel bank ($F_{(1,381)} = 48.19$, $P < 0.01$), which caused these areas to endure higher inundation frequencies ($F_{(1,381)} = 21.76$, $P < 0.01$) and durations ($F_{(1,381)} = 8.06$, $P < 0.01$), mean soil redox potential was significantly higher on the channel banks ($F_{(1,381)} = 11.323$, $P < 0.01$) at 50.3 ± 7.1 mV as opposed to 16.4 ± 7.2 mV in measurements 5 m away from the channel edge (Fig. 7.3). However, Shannon entropy and percentage cover of bare ground were not influenced by overall channel proximity ($P > 0.05$).

The effects of channel proximity on the measured variables were highly site-specific (Wilks' $\lambda = 0.76$, $F_{(30,1506)} = 3.62$, $P < 0.01$). Independent *t*-tests were used to further investigate these within-site effects. Channel banks were generally lower in elevation at all sites than 5 m away from the channel bank (Fig. 7.4). Assuming elevational differences, inundation frequency and/or duration at most sites should be correspondingly higher on the channel bank. SEM and SEN were the only sites where hydrodynamics did not differ with proximity to the channel. However, redox was significantly higher on the channel banks at SEM ($t_{(76)} = 3.25$, $P < 0.01$). Redox potential was generally higher on the channel banks at every site (Fig. 7.4), but BN was the only other site at which this difference was statistically significant ($t_{(51)} = 2.62$, $P < 0.05$).

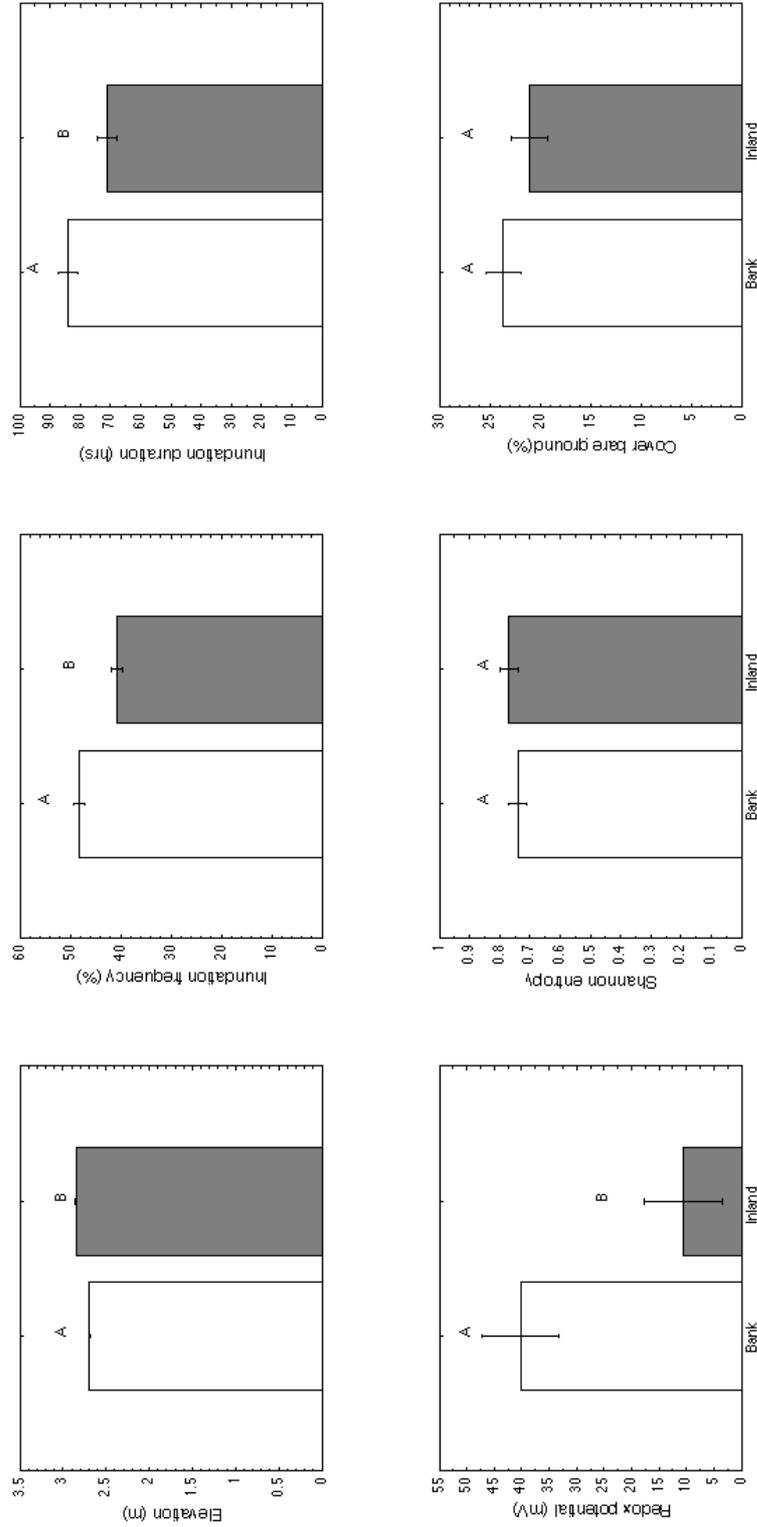


Figure 7.3 - Variations in (a) Elevation; (b) Inundation frequency; (c) Inundation duration; (d) Redox potential; (e) Shannon entropy and (f) Percentage cover bare ground between measurements taken from all sites on the channel edge ('Bank'; white bars) and 5m inland ('Inland'; grey bars). Significant differences between creek location means ($P < 0.05$) are marked by different letters.

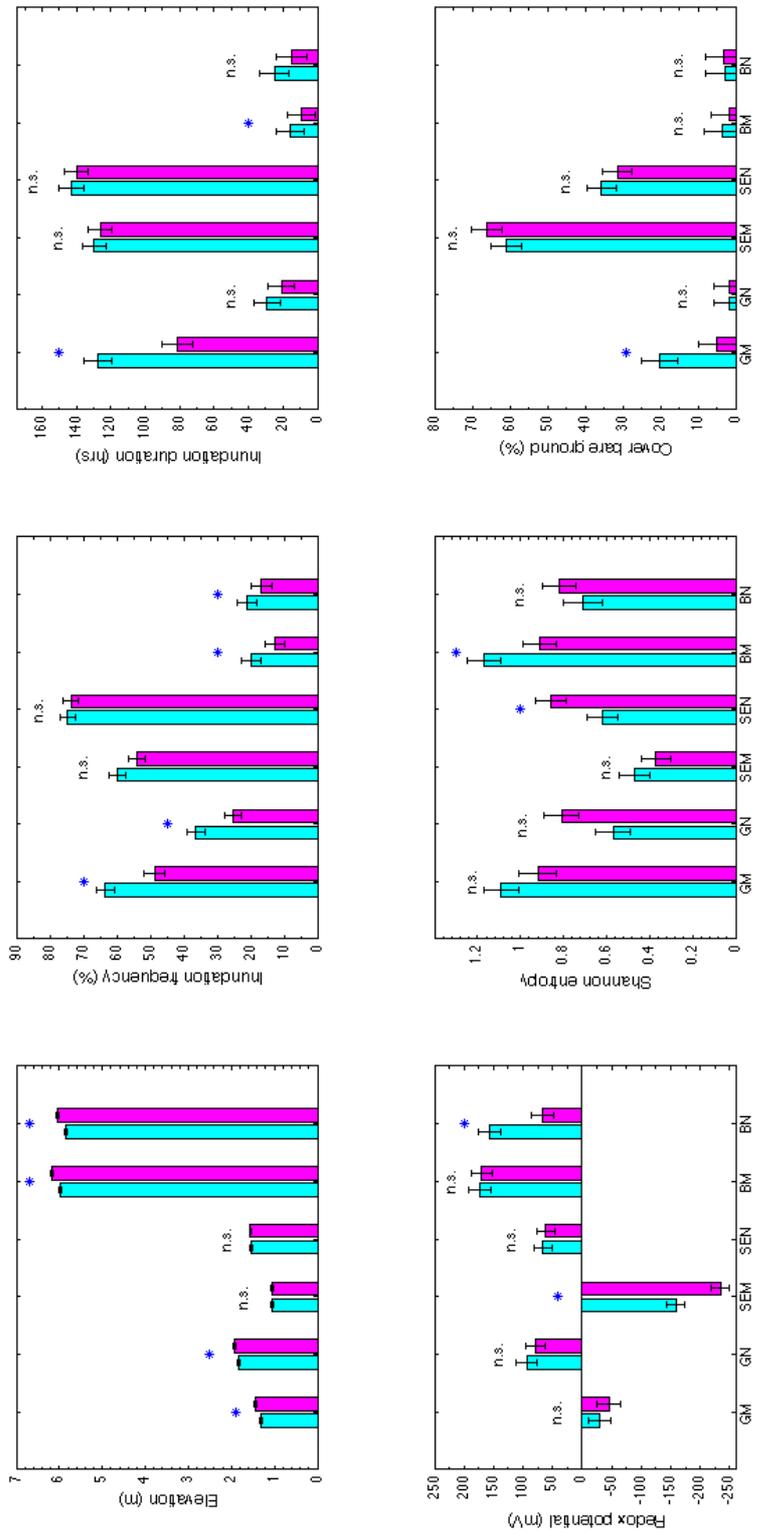


Figure 7.4 – Variations in (a) Elevation; (b) Inundation frequency; (c) Inundation duration; (d) Redox potential; (e) Shannon entropy and (f) Percentage cover bare ground between measurements taken from all sites on the channel edge ('Bank'; blue bars) and 5m inland ('Inland'; red bars) at individual sites. Significant differences ($P < 0.05$) marked with an asterisk (*); not significant marked as n.s..

At all managed realignment sites (GM, SEM, BM), Shannon entropy tended to be higher on the channel bank (Fig. 7.4), although BM was the only site where this difference was statistically significant ($t_{(58)} = -3.91, P < 0.01$). In contrast, at all natural sites (GN, SEN, BN), Shannon entropy was lower on the channel bank and at SEN this difference was statistically significant ($t_{(79)} = 2.74, P < 0.01$). GM is the only site at which percentage cover of bare ground is significantly higher on the channel edge ($t_{(51)} = 3.50, P < 0.01$).

Fig. 7.5 is a series of CCA ordination plots showing the distribution of species and samples in relation to each other and selected environmental variables at (a) GM and GN; (b) SEM and SEN and (c) BM and BN. Tables containing CCA ordination results can be viewed in Appendix 2. In Fig 7.5a, it is clear that hydrological variables and redox potential are highly correlated on the primary axis, explaining 73 % of the variation in sample distribution at the Goosemoor sites ($P < 0.01$; Appendix 2a). This explains the clear separation in sample distribution from GM and GN (Fig. 7.5aii), as GM has higher inundation frequency and duration, and lower soil redox potential. Although GM and GN have similar species richness, with 15 species present at both sites, higher-elevation marsh species such as *Elymus repens*, *Festuca rubra* and *Agrostis stolonifera* dominated quadrats in GN, whilst GM was dominated by lower marsh species such as *Puccinellia maritima* and *Spartina anglica* (Fig. 7.5ai). Some slight differences in community composition were also apparent within GM, as channel quadrats are more clustered in the top right quarter of the plot (Fig. 7.5aii). This is due to greater cover of bare ground and *Spartina anglica* in channel quadrats and lower cover of grass species such as *Agrostis stolonifera* and *Puccinellia maritima* (Table 7.2).

Fig. 7.5b shows a clear (primary axis) separation between data collected at SEM and SEN, mostly reflecting differences in elevation and redox potential between the sites

(this explains 63 % variation ($P < 0.01$); see Appendix 2b). Inundation frequency and duration determine variation on the second axis, causing much within-site variation (Fig. 7.5bii). This indicates that elevation and redox are the main factors influencing observed differences in species composition between the managed and natural South Efford sites, but hydrodynamics strongly influence within-site variation in species composition. All sample sites at SEM (particularly those further from the channel) were characterised by lower sediment redox potential than those at SEN, despite overlap in hydrological characteristics (Fig. 7.5bii). Although mostly dominated by bare ground, 12 species were recorded at SEM, with *Juncus gerardii* and *Agrostis stolonifera* being the most common (Table 7.2). Vegetation community composition does not appear to vary with proximity to the tidal channels at SEM. Seven plant species were recorded in quadrats at SEN, including *Puccinellia maritima*, *Spartina anglica* and *Atriplex portulacoides*; the latter dominated channel quadrats, but became less common with distance from the channel edge, while *Puccinellia maritima* showed the opposite trend (Table 7.2).

The first axis in the CCA assigned to data from BM and BN is mainly associated with highly correlated elevation and hydrological variables (Fig. 7.5c). However, the first axis only explains 56 % of variation in the dataset, whilst in conjunction with the second axis (correlated with redox potential), 79.7 % is explained (Appendix 2c). This indicates that redox potential had an independent effect on vegetation composition, separate from elevation and associated hydrology. Samples from BM and BN were highly dispersed in the CCA ordination plot (Fig. 7.5cii) and a wide range of species are present at both sites (Fig. 7.5ci); 15 and 17 species were recorded at BM and BN respectively, including *Armeria maritima* at BN, which was not recorded at any other site. Nevertheless, *Festuca rubra* appears to dominate both of these sites. Most BM samples are present in the southwestern part of the plot, reflecting higher elevation and

redox potential. Quadrats further from the channel are mostly dominated by *Elymus repens*, containing 16.2 % higher cover than on the channel bank (Table 7.2). Similarly, *Elymus repens* was not found in any channel quadrats at BN, whilst 8.2 ± 5.0 % was recorded in quadrats further from the channel. The ‘inland’ quadrats also contained a higher percentage cover (by 14.1 %) of *Plantago maritima*. BN channel quadrats are slightly clustered in the southern part of the plot, indicating higher redox potential and higher percentage cover of *Festuca rubra*.

(a)(i)

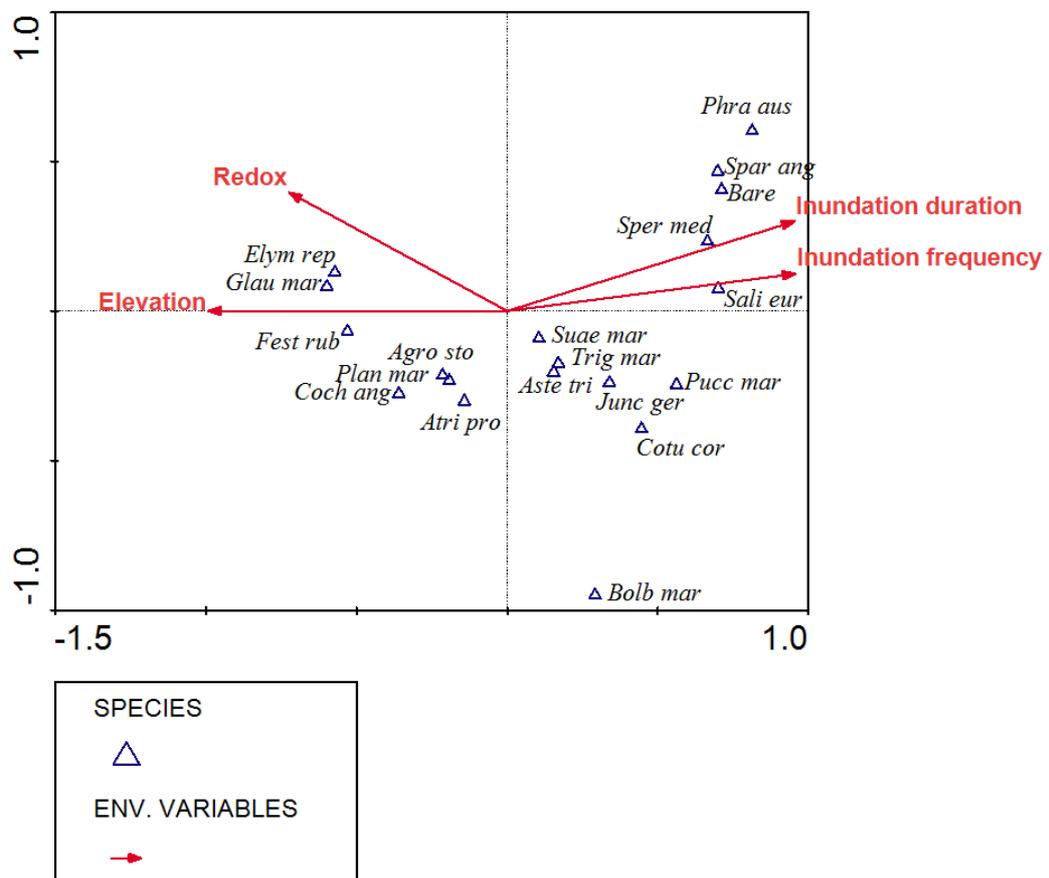
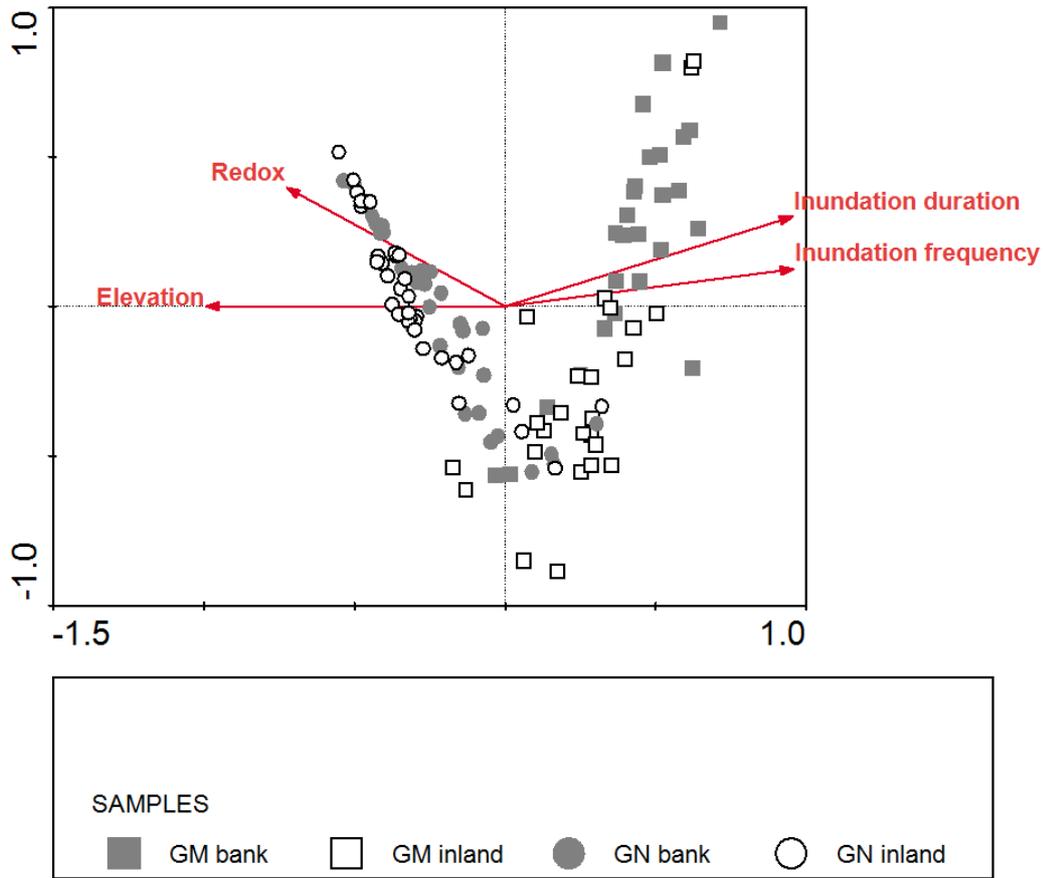


Figure 7.5 - CCA biplots showing the distribution of (i) species and (ii) samples in relation to each other and selected environmental variables at (a) GM and GN; (b) SEM and SEN and (c) BM and BN.

(a)(ii)



(b)(i)

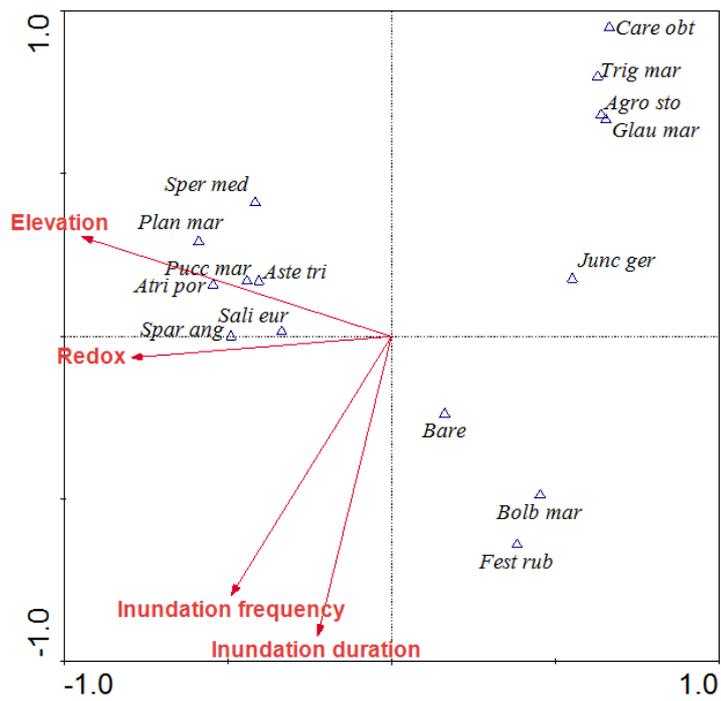
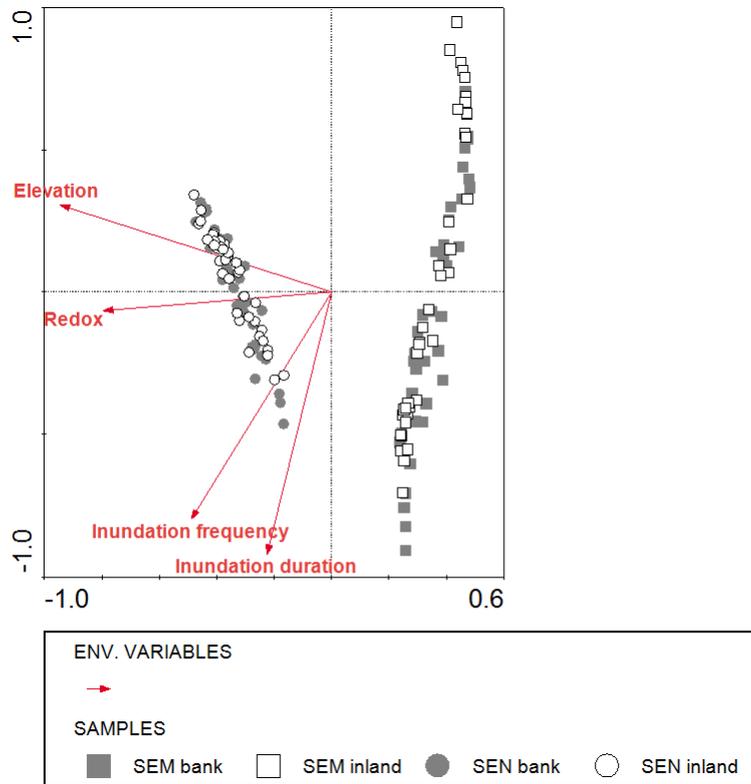


Fig. 7.5 ctd

(b)(ii)



(c)(i)

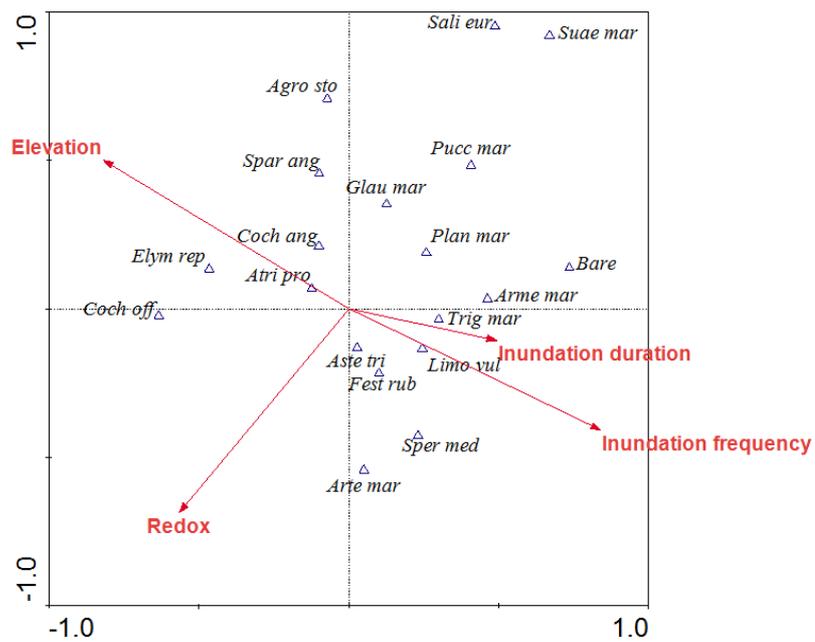


Fig. 7.5 ctd

(c)(ii)

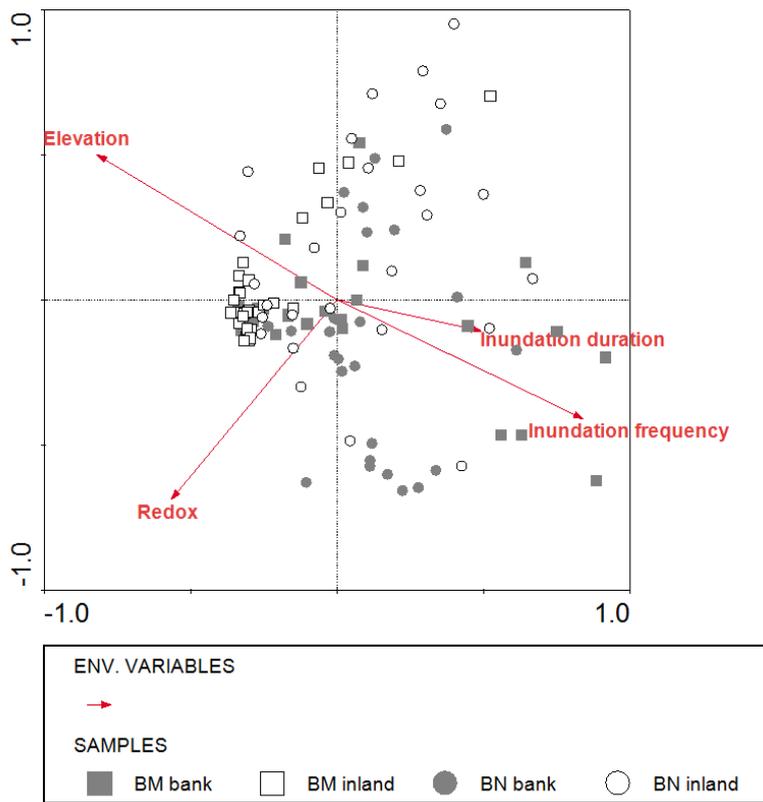


Fig. 7.5 ctd

	GM		GN		SEM		SEN		BM		BN	
	Creek	Interior										
<i>Agrostis stolonifera</i>	2 ± 2.0	10 ± 4.6	7.5 ± 3.2	8.1 ± 2.9	16.6 ± 4.2	15.9 ± 4.2	0	0	0	0.3 ± 0.3	0	0
<i>Aster tripolium</i>	7.9 ± 1.8	5.4 ± 1.5	8.6 ± 3.0	6.2 ± 1.6	1.4 ± 0.6	0.1 ± 0.1	1 ± 0.6	7.1 ± 1.3	7.2 ± 1.3	5.5 ± 1.3	6.1 ± 1.2	3.5 ± 1.0
<i>Atriplex portulacoides</i>	0	0	0	1.2 ± 1.2	0	0	43.5 ± 6.0	28.9 ± 5.7	0	0	0	0
<i>Atriplex prostrata</i>	0	0	4.4 ± 1.5	4 ± 1.1	0.3 ± 0.2	0	0	0	0.3 ± 0.2	0.6 ± 0.4	0.1 ± 0	0.1 ± 0.1
<i>Elymus repens</i>	3.2 ± 3.2	4 ± 3.5	59.3 ± 7.5	46.8 ± 7.5	0	0	0	0	12.2 ± 3.9	28.4 ± 5.7	0	8.2 ± 5.0
<i>Festuca rubra</i>	0.4 ± 0.4	5 ± 3.6	8 ± 3.1	13.4 ± 3.8	0.3 ± 0.3	0.4 ± 0.4	0	0	42 ± 4.5	47.3 ± 3.9	61.3 ± 7.4	44.1 ± 7.6
<i>Juncus gerardii</i>	0.4 ± 0.4	1.5 ± 0.9	0	0	17.6 ± 4.5	10.9 ± 3.5	0	0	0	0	0	0
<i>Plantago maritima</i>	1 ± 0.6	1 ± 0.6	0.2 ± 0.2	1.5 ± 1.2	0	0	6.5 ± 3.7	0.4 ± 0.3	14.7 ± 1.8	5 ± 1.6	10.6 ± 2.4	24.7 ± 4.7
<i>Puccinellia maritima</i>	30.8 ± 5.4	43.7 ± 7.0	3.1 ± 1.8	3.4 ± 1.8	1.4 ± 0.7	2.1 ± 1.2	4.8 ± 2.1	21.6 ± 4.3	2.5 ± 1.0	0.4 ± 0.3	12.2 ± 4.1	8.1 ± 2.9
<i>Spartina anglica</i>	17.1 ± 4.6	5.1 ± 2.7	1.2 ± 1.2	4.1 ± 1.8	0	0	6.3 ± 1.8	8.7 ± 1.6	0	0.3 ± 0.3	1.7 ± 1.0	0.6 ± 0.4
<i>Triglochin maritima</i>	8.8 ± 2.8	14.6 ± 4.1	4 ± 1.8	7.8 ± 2.4	1.1 ± 0.7	2.2 ± 1.6	0	0	17 ± 2.7	9.2 ± 2.2	3.1 ± 1.5	3.5 ± 1.3
<i>Bare ground</i>	20.2 ± 3.9	4.9 ± 1.6	1.6 ± 0.8	1.6 ± 0.8	60.9 ± 6.3	66.2 ± 6.9	35.6 ± 5.2	31.4 ± 5.3	3.7 ± 1.5	1.8 ± 1.7	3 ± 1.6	3.1 ± 1.0

Table 7.2 – Mean percentage cover ($\pm SE$) values of the main species present in quadrats at each site in relation to distance from the channel.

Although all sites were found to be highly variable, some interesting main conclusions can be recapitulated from this section: -

(1) Natural salt marshes were similar in soil redox potential and plant species diversity, despite higher levels of inundation at SEN. The sites did, however, vary in plant community composition.

(2) Managed realignment sites did vary in soil redox potential. Soils at GM and SEM were lower in redox potential than the natural sites, whilst soils at BM were highest in redox potential out of all sites. Managed realignment sites also varied in plant species diversity. BM had the highest plant species diversity of all study sites, closely followed by GM. The plant community at SEM was the least diverse.

(4) Vegetation community composition varied between (a) location and (b) natural and managed sites. BM and BN were fairly similar, dominated largely by *Elymus repens* and *Festuca rubra*. GN was also dominated by the latter two species, whilst lower-marsh species dominated at GM. SEM was largely unvegetated, differing from a fairly diverse salt marsh community at SEN.

(5) Soil redox potential was generally higher on the channel banks at all sites, even at lower elevations in the tidal frame. Shannon entropy tended to be higher on the channel banks in managed realignment sites, but lower on the banks in the natural salt marshes. At different sites, certain species appear to thrive on the channel bank, whilst others appear scarce.

7.3.2 Channel order

Stream order had little influence on species composition on the channel banks, although slight clustering was evident on the CCA ordination plots at SEN, SEM, BN and BL.

Fig 7.6a shows a triplot of samples (classified by stream order) in relation to environmental variables and species composition at SEN (see Appendix 3a for CCA table). Elevation and hydrological variables are highly positively correlated on the first axis (explaining 66 % variation), whilst although redox potential is slightly positively correlated with inundation duration/frequency, redox potential also independently explains some variation in species composition on the second axis (explaining 20 % variation; Appendix 3a). Fourth order samples are mainly grouped to the right side of the plot, which reflects high inundation frequency/duration (as a result of lower elevation) and surprisingly, a tendency for higher soil redox potential. These samples are dominated by *Salicornia europaea*, *Spartina anglica* and bare ground. In contrast, second and third order channels are mainly grouped to the left side of the plot, where *Puccinellia maritima* and *Aster tripolium* are abundant. *Atriplex portulacoides* was more abundant on the banks of second and third order channels, in less frequently inundated areas.

At BN, samples from second (highest) order channels appear to be associated with higher redox and lower elevation on the left side of the plot, where *Elymus repens* and *Festuca rubra* are present, whilst first order channels are more interspersed (Fig. 7.6b; see Appendix 3b for CCA table). At BM (Fig. 7.6c and Appendix 3c for CCA table), the slight positive correlation of redox potential with elevation on the first axis plus the highly dispersed nature of the samples causes difficulty in deciphering the effects of channel order. However, more first order samples occur on the left side of the plot, indicating higher elevation, soil redox potential and abundance of *Elymus repens*.

Fig. 7.6d presents the distribution of channel bank samples at SEM (see also Appendix 3d). Redox potential does not appear to be associated with elevation in the triplot and a slight grouping of second order channels to the south west of the plot indicates that

these samples in general have more reduced soils. In contrast, fourth order channels are grouped on the opposite side, where species such as *Salicornia europaea*, *Aster triplolium* and *Puccinellia maritima* are present at higher redox potentials. Redox potential is highly variable between samples from third order channels, despite little variation in elevation and hydrological variables. This indicates that another factor may be influencing within-order variation in redox potential and resulting species composition.

(a)

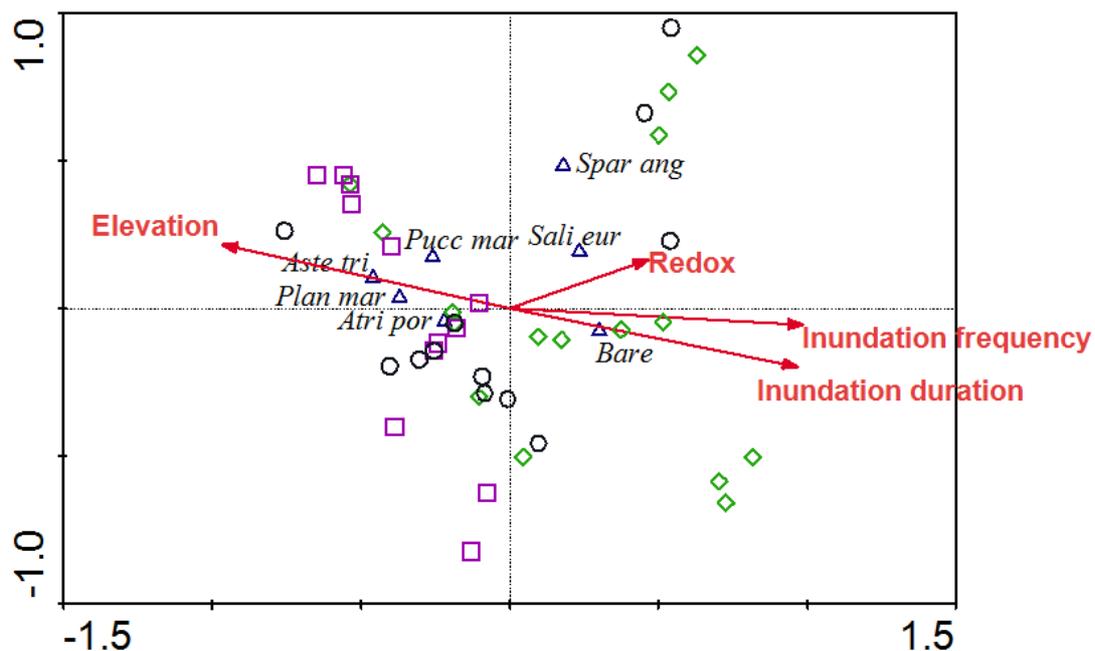
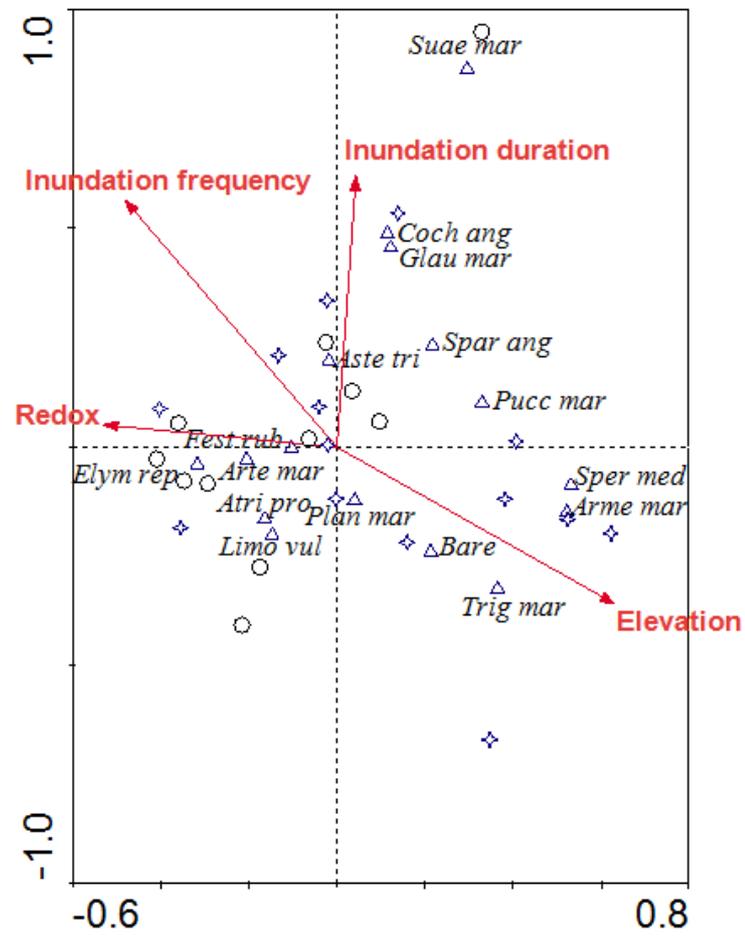
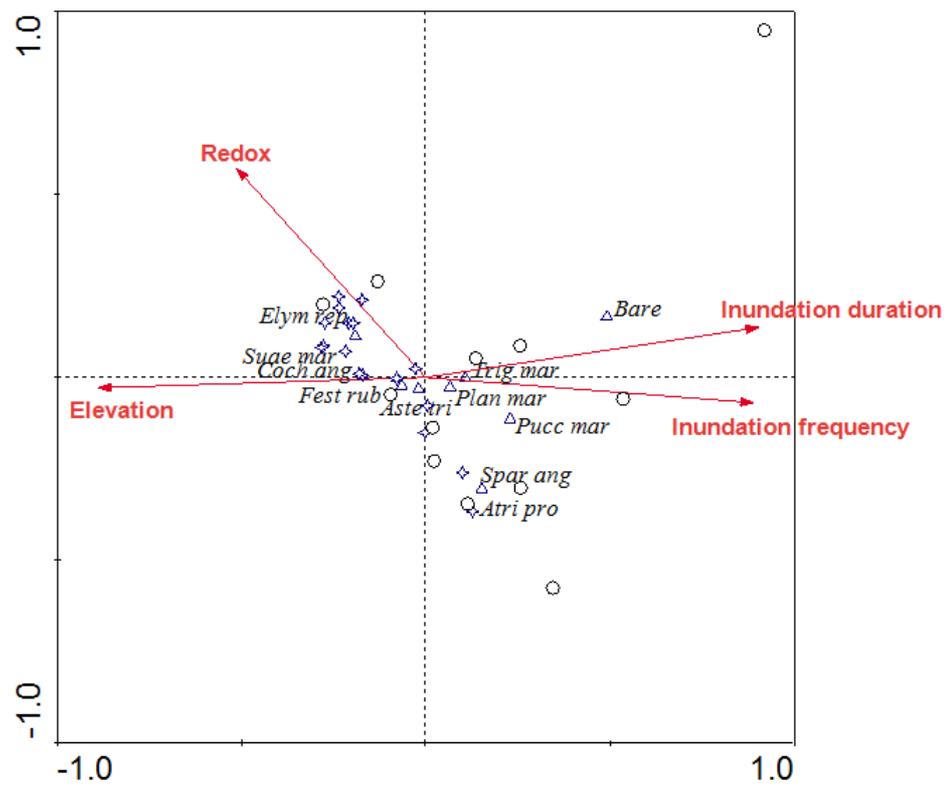


Figure 7.6 - CCA triplots showing the distribution of species and samples in relation to stream order at (a) South Efford natural marsh (SEN); (b) Brean Down natural marsh (BN); (c) Bleadon Levels managed realignment (BM); (d) South Efford managed realignment (SEM). First order channels = Stars (blue outline); Second order channels = Circles (black outline); Third order channels = Squares (purple outline); Fourth order channels = Diamonds (green outline).

(b)



(c)



(d)

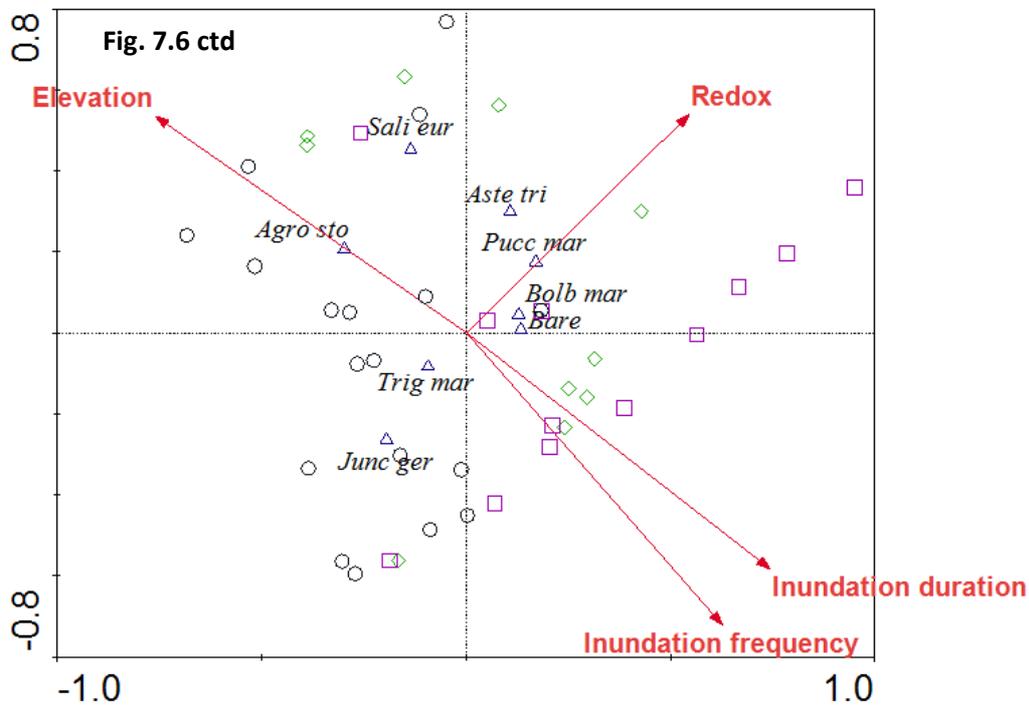


Fig. 7.6 ctd

To summarise, soils on the banks of higher order channels generally appear to be higher in redox potential, even if they are lower in elevation. BM is an exception to this generalisation, as higher order channels were lower in elevation and lower in soil redox potential. The vegetation community composition on higher order channels varies from site to site. For example, higher redox soils on higher order channels at SEN are dominated by relatively low marsh species (e.g. *Salicornia europaea*), whilst high marsh species (e.g. *Elymus repens*) dominate high redox soils on higher order channels at BN.

7.3.3 Channel width

The mean channel width at SEN was 2.44 ± 0.36 m (N = 41), ranging between 0.3 - 10.85 m. The two main axes of a CCA on the environmental and species distribution datasets explained 89 % of variation (Axis 1 – 48 %, $P < 0.05$; Axis 2 – 41 %; Appendix 4). Fig. 7.7 presents the results of the CCA in an ordination triplot. On the first axis, channel width has a greater influence than elevation on species composition, but a slight negative correlation between the two variables is also evident. Sediment particle size also has a large influence on the first axis, as median particle size (ϕ) increases with channel width. This is due to a negative relationship between organic content and channel width (and thus a positive correlation between channel width and sand content (%) and a negative correlation with silt and clay content (%)). Channel width was also negatively correlated with soil moisture content (%). Variation along Axis 2 is explained by salinity, but apart from a slight correlation with elevation, this effect appears to be independent of any other measured variable. Soil redox potential has a slight influence on the second axis, but has relatively little influence on species composition.

Bare ground was more abundant on the banks of wider channels, at lower elevations (Fig 7.7). As channels narrow, species such as *Salicornia europaea* and *Spartina anglica* become more abundant, whilst *Puccinellia maritima* tended to be more abundant on the banks of the narrowest channels, where soil organic content was relatively high. *Atriplex portulacoides* generally occupied areas of high salinity, with relatively high sand content and low soil moisture content.

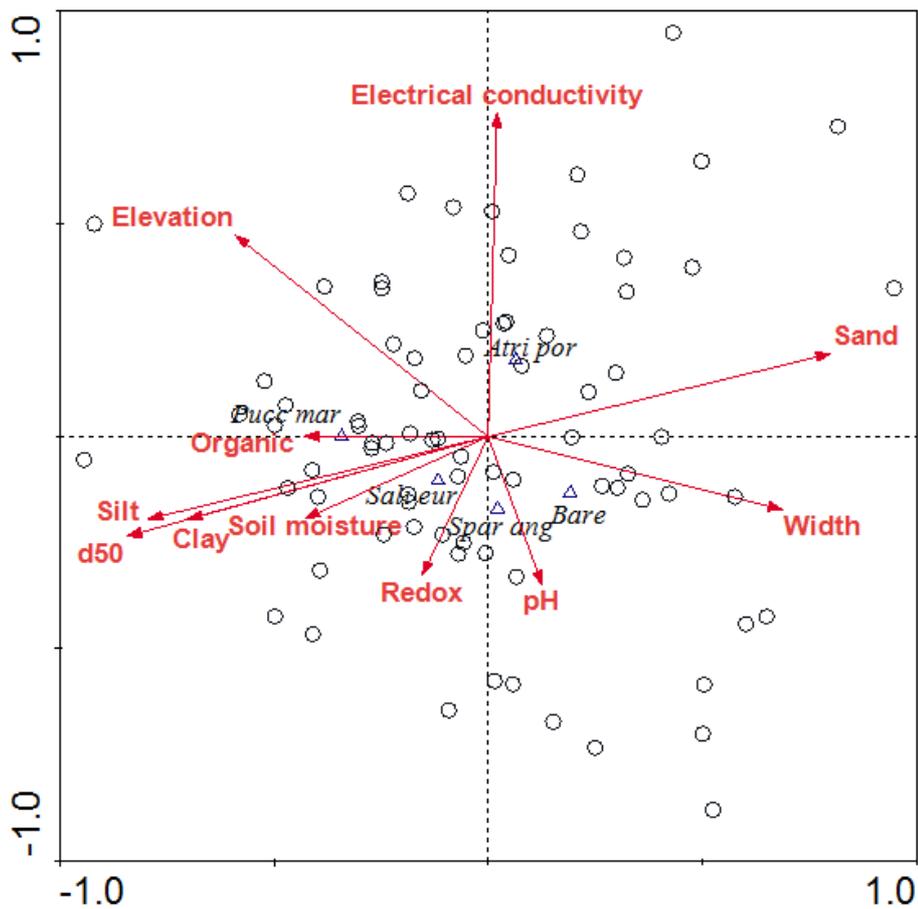


Figure 7.7 - CCA triplot showing the distribution of species and samples in relation to channel width at South Efford natural marsh (SEN). Circles = samples; triangles = species.

7.4 Discussion

7.4.1 Landscape-scale patterns in site variability

Salt marshes are extremely site-specific landforms, due to their high dependence on a complex range of biogeomorphological interactions (Viles et al. 2008; Reed et al. 2009). A landscape-scale comparison revealed great variability between the study sites; but some key overriding patterns can be recapitulated from the investigation.

All the natural salt marshes (SEN, GN, BN) were similar in soil redox potential, despite SEN lying significantly lower in the tidal frame. This may be due to the high density of the channel network at SEN, possibly causing overall higher aeration of the soil (Morzaria- Luna et al. 2004). As a result, all the natural sites also have similar values of plant species diversity. This contrasts with other studies, where there has been high variability between reference natural sites (e.g. Garbutt & Wolters 2008), which has made it difficult to extract differences between natural and restored sites. However, plant species composition does vary between the natural salt marshes, indicating that there are additional factors involved in the determination of plant species distribution besides redox potential. These factors are most likely associated with their differing elevations in the tidal frame, impacting soil salinity (Silvestri et al. 2005), exposure to tidal currents (Bouma et al. 2009) and rates of seed deposition (see Chapters 6).

In contrast, the managed realignment sites in this study did vary from each other, in terms of soil redox potential and plant species diversity/composition. In general, managed realignment sites in the UK are generally lower in soil redox potential than equivalent elevations in the tidal frame on reference natural salt marshes (Mossman et al. 2012b). Therefore, it is perhaps unsurprising that the two most recently implemented managed realignment sites (GM and SEM) had the lowest mean soil redox potentials overall and were significantly lower in redox potential than their natural reference salt marshes (GN and SEN). However, soils at BM (the oldest and only unregulated managed realignment site) had higher redox potential than any other site. Soil redox potential has been shown in other studies (e.g. Baldwin & Mendelssohn 1998) to decrease with increased flooding duration, as low oxygen levels in the soil cause the reduction of sulphate into toxic hydrogen sulphide (Ponnamperuma 1972). At Goosemoor, the difference between managed and natural sites may therefore be attributed to comparatively higher inundation frequency and duration of the managed

realignment site (as controlled by the self-regulating tidal gate). Similarly, BM was located relatively high in the tidal frame; therefore, subject to infrequent and short-duration inundations.

However, the tidal regime at SEM was similar to GM and SEN, yet soils at the former site were lower in redox potential. The recent decomposition of pre-alignment vegetation is likely to have reduced oxygen concentrations in the soil and overall redox potential at SEM (French 2006), causing bare ground to become widespread. Low colonisation and establishment of vegetation may be attributed to these reducing conditions (Chapter 5; Mossman et al. 2012b), but on the flip-side, a lack in vegetation cover may also contribute to low soil redox potential. Ursino et al. (2004) found that where pioneer species were able to colonise anoxic soils, evapotranspiration rates increased oxygen availability in the soil, therefore improving conditions for root respiration of future colonisers. If soils are extremely reduced, the colonisation of catalytic pioneer vegetation may be completely inhibited, preventing the establishment of such a positive feedback. Additionally, although inundation duration at SEM was similar to SEN during this period (see Chapter 4 for a time series of water levels at SEM imposed by the SRT), this does not reflect the amount of time that the soil at either site remains waterlogged. It is possible that soils at SEM remain waterlogged between inundations, due to inefficient drainage (White, Pers. Obs.). Hazelden and Boorman (2001) found that the differences in soil composition between formerly reclaimed salt marshes and natural salt marshes are the main explanation for drainage inefficiencies on managed realignment sites, especially where sedimentation rates are limited. Indeed, in Chapter 6, the paucity of mineral sediment being transported onto the marsh surface at SEM contrasted markedly with sediment deposition on the adjacent natural marsh (SEN). Additionally, the drainage density at SEN is much higher than that of SEM, where linear ditches are currently the only form of drainage channels. As the channel

network is so dense at SEN, locations surveyed away from the channel would have been closer to another channel than they would have been at SEM, possibly causing overall higher aeration of the soil (Morzaria- Luna et al. 2004).

All managed realignment sites significantly differed from each other and their natural counterparts in terms of plant species diversity and composition. Not surprisingly, as the most recent realignment site with highly reduced soils, plant species diversity at SEM was low, reflecting the high cover of bare ground and only sporadic presence of opportunistic, transitional species such as *Agrostis stolonifera* and *Juncus gerardii* where inundation frequency/duration were slightly reduced (Rozema & Blom 1977). This is very different from the more varied salt marsh community at SEN. Providing the existence of a sufficient seed supply; similar species richness between restored and natural sites can be attained. For example, Brancaster managed realignment site, Norfolk, UK attained similar species richness to natural reference marshes within five years of the initial breach (Mossman et al. 2012a). Likewise, salt marsh species quickly colonised a new restoration site on the Yzer estuary, Belgium within five years (Erfanzadeh et al. 2009). However, differences in species composition between managed realignment sites and natural salt marshes often exist even after 50-100 years (Mossman et al. 2012b). GM and BM have similar species richness to their natural references, but surprisingly, they also have significantly higher diversity than all other sites, indicating that the abundance of individuals within species types was more equal than on the natural sites. As the oldest managed realignment site in this study, BM has had thirteen years for a range of species to colonise and the environment to equilibrate to optimise conditions for their establishment. Quickly spreading species *Elymus repens* and *Festuca rubra* dominate the site as they are suited to infrequently flooded, aerated, high marsh soils (Rozema & Blom 1977; Armstrong et al. 1985). However, deep channels with gently sloping sides that were dug at the site prior to inundation have

enabled a range of other species more tolerant of occasional flooding to colonise the site in absence of competition. Species with long reproductive cycles such as *Triglochin maritima* and *Plantago maritima* have been able to colonise over this time period, shown to be limited in abundance at other managed realignment sites over a range of timescales (Garbutt et al. 2006; Mossman et al. 2012b). However, *Armeria maritima* is generally absent or infrequent at many managed realignment sites (Mossman et al. 2012b; Garbutt et al. 2006; Wolters et al. 2008) and was not recorded at BM, even though the species was present at nearby BN. Relative to other salt marsh species, *Armeria maritima* has a lower tolerance of salinity (Wolters et al. 2008), therefore may have been outcompeted by *Elymus repens* at higher elevations and outcompeted by more saline-tolerant species on the sloping channel banks at lower elevations. However, BN is not as topographically heterogeneous as BL, therefore most of the site is dominated by *Festuca rubra*, reducing overall species evenness and therefore diversity.

Elymus repens may also be responsible for reducing overall species diversity at GN via inhibition succession (i.e. outcompeting potential future colonists: Connell & Slatyer 1977), whilst soils at GM are generally too reduced (i.e., low soil redox potential) to support the spread of this high-marsh species (Rozema & Blom 1977). Halophytes vary greatly in their ability to tolerate reduced soils, depending on their ability to oxygenate their rhizospheres (e.g. producing aerenchyma), response to nutrient depletion, effectiveness of internal ventilation and anaerobic metabolism (Armstrong 1982; Armstrong et al. 1985). *Elymus repens* does not possess such adaptations, therefore is known to colonise aerated soils (Armstrong et al. 1985; Davy et al. 2011). Slightly reduced soils may therefore act in the favour of halophyte species diversity at GM, as a greater diversity of species (more able to tolerate slightly reducing conditions) is able to colonise the site in the absence of spreading species such as *E. repens*, consequently creating a more heterogeneous habitat.

7.4.2 The influence of tidal channels on salt marsh functioning

Tidal channels are known to be a major provider of topographic heterogeneity on salt marshes (Larkin et al. 2006). It is common for levees to form adjacent to tidal channels over time, as transported sediment quickly falls out of suspension when tidal flows lose velocity on contact with the channel banks causing a gradual increase in elevation (Friedrichs & Perry 2001). However, the channel banks investigated in this study were generally of low elevation, perhaps because all marshes were located high in the estuary where low tidal amplitudes and corresponding high rates of organic sedimentation likely limit levee development (Zedler & Callaway 1999; Mudd et al. 2004).

The lower elevated channel banks therefore differ hydrologically from locations further inland, as lower elevations in the tidal frame are inundated more frequently and for longer. Therefore, it was surprising to find that overall soil redox potential on the channel banks was higher than further inland. These findings suggest that channels do aerate adjacent soils, likely due to increased drainage capabilities via horizontal and vertical flows of subsurface water (Ursino et al. 2004). The transition from two-dimensional to one-dimensional flow happens rapidly, within metres of the channel, explaining the differences in redox found within 5m of the channel in this study (Ursino et al. 2004).

At SEM, higher redox potential on the channel banks may be crucial for the future salt marsh development. As soils are extremely reduced across the whole area, the channel banks may act as a refuge for potential salt marsh colonisers. A number of studies have found that species richness is enhanced on the channel banks of salt marsh creeks (Hopkins & Parker 1984; Zedler et al. 1999; Sanderson et al. 2000) and here plant species diversity was generally higher on the channel banks at all managed realignment sites (although significantly elevated only at BM). Whether increased plant diversity is

due to better propagule dispersal (Diggory & Parker 2011), seedling germination or establishment (Zedler et al. 1999), more benign environmental conditions for plant growth (Balling & Resh 1983), or a combination of these is unclear. However, at BM, a range of species is found on the long, sloping sides of constructed channels, whilst *Elymus repens*, a dominant species on the rest of the marsh is greatly reduced in cover. Unlike other studies (e.g. Armstrong et al. 1985), soil redox potential cannot be the limiting factor for *Elymus repens* cover, as redox is as high if not higher on the channel banks, and other factors associated with higher inundation frequency/duration must be key. Wolters et al. (2005), for example, suggest that *Elymus repens* may be limited to brackish locations. Indeed, salinity appeared to be a main influence on vegetation community composition in the single-site channel width investigation at SEN. The relatively low *E. repens* cover on the channel banks at BM allows less competitive species, such as *Plantago maritima*, to thrive in the absence of this aggressive competitor (Larkin et al. 2006). This may also be the case at GM, where some drainage channels were constructed prior to initial flooding. Topographic heterogeneity on the channel edge causes bare ground to open up, creating suitable germination microsites for a range of other species to colonise and likely facilitating the development of a heterogeneous plant community (*sensu* Grubb 1977).

In contrast, plant species diversity was lower on the channel banks at all natural sites. On these sites, more competitive perennial species have opportunistically colonised the channel edges. Although the establishment of perennials improved species diversity close to channels, Morzaria-Luna et al. (2004) reported how halophytic perennial species outcompeted other salt marsh species in the main marsh. At SEN, *Atriplex portulacoides* was more abundant on the channel bank, compatible with its known sensitivity to soil aeration and soil redox potential, and preference for well drained areas (Armstrong et al. 1995). In the channel width investigation at SEN, *A. portulacoides*

occupied sandy soils where moisture content was reduced. Where the species is able to colonise, it is extremely quick to spread and is reproductively efficient, therefore may prevent the establishment of future colonisers (Mossman et al. 2012b). This may explain observed reductions in species diversity on the channel banks at SEN. Similarly; the channel banks at BN are higher in redox potential, encouraging the domination of *Festuca rubra*, which is sensitive to soil waterlogging (Davies & Singh 1983). This species may also be responsible for competitively excluding less abundant salt marsh species (Krahulec et al. 2001).

The vegetation communities of the managed realignment sites are likely to be still developing since their initial inundation. It is possible that high plant species diversity may be maintained as salt marsh colonisers fill patches of bare ground adjacent to the salt marsh creeks. For these sites, it is essential that topographic heterogeneity is retained so that a variety of plants can establish in specific microsites, in the absence of competitive exclusion (Larkin et al. 2006).

7.4.3 The influence of tidal channel morphology on local functioning

In a more focussed investigation at SEN, I attempted to disentangle the effects of elevation and channel width on a range of environmental variables and plant species composition on the channel banks. Channels tend to become wider at lower elevations in order to accommodate increased tidal flows (Fagherazzi & Furbish 2001; Friess et al. 2014) a tendency confirmed in my results. However, width explained more variation in plant distribution/vegetation composition than elevation, with strong associations with sediment particle size, soil organic content and soil moisture content. Sediment mineral content and particle size increased with channel width, mainly due to the elevated sand content associated with higher tidal flows and energies (Stoddart & Reed 1989; Friedrichs & Perry 2001). Coarse sediment grains are often deposited on the channel

banks during overmarsh tides, as velocities of tidal flows are suddenly reduced on contact with the marsh surface (Stoddart & Reed 1989). Coarser particle sizes increase the permeability of channel banks, therefore improving drainage (Brophy 2011). The strong influence of channel width and sediment particle size on drainage is evident in the results of this study, as soil moisture content increased with finer sized sediment, which contributed to a greater proportion of overall sediment composition on the banks of narrower channels.

Higher order channels are usually wider, as they are lower in elevation on the marsh edge, having to accommodate greater discharge during the ebb tide (Fagherazzi & Furbish 2001). It is therefore surprising that channel order did influence soil redox potential, whilst channel width had no influence on redox, which in turn had extremely limited influence on vegetation composition (salinity had a greater influence). Soils on the banks of many higher order channels (at BN, SEM and SEN) had higher redox potential, regardless of elevation and relative increases in inundation frequency/duration. Variation in soil moisture content with width, in tandem with soil redox potential associated with channel order suggest that wider channels (or simply those of a higher order receiving higher volumes of water on the ebb tide), may have a greater influence on the drainage of adjacent sediments. This was not the case at BM, as first order channels were not constructed with the same sloping banks as second order channels, therefore soils on the banks of lower order channels were generally both higher in redox potential and higher in elevation.

Vegetation composition on the channel banks was not necessarily reflective of soil redox or soil moisture. For example, bare ground and pioneer vegetation was widespread on the banks of higher order channels at SEN, which were higher in redox potential than lower order channels (which were colonised by higher marsh vegetation

such as *Aster tripolium*). Wider channels were associated with a greater amount of bare ground and thus negatively linked to the cover of plants such as *Puccinellia maritima*. This contrasts with the results of another study on Petaluma Marsh by Sanderson et al. (2000), where species richness tended to increase with channel width and stream order, except on the very widest/highest order creeks. It is possible that large tidal flows in very wide creeks cause mechanical disturbance events such as channel scour, which opens up bare space on the channel bank (Tessier et al. 2002). It is also suspected that elevation may act in unison with channel width to affect species composition, as although wider/higher order channels aerate the channel banks (as well as potentially receiving a greater propagule supply (Reed et al. 1999)); increased inundation frequency at lower elevations causes a multitude of stresses on the plant community (Silvestri et al. 2005).

Overall, the effects of stream order on redox potential and species composition in the multi-site investigation were not so pronounced, indicating that other factors such as channel dimension and distance from source work in accordance with position in the drainage network. In future studies, a larger sample size of channels may be required to make definite conclusions on the effects of stream order. However, a specific stream ordering process for salt marsh channels may be required to allow patterns to be deduced, as current methods, including those by Strahler (1965) do not accommodate for variability in salt marsh channels caused by bi-directional flow.

7.5 Conclusions

Results in this chapter reflect the variability of salt marshes over a range of different scales. Managed realignment sites were particularly variable in soil redox potential and plant species diversity/community composition. This was assumed to be primarily due to differences in inundation regime and the variable maturity of the sites, associated

differences in vegetation development and topographic heterogeneity. Tidal channels, particularly those of greater width and/or higher Strahler order, were shown to improve the drainage efficiency of adjacent soils. Higher soil redox potential reduced plant species diversity on the channel banks of natural salt marshes, as competitive species sensitive to soil aeration (e.g. *Atriplex portulacoides*) were able to establish and exclude a range of other halophyte species. In contrast, species diversity was generally higher on the channel banks on managed realignment sites. On sites with highly reduced soils, the aerated banks of tidal channels could favour the colonisation and establishment of halophytes. Additionally, where the banks of excavated channels are lower in the tidal frame; less competitive halophytes could thrive in the absence of competitive species that are sensitive to factors associated with high levels of tidal inundation, such as *Elymus repens*. Results from this chapter could contribute to the generation of a number of recommendations on different scales for the implementation of managed realignment, particularly with regard to the excavation of tidal creek networks, which will be discussed in Chapter 8.

Chapter 8 – Synthesis

8.1 Salt marsh development at South Efford managed realignment site

Following coastal realignment, the introduction of tidal flows to low-lying land incurs massive disturbance on biogeomorphological functioning (Viles et al. 2008). Whereas natural salt marshes form over long timescales, realignment sites experience sudden exposure to seawater flooding after years of reclamation, or in some cases having no previous experience of flooding. Realigned land may therefore require time to equilibrate with the new tidal regime, both ecologically and morphologically (French 2006). In many locations, recognisable salt marsh plant, invertebrate and bird communities have developed rapidly, within the first few years of realignment (Atkinson et al. 2004; Garbutt et al. 2006; Erfanzadeh et al. 2009; Mossman et al. 2012a). However, the plant species composition of these newly developed communities often differ from those on nearby natural salt marshes (Zedler et al. 1999; Crooks et al. 2002; Mossman et al. 2012a).

After three years of realignment, South Efford managed realignment site (SEM) had not yet developed into salt marsh. Due to the long timescales associated with salt marsh development, it is difficult to judge whether SEM will transition successfully in the long-term. However, by investigating alterations to natural geomorphological functioning imposed by the newly designed self-regulating tidal gate (in tandem with short-term vegetation change), it has been possible to identify possible limitations of the design in the short-term. Consequently, recommendations can be provided to assist the long-term transition of SEM into salt marsh.

In the first year of realignment, SEM was rarely inundated, as the SRT was adjusted to close on rising tides before water levels became high enough to cover the restored

marsh surface. Although gaps did appear in the pre-realignment vegetation, some glycophyte species persisted. Indeed, in Chapter 3, it was found that some *Trifolium repens* ecotypes with higher resistance to salinity might survive occasional short-term flooding (albeit with compromised growth and reproductive potential) (White et al. 2014). However, *T. repens* rapidly disappeared following initial flooding at SEM and *Juncus gerardii* and *Agrostis stolonifera* became dominant. In contrast, all pre-realignment vegetation was rapidly killed by heavy sedimentation caused by excessive inundation at Orplands managed realignment site (Essex, UK), which was deliberately breached in 1995. Mass decomposition of terrestrial vegetation created anoxic soil conditions, inhibiting the establishment of halophytic pioneers (Macleod et al. 1999). The persistence of some pre-alignment vegetation following realignment may prevent widespread soil anoxia and indeed maintain soil aeration and nitrogen levels, as well as promote sediment stability and accretion (French 2006), which could be pivotal in the future establishment of halophytic vegetation. However, at SEM, competition from opportunistic species *Juncus gerardii* and *Agrostis stolonifera* may have also inhibited the establishment of any of the few halophytic seedlings that were tidally dispersed onto the site in the first year of realignment (Chapter 5).

Water levels were raised after the first year of realignment and the cover of glycophytic species consequently decreased. In addition, the increased settlement of hydrochorous propagules in the third year of realignment (Chapter 6) enabled SEM to attain a similar number of salt marsh species as in the natural species pool (Chapter 5). Plant community development occurs rapidly on many other managed realignment sites (Atkinson et al. 2004; Garbutt et al. 2006; Wolters et al. 2008; Erfanzadeh et al. 2009; Mossman et al. 2012b), but at SEM, halophyte colonization was restricted to higher elevations and channel banks, leaving much of the site unvegetated and more similar to a tidal flat than a salt marsh. This particular SRT design causes water levels to peak and

plateau in the restored area for longer than on a natural tidal cycle. Therefore, increasing the tidal prism in the MR site not only increased the frequency of marsh surface inundation, but also lengthened the hydroperiod. By the third year of realignment, the restored site was inundated for significantly longer periods than the tidal flat. Prolonged inundation duration of lower elevations at SEM reduced oxygen levels in the marsh soil, lowering soil redox potential (Chapter 7). Therefore, it is likely that colonizing halophytes were limited to areas of higher soil aeration.

Research at SEM reflects the importance of considering the impact of the prolonged hydroperiod on vegetation development in RTE schemes, as well as inundation frequency alone. For example, controlled-reduced tide techniques used on the tidal Schelde, Belgium similarly extend the hydroperiod, approximately doubling the amount of time the restored marsh surface is inundated in comparison with natural salt marshes (Cox et al. 2006). Even if RTE sites are inundated at a similar frequency as nearby natural salt marshes, plant community development is often characterized by halophytes suited to lower elevations in the natural tidal frame. In addition, Mossman et al. (2012b) suggest that due to inadequate drainage, soils are generally lower in redox potential on coastal realignment sites than in natural salt marshes. Drainage problems are usually caused by alteration to the sediment structure following reclamation (Crooks et al. 2002; Blackwell et al. 2004) and/or an inefficient tidal creek network (Chapter 7; Crooks et al. 2002). A combination of a prolonged hydroperiod with poor drainage in RTE sites is likely to cause even greater shifts in the development of vegetation communities and may even inhibit vegetation establishment in extreme cases. This needs to be considered when planning the spatial development of vegetation communities in RTE schemes, and certain management techniques (such as the construction of tidal channels, general topographic heterogeneity and vegetation transplanting) may be required more often than on sites with a simple breach.

Sufficient sediment accretion is required in order to allow parts of the marsh surface to rise in the tidal frame, which reduces the frequency and duration of tidal inundation in these areas, and encourages the establishment of a range of salt marsh vegetation (depending on their adaptations to prolonged inundation) (Reed 2002). Sedimentation rates at SEM did increase over time as the tidal prism increased, yet regular inundations were not deep enough to encourage similar sedimentation rates to those on the natural salt marsh (SEN) and on an unmanaged realignment site (GOF) where seawater flows through a simple breach (Chapter 6). Additionally, sediment was finer and higher in organic matter on the restored site; characteristics that reduce soil porosity and impede further drainage (Brophy et al. 2011). Shallow tidal flows are generally unable to entrain large particles; Crowther (2007) and Boumans et al. (Boumans et al. 2002) state that narrow culverts, such as that at SEM, may reduce inorganic sediment fluxes. Therefore, if sedimentation rates remain low at SEM following further increases in water depths, an expansion of the culvert may be required in order to increase the input and particle size of mineral sedimentation to the restored area.

The challenge for the future of SEM is that different aspects of salt marsh functioning require contrasting SRT adjustment. Water levels need to be raised on the site to increase depths, in order to increase hydrochory, sediment accretion and morphological development. However, this would also cause extended periods of waterlogging, which could impede future vegetation development. Therefore, the drainage efficiency of the site needs to be increased before any other adjustments are made to the tidal prism. This may be achieved through increasing the size of the current culvert (Boumans et al. 2002) or constructing extra outfalls (Crowther 2007). If adopted, these measures would promote ecological development of the site and stimulate the transition into salt marsh habitat. However, vegetation communities would still likely differ from nearby natural communities at the same elevation in the tidal frame, due alterations to the tidal cycle

imposed by the SRT. These differences need to be considered when using managed realignment to create compensatory habitat and the functional consequences of such community alterations need to be considered in the planning of future RTE designs.

8.2 Lessons for future managed realignment practice and research

Salt marshes are complex biogeomorphological systems, where disturbance to one process can de-stabilise the whole system (Viles et al. 2008). As the initial formation of restored salt marshes differs greatly from the gradual accretion of natural salt marshes, it is unlikely that equivalency in biogeomorphological functioning will be achieved in the short-term, if at all (Mossman et al. 2012b).

However, managed realignment is one of the only habitat restoration/creation options available to coastlines where salt marsh habitat has been depleted. In addition, managed realignment is a great provider of accommodation space for floodwater, reducing the risks of seawater flooding in other areas of the estuary (Cox et al. 2006). Vegetation communities on restored sites may not become absolutely equivalent to those on natural salt marshes, but a top priority should be to ensure development of diverse, self-sustaining communities. Such communities have been proven to maximise ecosystem functioning and the resulting provision of ecosystem services (Zedler et al. 2001; Sullivan et al. 2007). Evidence of the latter is crucial to gain in light of social, economic and political pressures associated with many schemes (Nicholson-Cole & Riordan 2009).

The question is: how can we *optimise* habitat creation following managed realignment? My research suggests that achieving geomorphological similarity to natural salt marshes will facilitate the ecological development of managed realignment sites. In the following sections I outline key areas requiring particular attention in future managed realignment practice and research: a) Tidal regime, (b) Tidal channels and (c)

Vegetation transplanting. Within each section, I formulate recommendations on how to enhance the transition of coastal land into salt marsh, and where future research is required to fill key knowledge gaps.

8.2.1 Tidal regime

Evidence from SEM demonstrates the fundamental importance of designing a tidal regime suitable for the morphological, sedimentological and ecological requirements of managed realignment sites. It is essential that the tidal regime is prioritised in the planning process of individual sites (Maris et al. 2007), as tidal requirements vary according to site geomorphology and habitat targets (Boumans et al. 2002).

It is well established that the zonation of salt marsh plants is determined by their adaptations to survive and function efficiently under different levels of seawater inundation (e.g. Silvestri et al. 2005). In natural salt marshes, halophytes and salinity-tolerant glycophytes occupy different elevations of the tidal frame according to species-specific tolerance of local abiotic conditions. Coastal grassland is vulnerable to rising sea levels and may be increasingly exposed to sudden seawater flooding following storm surges (Nicholls & Cazenave 2010; Martin et al. 2011; Zappa et al. 2013; Hoggart et al. 2014). Chapter 3 revealed that slightly more saline-tolerant individuals of some terrestrial species, such as *Trifolium repens*, may be selected for in these transitional areas. Further research should be directed into the responses of typical grassland species belonging to a range of functional groups (with varying levels of salinity tolerance) to increasing rates of seawater flooding, as it has been suggested that a more species-rich vegetation community may be more resilient to seawater flooding (Hoggart et al. 2014). Such research will enable coastal managers to predict spatially variable rates of initial vegetation change under different tidal scenarios following managed realignment and also anticipate how terrestrial grassland

surrounding managed realignment sites may respond to increased exposure to seawater flooding.

Both excessive and insufficient tidal inundation can inhibit salt marsh development on managed realignment sites. Where water levels are too low, hydrochory is limited (Chapter 6) and terrestrial vegetation may dominate and outcompete halophytic colonisers (Chapter 5). However, where poor drainage or low relative elevation causes waterlogging, plant community development is adversely affected by low soil redox potential (Mossman 2012b). Factors such as previous land use, drainage density of relic creek networks/excavated channels and sediment structure will affect the drainage of formerly reclaimed land and should all therefore be considered alongside the tidal regime prior to managed realignment. RTE mechanisms may be adjusted to prevent excessive water levels on a site, yet such mechanisms impact upon certain aspects of the tidal cycle in the restored area (Chapter 4). These deviations from the natural tidal cycle, such as the increased hydroperiod and extended submersion further contribute to the development of a vegetation community more tolerant of increased flooding duration than at equivalent elevations on natural marshes.

It is of utmost importance that the tidal regime is appropriate for morphological development to take place via sediment accretion and creek erosion, as these processes will improve site hydrology, ensuring the future establishment of a self-sustaining vegetation community. Therefore, it must also be ensured that the tidal flows are regular and deep enough to incur sediment accretion (alongside hydrochory) and ‘channel-forming flows’ (Chapter 4; Chapter 7; Williams et al. 2002). However, on sites where drainage is poor, increasing the tidal prism in order to achieve morphological change may cause waterlogging and inhibit vegetation development in the short-term (Chapter 4 and 5). Therefore, additional management techniques are required to facilitate

morphological development and promote the establishment of diverse salt marsh communities.

8.2.2 Tidal channels

Tidal channels play a major role in salt marsh functioning, primarily by draining water from the salt marsh surface. Results presented in Chapter 7 show that soils adjacent to channel banks had higher redox potential than soils further away. This may have great functional benefit in managed realignment sites, where soils tend to be more reduced than those at equivalent elevations in the tidal frame on natural salt marshes (Mossman et al. 2012b). The natural establishment or excavation of creek networks may allow a range of halophytes generally intolerant of reduced soils to colonise managed realignment sites. Indeed, plant species diversity was generally elevated on the channel banks at all managed realignment sites in Chapter 7, including SEM.

Tidal creek networks may be slow to develop on managed realignment sites, particularly on sheltered sites, or where ebbing currents are limited by a RTE mechanism or breach size (Bowron et al. 2009; Friess et al. 2014). Tidal channels may be therefore constructed prior to realignment, so that drainage is enhanced from the start of tidal exchange and as a catalyst for future morphological development (Wallace & Callaway 2005). Other studies have proven the success of excavating creeks based on the modelled likely path of tidal flows through relic creek networks and topographic depressions (Williams et al. 2002). Although the banks of wider and higher order channels are better drained (Channel 7), these areas often have higher cover of bare ground and pioneer species, possibly due to increased mechanical disturbance events such as channel scour (Tessier et al. 2002). It is therefore essential to excavate a range of channel widths within a base network of different order channels, in order to enhance site drainage and also facilitate the colonisation of a variety of plant species on channel

banks. Further investigation will be required into optimum creek design and how much of a network it is necessary to excavate in order to efficiently drain soils on a managed realignment site and catalyse future morphological development. Additionally excavated channel networks are often linear and uniform, whilst natural salt marshes often have high density, sinuous creek networks, such as those on SEN. Future research needs to focus on the potential effects that channel sinuosity (alongside other morphological variables) has on drainage and vegetation composition. Other morphological variables may be identified from LIDAR data, by comparing how tidal channel networks on managed realignment sites may differ from those on natural salt marshes.

Tidal channels may offer the additional benefit of topographic heterogeneity on restored salt marshes. Low topographic heterogeneity has been linked with poor plant species diversity on managed realignment sites (Brooks et al. in press), as different plant species are both adapted to and limited by specific environmental conditions associated with the tidal regime (Huston 1999). Therefore, a vertical environmental gradient caused by differing elevation in the tidal frame will encourage the development of a biotic gradient, reducing the risk of competitive exclusion by one dominant species (Zedler et al. 1999). In Chapter 7, the flat inland topography of Bleadon Levels managed realignment site was dominated by *Elymus repens* and *Festuca rubra*, inhibiting the establishment of lower salt marsh species. However, on the sloping banks of constructed channels, *E. repens* and *F. rubra* were unable to dominate, allowing a range of species to colonise according to the gradient of abiotic conditions associated with different elevations on the slope. In the design of constructed creek networks, considering channels as a provider of topographic heterogeneity as well as drainage may allow managed realignment sites to attain higher species diversity than otherwise possible. Topographic heterogeneity has been incorporated into the design of the new largest managed realignment site in the UK, at the Steart Peninsular (Somerset, UK), which was

breached in September 2014. Tidal channels with sloping banks have been excavated, as well large areas of low elevation adjacent to channels and hummocks and depressions of various scales throughout the remainder of the site. It is likely that the creation of horizontal and vertical environmental gradients over a range of scales will facilitate the development of a diverse plant community (Huston et al. 1999). However, the impact of such manipulation on both morphological and ecological development will need to be closely monitored in future years.

8.2.3 Vegetation transplanting

Transplanting halophytic vegetation into salt marshes should be considered as a last resort, as the main focus should be on attaining the correct environmental conditions for the colonisation and establishment of the desired target species. Additionally, managed realignment sites should always be in close proximity to a seed supply and breached in early autumn to coincide with peak seed dispersal (Chapter 6). However, vegetation transplanting may stimulate the development of a diverse plant community on managed realignment sites where certain halophytic species have been slow to colonise. In addition to benefitting the local seedbank, transplanted species may prevent erosion and maintain soil aeration (Ursino et al. 2004). For example, despite high abundance on the natural salt marsh at South Efford, *Atriplex portulacoides* was not recorded on SEM (Chapter 5) and did not germinate on any of the Astroturf mats from either the site in Chapter 6. Therefore, transplanting plant species with lower seed germination rates may be beneficial in accelerating colonisation of managed realignment sites. This would require further investigation into which salt marsh species have slower reproductive cycles and should be therefore prioritised in transplanting schemes.

Chapter 5 highlighted the importance of ensuring that environmental conditions are within the tolerance thresholds of transplanted species, as the majority of transplants at

SEM did not survive, whilst survival rates were much higher on Great Orcheton Fields unmanaged realignment site (GOF). If neglected in the planning of such schemes, valuable resources may be wasted when transplants fail to establish. On managed realignment sites where soils are generally reduced, it may be desirable to transplant species that are sensitive to soil aeration on channel edges, as these areas tend to be better drained (Chapter 7). This may not only improve transplant success but also have a morphological benefit in stabilising channel edges (Reed et al. 1999).

Some species may also respond better than others to transplanting, especially if they are better adapted to the local abiotic environment. For example, more *Puccinellia maritima* than *Spartina anglica* transplants survived at GOF (Chapter 5), possibly due to the ability of *P. maritima* to withstand higher current velocities. As transplanting schemes are often implemented with the intention of instigating morphological development through sediment trapping, and stabilizing and aeration, further research is required into species-specific functioning under different abiotic conditions and planting formations. For example, *Spartina anglica* is usually the ‘default option’ in transplanting schemes, due to the ability of the species to prevent erosion and enhance sedimentation on natural salt marshes (Adnitt et al. 2007). However, the species may not function as an efficient ecosystem engineer where it is not adapted to the local environment; therefore, it may be more beneficial to transplant other species that may be able to function more effectively (such as *P. maritima*). In addition, it has been suggested that *Spartina anglica* causes its own dieback by altering the sediment and drainage characteristics of salt marshes; therefore, creating unsuitable environmental conditions for its own survival (Cornick et al. 2005).

Future investigation is also required into the functioning of different species when transplanted in various formations, as certain species (such as *Spartina* species) may

better establish when planted in large, tightly spaced groups (O'Brien & Zedler 2006), whilst others (e.g. *P. maritima*; Langlois et al. 2001; 2003) may be less dependent on such a buffering effect. As a result, coastal managers will be able to adopt 'informed transplanting' schemes on managed realignment sites, where different species are planted in a way they are most likely to deliver maximum functional benefit.

8.3 Conclusion

Managed realignment is now widely seen as an important part of coastal management strategy, as an environmentally sustainable, cost-effective alternative to traditional, hard defences (Hoggart et al. 2014). However, the trajectory of salt marsh development in managed realignment schemes remains uncertain and it is unclear how sites should be managed to fulfil both coastal defence and biodiversity objectives.

My work shows that salt marsh development is highly linked to different tidal attributes. Understanding the response of pre-realignment vegetation to seawater flooding is extremely important in the prediction of the transition into salt marsh following managed realignment, and also in the development of a saline-freshwater gradient with distance from the breach. Regular, deep tidal flows are required in order to instigate morphological development, sediment accretion and hydrochory, yet site drainage must be efficient enough to prevent waterlogging, especially on RTE sites where the hydroperiod is often already extended on every tidal cycle, as vegetation establishment may otherwise be inhibited. Balancing the tidal regime with the drainage efficiency of sites may enable hydrology to resemble that of natural salt marshes. This is the most likely scenario under which managed realignment sites will develop with maximum biodiversity benefits. However, due to differences in the initiation of natural marshes and realignment sites, further management techniques may need to be employed to help sites to meet restoration targets.

Wider adoption of a biogeomorphological approach to the planning and implementation of coastal realignment projects will allow more accurate predictions of salt marsh development and fine-tuning of management techniques, including regulated tidal exchange, creek excavation and vegetation plantings. Well-informed management decisions will consequently enhance and optimise the provision of vital ecosystem services from salt marshes in managed realignment sites.

Appendix 1 – Description of vegetation communities in each field at Great Orcheton Fields

Field 1 closest to the breach is approximately 50% bare ground and 50% *Salicornia europaea* with some *Spergularia media* alongside *Salicornia europaea*. This site is typical of the pioneer zone of salt marshes.

Field 2 is approximately 60% *Salicornia europaea* and 40% bare ground, within the *S. europaea* there is some *Aster tripolium*. This site is typical of the pioneer zone of salt marshes.

Field 3 is approximately 40% vegetation and 60% bare ground. The vegetation consists of a mix of *Salicornia europaea*, *Aster tripolium*, *Atriplex portulacoides*, *Spergularia media* and a small patch of *Spartina anglica*. This field can be regarded as typical low-mid salt marsh environment.

Field 4 is approximately 65% vegetation including *Aster tripolium*, *Plantago maritima*, *Spergularia media*, *Atriplex portulacoides*, *Puccinellia maritima*, *Salicornia europaea* and a small patch of *Spartina anglica* and 35% bare ground. This field can be regarded as typical mid salt marsh environment.

Field 5 is approximately 80% vegetation, including *Aster tripolium*, *Plantago maritima*, *Spergularia media*, *Atriplex portulacoides*, *Puccinellia maritima*, *Salicornia europaea*, *Atriplex prostrata*, *Agrostis stolonifera* and *Carex* spp. In this field the proportion of *Salicornia europaea* is much lower than the preceding fields and the field itself is much drier overall, the top of field dominated by *Puccinellia maritima*. This field can be regarded as typical mid salt marsh environment.

Field 6 is 95% vegetation excluding the large quantities of litter that have accumulated at the top of the field. The plant species found were: *Puccinellia maritima* (dominant), *Agrostis stolonifera* (substantial), *Triglochin maritima*, *Atriplex prostrata*, *Aster tripolium*, *Spartina anglica* (minimal), *Phragmites australis* (minimal), *Glaux maritima*. This field can be regarded as typical upper marsh environment.

Appendix 2 – Summary of canonical correspondence analyses (CCA) and Monte Carlo permutation tests for samples from (a) Goosemoor managed and natural sites; (b) South Efford managed and natural sites and (c) Bleadon managed and natural sites.

(a)

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.66	0.15	0.07	0.02
Species-environment correlations	0.89	0.56	0.47	0.22
Cumulative % variance				
of species data	15.7	19.2	21.0	21.3
of species-environment	73.7	90.1	98.4	100.0

Significance of species-environment correlation (Axis 1): $F = 21.64$, $P = 0.002$

Significance of species-environment correlation (all canonical axes): $F = 7.86$, $P = 0.002$

(b)

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.56	0.28	0.04	0.01
Species-environment correlations	0.86	0.66	0.31	0.17
Cumulative % variance				
of species data	16.1	24.0	25.1	25.4
of species-environment	63.1	94.4	98.9	100.0

Significance of species-environment correlation (Axis 1): $F = 29.46$, $P = 0.002$

Significance of species-environment correlation (all canonical axes): $F = 13.13$, $P = 0.002$

(c)

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.26	0.11	0.05	0.04
Species-environment correlations	0.59	0.46	0.48	0.54
Cumulative % variance				
of species data	9.3	13.2	15.1	16.6
of species-environment	56.2	79.7	91.1	100.0

Significance of species-environment correlation (Axis 1): $F = 11.09$, $P = 0.002$

Significance of species-environment correlation (all canonical axes): $F = 5.37$, $P = 0.002$

Appendix 3 – Summary of canonical correspondence analyses (CCA) and Monte Carlo permutation tests for channel bank samples from (a) South Efford natural site; (b) Bleadon natural site (c) Bleadon managed realignment site and (d) South Efford managed realignment site.

(a)

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.38	0.12	0.07	0.02
Species-environment correlations	0.84	0.68	0.41	0.21
Cumulative % variance of species data of species-environment	18.4	24.0	27.2	27.9
	65.9	86.0	97.4	100.0

Significance of species-environment correlation (Axis 1): $F = 8.12$, $P = 0.004$

Significance of species-environment correlation (all canonical axes): $F = 3.48$, $P = 0.002$

(b)

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.32	0.16	0.08	0.02
Species-environment correlations	0.68	0.76	0.75	0.40
Cumulative % variance of species data of species-environment	21.6	32.4	37.5	38.8
	55.6	83.3	96.6	100.0

Significance of species-environment correlation (Axis 1): $F = 5.78$, $P = 0.03$

Significance of species-environment correlation (all canonical axes): $F = 3.33$, $P = 0.006$

(c)

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.26	0.05	0.03	0.003
Species-environment correlations	0.80	0.44	0.48	0.20
Cumulative % variance				
of species data	24.4	28.8	31.4	31.7
of species-environment	77.1	91.0	99.0	100.0

Significance of species-environment correlation (Axis 1): $F = 8.07$, $P = 0.006$

Significance of species-environment correlation (all canonical axes): $F = 2.90$, $P = 0.01$

(d)

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.25	0.17	0.03	0.004
Species-environment correlations	0.59	0.64	0.47	0.23
Cumulative % variance				
of species data	16.9	28.0	29.7	30.0
of species-environment	56.5	93.5	99.2	100.0

Significance of species-environment correlation (Axis 1): $F = 7.14$, $P = 0.01$

Significance of species-environment correlation (all canonical axes): $F = 3.75$, $P = 0.002$

Appendix 4 – Summary of canonical correspondence analyses (CCA) and Monte Carlo permutation tests for channel width samples from South Efford natural site.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.20	0.17	0.04	0.01
Species-environment correlations	0.63	0.58	0.41	0.37
Cumulative % variance				
of species data	15.3	28.4	31.4	32.1
of species-environment	47.5	88.3	97.8	100.0

Significance of species-environment correlation (Axis 1): $F = 11.89$, $P = 0.008$

Significance of species-environment correlation (all canonical axes): $F = 2.84$, $P = 0.002$

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