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FACULTY OF ENGINEERING, SCIENCE AND MATHEMATICS

National Oceanography Centre School of Ocean and Earth Science

The Role of Coastal Defence Structures in Channeling Production in Coastal Ecosystems

By

Elizabeth Charlotte Jolley

Thesis for the degree of Doctor of Philosophy

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Graduate School of the National Oceanography Centre, Southampton

This PhD dissertation by

Elizabeth Charlotte Jolley

has been produced under the supervision of the following persons:

Supervisor/s:

Dr. Antony C. Jensen University of Southampton

Prof. Steve Hawkins Marine Biological Association

Chair of Advisory Panel:

Prof. Paul A. Tyler University of Southampton

Member/s of Advisory Panel:

Dr. Antony C. Jensen University of Southampton

Prof. Steve Hawkins Marine Biological Association

Dr. Rona A. R. McGill Scottish Universities Environmental Research Centre

Prof. Martin Attrill University of Plymouth

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Coastal Ecosystems

ABSTRACT

This study assessed the interaction of coastal defence structures (CDSs), namely shore-parallel 'low crested breakwater structures' (LCSs), design features and hydrodynamic regime on the quantity and timings of macroalgae deposition. The employed sampling strategy comprised a spatially and temporally stratitified approach of time-lapse photography of macroalgae deposition, verified with field observations. Field surveys determined the associated ecological assemblages of the sediment infauna and rocky shore epifauna associated with the breakwater scheme, as well as for two nearby beaches with groynes. Further analysis determined decay rates, decay processes, changes in C and N stable isotope values of dominant macroalgal species and the dependence of the faunal assemblages on the decaying macroalgae deposits. Temporal analysis highlights the main factors driving macroalgal deposition were differences in spring and neap tidal range, wave height and sea temperature. Greatest deposition occurred during months of lower wave height and fewer storms, when filamentous red algae and ephemeral green algal species dominated. Results indicated to greater amounts of macroalgae deposits around LCSs than around wooden or granite groynes. Beach elevation best explained the spatial variation, both vertically and horizontally, in the benthic assemblages within the breakwater scheme, with the abundance of detritivorous deposit feeders being significantly correlated with abundance of macroalgae deposits. Orientation of LCSs, relative to wave action, was an important driver of epifaunal assemblages on the CDSs, with the eastward ends of the breakwaters providing the optimum intermediate environment with regards to wave action, exhibiting the greatest abundances of epifauna. Stable isotope analysis showed that the carbon and nitrogen isotopic values of macroalgae changed during the decomposition and were both species and time dependent. Isotope analysis illustrated that decaying macroalgae deposits were of greater trophic importance to species within the LCS ecosystem where there was large macroalgal deposition, than to species within the groyne ecosystem where macroalgal deposition was lower. Key findings of the study illustrate the importance of decaying macroalgae deposits for the local ecosystem via modification of food chain energy flows. Though the ecosystem benefits from this allochthonous resource, deposits may be a nuisance requiring controlled human intervention.

Declaration of Authorship

I, Elizabeth Charlotte Jolley, declare that the thesis entitled "The Role of Coastal Defence Structures in Channeling Production in Coastal Ecosystems" and the work presented in it are my own. I confirm that:

- this work was done wholly or mainly while in candidature for a research degree at this University;
- where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
- where I have consulted the published work of others, this is always clearly attributed;
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- I have acknowledged all main sources of help;
- where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;

Signed:	 	 	· • •	 	٠.	٠.	٠.	 	 	 	 	 ٠.	٠.	 •	 		 		٠.
Date:	 	 		 				 	 	 	 	 				 	 	 	

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"Keep on beginning and failing.
Each time you fail,
start all over again,
and you will grow stronger
until you have accomplished a purpose
not the one you began with perhaps,
but one you'll be glad to remember."

Anne Sullivan

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Chapter 1: Introduction - A Review of Sea Defences and their Environmental Impact

1.1 Scope of Thesis and Introductory Remarks

Climate change will lead to rising sea levels and stormier seas (Marshall et al. 2001); hence coasts need to be defended more. The rapid urban development of coastal areas around the world and subsequent man-made coastal defence schemes makes research into their effects all the more urgent, additionally, there is a growing need to understand their impact on the local ecosystem in order to implement impact minimisation and/or mitigation measures (e.g. Airoldi et al. 2005, Martin et al. 2005, Moschella et al. 2005, see Burcharth et al. 2007 for a review). This thesis examines the ecology of sea defences on the south coast of England.

This introductory chapter reviews research relevant to this thesis, beginning with detailing the need for coastal protection during the current period of rapid climate change and reviewing the types of coastal defence structures (CDSs) that exist and their function. Following this, a summary of the history of low crested breakwater structures (LCSs) around the world, in the U.K. and on the south coast of England are given, focusing on the sea defences at Elmer in West Sussex: the main study site used. Past research on how the low crested breakwater scheme at Elmer has modified the environment is reviewed; particularly focusing on the ecological impacts. Knowledge gaps in the existing research and consequently what is further required for a better understanding of the ecological impacts of LCSs are then identified. This chapter concludes with the aims, objectives and rationale of the structure of the thesis.

1.2 Why the Need for Coastal Protection?

Coastlines are highly dynamic and complex systems, representing the intersection between the marine and terrestrial environments. These two environments are constantly interacting, leading to erosion or accretion in response to natural geo-morphological and hydrodynamic processes such as sediment transport, vertical land movement (Simeonova 1992) and changes in the pattern of waves and storms. These natural processes lead to continuous changes in the

coastline, depending on the exposure of the coast and the underlying physical geology (Pethick & Burd 1993). Human activities such as excavation of the sand and gravel, offshore and in the nearshore beach environment, as well as the construction of harbour breakwaters, groynes and other structures, all modify the effects of natural coastal processes. On a global basis, more than 70 % of the world's sandy beaches have experienced net erosion over past decades (Bird 1985). The three possible reasons for this global pattern are: sea level rise, changes in storm climate, and human activity (Zhang et al. 2004).

Global surface temperature has increased since the middle of the 19th Century (IPCC 2007) and is expected to accelerate through the 21st Century due to human emissions of greenhouse gases, primarily through the burning of fossil fuels. Coastal communities are more vulnerable to climate change than inland communities because, in addition to changes in meteorological parameters, they are also affected by changes in oceanic parameters especially increases in sea level and wave heights (Tsimplis 2004). Even given substantial reductions in these emissions, sea-level rise will be significant through the 21st Century and beyond (Church et al. 2001, Nicholls & Klein 2005).

The most obvious effect of climate change will be that increasing sea levels will reduce the effective crest height of sea defences. Also, changes in weather patterns may cause more frequent surges, and therefore greater potential for overtopping and other damage. Alterations in patterns of storminess including storm frequency, intensity and tracking, cause changes to the storm-induced waves and surges, which will in turn, alter the response of the coastal environment (Lozano et al. 2004). Although future sea levels are difficult to predict, all scenarios point to a substantial increase in the risk of flooding (Nicholls et al. 1999, Nicholls & Klein 2005), due to more frequent extreme natural events such as storms and tidal surges. This is likely to have a profound impact on coastal erosion and serious consequences for the effectiveness of coastal protection and sea defence schemes in the near future (Thomalla & Vincent 2003).

Some 37 % of the world's population resides close to coastal areas (Cohen et al. 1997, Kay & Alder 2005), developing widespread economic activities. This figure varies from country to country, according to Nicholls & Klein (2005), with 75 % of the UK's population living within 50 km of the coast. The economic development and urbanization of coastlines has led to

increased land use, natural resource exploitation and impacts on these coastal environments. This has been particularly evident in many developed nations during the last four decades (Pilkey & Cooper 2004). In highly developed coastal areas, erosion and flooding cause socioeconomic losses in terms of damages to property, infrastructure such as roads and railways, industries, farmland and the local economy. There are also threats to the nature heritage value of important coastal habitats and ecosystems. Levels of development and economic activity in coastal regions have intensified in recent years so a range of pressures have emerged in the coastal zone, as people move to the coast for what is viewed as an enhanced lifestyle (Yapp 1986, Glasby & Connell 1999). Associated with coastal development and urbanisation are new and often novel engineered structures in intertidal and subtidal habitats such as marinas, ports, piers, seawalls and coastal defence structures (Glasby & Connell 1999, Bulleri et al. 2000, Chapman & Bulleri 2003). For example, in 1994, 23 % of England's eroding coastlines were already modified by man-made structures (MAFF 1994), and this proportion is certain to have increased over the last decade and will continue to in the future. These hard defences lock the coastal position and hence, contribute to the coastal squeeze of intertidal habitats on retreating shorelines (Nicholls 2000, French 2001). In Britain, it has been reported that the most rapid relative sea-level rise is along the English Channel from the Solent eastwards (Tubbs 1995).

The importance of flood defence is reflected in the large financial investment made to contend with flood risk, for example, in the Thames Barrage in the UK. Following a storm surge in 1953, floods in the UK cost between £240 million and £400 million at 1982 values (Arnell et al. 1984). High population densities around the whole North Sea are at high risk from coastal storm surges. For example, the 1953 floods claimed over 300 lives (Karas et al. 1991) in East Anglia, a low-lying area separated from the sea by soft, erodible cliffs. The Dutch have spent centuries defending themselves from the sea with a massive series of dykes. In spite of this, 1800 people died when a surge overpowered the dykes and levees in the lower Rhine Valley in 1953. Currently, coastal flooding threatens nearly 2 million properties in floodplains along rivers, estuaries and coasts in England alone (Anon 2006). The cost of protecting urban and coastal areas from sea level rise has been estimated as £6 billion for a 1 m rise in level (IPCC: Delft Hydraulics 1990 cited by Karas et al. 1991). In the Netherlands, \$5 billion was spent on the Delta Project, which took 4 decades to complete. Its centrepiece being a pair of 'doors', each about 20m high, that can close off the Rhine if a major coastal storm looms. In Italy, a set of 79

hinged inflatable steel gates are being built to protect Venice from rising waters, costing an expected \$2.6 billion. The project is due to be completed in early 2010 (Henson 2006).

Relative sea-level rise, irrespective of cause, has a number of impacts such as increased erosion and flood risk. In turn, these can have direct and indirect socio-economic impacts depending on the human exposure to these changes (Nicholls & Klein 2005). This clearly means there is a need for a more flexible, innovative and strategic approaches to coastal management. Such an approach requires a comprehensive scientific understanding of the controlling coastal processes and, likewise, how such problems can be mediated (Plomaritis 2006).

1.3 Definitions and Types of Coastal Defence Structures

A coastal defence structure (CDS) is an artificial structure whose primary function is to avert flooding by preventing erosion of sedimentary beaches. These should not be confused with either 'artificial reefs', whose primary purposes are habitat management, nature conservation, fisheries management and enhancement (Jensen 2002) through increasing biodiversity and production, or with urban structures such as marinas, piers and pilings, whose primary purpose is not for coastal defence but amenity use. In addition, artificial reefs are subtidal structures, whereas, coastal defence structures extend from the subtidal zone through the intertidal zone and into purely terrestrial realms (Davis et al. 2002). There has been considerable literature on the purpose, function, design, ecological implications and policy of artificial reefs since the pioneering of European artificial reefs in Monaco in the late 1960s (see Jensen's (2002) review of the artificial reefs of Europe).

The use of CDSs is ubiquitous and extensive, particularly since the mid 18th Century (Charlier et al. 2005). Nevertheless, despite the long history of urbanisation and coastal defence of the coastal environment, there understanding of the impact of such constructions on the ecology of intertidal habitats has only been in recent years (but see Airoldi et al. 2005, Martin et al. 2005, Moschella et al. 2005, Pinn et al. 2005, Airoldi & Beck 2007, Bertasi et al. 2007, Birben et al. 2007, Blockley 2007, Burcharth et al. 2007). In the last 20 years, published literature has increased on engineering design and structure and how this affects the performance, hydrodynamics and sediment transport surrounding CDSs (e.g. CERC 1984, Barber & Davies 1985, Brampton & Smallman 1985, Pope & Dean 1987, Koike 1988, Kaji et al. 1989, Pilarczyk

& Zeidler 1996, Bull et al. 1998, French & Livesey 2000, Black & Andrews 2001, Thomalla & Vincent 2003, Ranasinghe & Turner 2006, Birben et al. 2007). In comparison, the ecological implications of the layout of these structures (e.g. Smith et al. 2001, Davis et al. 2002, Bacchiocchi & Airoldi 2003, Martin et al. 2005, Moschella et al. 2005, Burcharth et al. 2007) has only been of relatively recent interest.

Coastal defence construction features generally fall into two categories, either soft or hard defences. Soft defences are mobile, responsive measures, which are intended to work with nature rather than control it (CERC 1984). Such structures may consist of natural or constructed sand or shingle beaches, and dunes or banks through beach nourishment, cliff/dune stabilisation, bypassing and managed retreat (Rosati 1990). Many types of hard CDSs exist, from bulkheads and seawalls, to groynes and breakwaters. Hard structures are some of the most common human-made constructions in coastal areas. CDSs are termed to be either located onshore or offshore as well as being attached or detached (CERC 1984). This thesis focuses on hard CDSs including groynes and shore parallel low crested breakwater structures (LCSs).

1.3.1 Onshore Structures

Bulkheads, seawalls and revetments are structures placed parallel, or nearly parallel, to the shoreline to separate a land area from a water area, in order to provide protection for the upper beach, which fronts backshore development or erodible sediments (Dally & Pope 1986). Both structures are expensive to build and maintain and may be built from many materials including steel, timber, or concrete pilings, gabions, or rubble mound structures (Dally & Pope 1986). Revetments armour existing slope faces of dunes, embankments and soft cliffs, acting to absorb wave energy (CERC 1984). They are slatted angled low walls parallel to the beach usually composed of one or more layers of wood, quarrystone or precast concrete. They are liable to rapid damage (Dally & Pope 1986).

There are no precise distinctions between these three structure types, and often the same type of structure in different localities will bear a different name (CERC 1984). These structures only afford protection to the land immediately behind them, not to the adjacent areas upcoast or downcoast. Furthermore, their height in the intertidal zone (above the MWS height) means that very little marine life will reside there, and more often than not, they fragment existing habitats.

1.3.2 Shore-connected Structures

There are several types of shore-connected structures, these being jetties, groynes and breakwaters. Jetties are structures that extend into the water to direct and confine river or tidal flow into a channel and prevent or reduce the shoaling of the channel by littoral material (e.g. Poole Harbour Training Bank, UK). Jetties located at the entrance to a bay or river also serve to protect the entrance channel from wave action and cross-currents. Unfortunately, jetties cause erosion of the downdrift beach (Dally & Pope 1986).

Groynes are barrier-type narrow structures of varying lengths and heights, extending from the backshore into the littoral zone (CERC 1984). They are built approximately perpendicular to the shoreline from various materials, such as timber, steel, concrete or quarrystone. Generally, they are constructed in a series along the entire length of beach, referred to as a 'groyne field'. The basic purposes of a groyne are to modify the longshore movement of sand and to either accumulate sand on the shore or impede sand losses. They trap sand in their lee, similar to jetties; this is at the expense of the adjacent downdrift shore (Rosati 1990). The interaction between the coastal processes and groynes is complicated and poorly understood (CERC 1984, Bull et al. 1998).

A shore-connected breakwater is a structure that protects a shore area, harbour, anchorage, or basin from waves (CERC 1984). They provide protection to harbours from wave action, creating calm water that provides protection for safe mooring, operating and handling of ships, and harbour facilities; there is the added advantage of a shore arm to facilitate construction and maintenance of the structure (Rosati 1990). They are generally of rubble-mound construction, but can also be made of composite, timber, steel, or concrete caisson, sheet-piling cell or crib.

1.3.3 Offshore Structures

Low crested breakwaters structure are stone wave energy barriers designed to protect any shoreline, landform or water area behind them from the direct assault of waves and thereby reduce coastal erosion (Rosati 1990; Fig. 1.1). Unlike groynes, breakwaters can be used to

reduce erosion at a beach that has no net longshore transport. However, if longshore transport exists, an offshore breakwater may act like a groyne and cause downdrift erosion if not engineered correctly (Loveless & Macleod 1999). Offshore breakwaters can be at a range of distances offshore and are orientated approximately parallel to shore and protrude above water level. They are referred to as "emergent" or be "submerged" low crested structures (LCSs) depending on whether they in the subtidal or intertidal (Burcharth et al. 2007). They may be continuous or consist of a series of structures. In the past however, because of the higher cost of these offshore structures over onshore structures (e.g. seawalls), breakwaters have been mainly used for harbour protection (e.g. Plymouth Breakwater, UK) and navigational purposes (French 2001). In recent years, LCSs have been used for shore protection, for example, in the UK there are emergent structures at Elmer, Sussex (Holland & Cooper 1994, Burcharth et al. 2007) and submerged structures at Sea Palling, Norfolk (Thomalla & Vincent 2003) and in Italy, emergent structures at Lido do Dante (Lamberti & Zanuttigh 2005). There are many different forms: singular units over 50 meters in length that protect a localized area such as a bay or harbour; obliquely positioned structures, offering enhanced protection from one particular direction; and multiple segmented system consisting of many components, designed to protect an extended length of coastline (e.g. Elmer and Sea Palling breakwaters).



Figure 1.1 An aerial view of the low crested breakwater scheme in the UK at Elmer, West Sussex. (Google Earth 2007). Map in British Grid.

Emergent detached breakwaters in multi-structure schemes are constructed in very shallow water of few metres water depth close to the shoreline, with the single objective of protecting a beach against erosion and flooding of low-lying areas (Environment Agency 2005). These can be costly to construct due to the inconvenience of constructing and maintaining offshore, therefore another design to counteract these issues is the "fish-tailed groyne" (e.g. The Wirral, Morecambe, UK), which it is connected to the shore (French & Livesey 2000). The objective of submerged structures built at some distance from the shoreline would most often be a combination of beach protection and creation of a suitable area for recreational usage.

The purpose of this thesis was to investigate the ecological implications of a multi-structured scheme of LCSs at Elmer in West Sussex. From this point on, CDSs are referring to groynes and LCSs, unless otherwise stated.

1.4 Low Crested Breakwater Function

The preliminary function of LCSs is to diminish the wave energy reaching the coastline, thus providing coastal protection (Burcharth et al. 2007). Generally, they are deployed as protective measures in response to erosion on sandy beaches and are often combined with beach renourishment (King et al. 2000). The structures reduce the incoming wave energy across the structure by triggering wave breaking at and on the structure, by partially reflecting the waves, and by dissipation related to the wave-induced porous flow in the structure (Burcharth et al. 2007). Shoreline changes occur through stabilisation and retention of existing sedimentary beach material, or natural sediment accumulation to form new beaches (King et al. 1996); this is because localised currents are altered, so changing the sediment transport pathways.

Predictions of the actual morphological changes imposed by LCSs, both local and distant, are difficult because of the complicated interaction between waves, water levels, currents and sediment transport. The tidal current patterns are different in the case of emergent and submerged structures (King et al. 1996). In multi-structured schemes, the currents around them will be manifested as concentrated and eroding rip currents in the gaps between the structures (see Plomaritis 2006). Dependent on the sheltering effect of LCSs, different amounts of littoral material are deposited and retained in the sheltered area behind the structures. If moderately sheltered, the sediment will typically appear as a bulge in the beach planform, termed as a

'salient', on the other hand if more protected, the resulting shoreline extends out to the structure thus forming a so-called 'tombolo' (Holland & Cooper 1994).

Though these LCSs are effective at protecting the coastline, they have like other hard structures some drawbacks. Salients or tombolos can interfere with longshore currents and sediment transport, almost always creating downdrift erosion on coastlines with one dominating sediment transport direction along the coast (Rosati 1990). Tombolos have a stronger negative effect than salients. Emergent breakwaters forming schemes with rather closed cells may result in stagnant water of poor quality. Furthermore, the visual impact of emergent structures can be negative at locations of high scenic value; however, these schemes have immediate relevance to local population by reducing localized risks. Evidently, there needs to be a balance between economics, aesthetics, objectives and negatives (Van Vuren et al. 2004).

1.5 Historical Development of Breakwaters

1.5.1 Worldwide

In latter half of the 19th Century, the development of coastal defences moved away from traditional longitudinal concrete seawalls and wooden groynes towards an increasing number of quarry rock structures, such as, groynes or emergent and submerged LCSs. Detached offshore breakwaters have been used successfully to control shoreline evolution for more than four decades worldwide. They began to be used as a form of coastal protection in the mid-1960s in Europe (Berenguer & Enriquez 1988, Lamberti et al. 2005, Lamberti & Zanuttigh 2005) and the United States (Dally & Pope 1986, Pope & Dean 1987, Rosati 1990, Rosati et al. 1992), subsequently proliferating in Japan (Uda 1988, Kaji et al. 1989) from the 1970s; by way of example, some 900 units were constructed by 1974 (Koike 1988), and 4,800 units by 1989 (Silvester & Hsu 1994). Until relatively recently, the use of submerged or emergent low crested breakwaters as coastal defence and protection structures has been restricted to micro- and mesotidal environments (Brampton & Smallman 1985).

1.5.2 U.K.

In macro-tidal areas (tidal range > 4 m), such as the UK, the use of breakwaters is relatively uncommon (King et al. 2000). The large tidal range and the severe wave conditions which can occur around most parts of the UK coast also make the construction of offshore structures costly and have therefore limited their use (Pilarczyk & Zeidler 1996). There are important differences between UK usage of LCSs and their previous use elsewhere. The large tidal range in the UK and their application to shingle beach protection being the main differences (King et al. 2000). To date, LCSs have only been used at a few sites in the UK, although the number of schemes is expected to rise in the future. Until recently, the largest scheme in the UK consisted of eight breakwaters constructed at Elmer on the south coast of England (Holland & Cooper 1994, Cooper et al. 1996a, King et al. 2000, Lamberti et al. 2005).

Along the east Norfolk coastline, from Happisburgh to Winterton (encompassing Sea Palling) a major low crested breakwater scheme has been partly constructed to protect the Norfolk Broads, a wetland area in East Anglia. When finished in 2012, this scheme will be twice as big as at Elmer. It will eventually consist of 16 units, around 300 m long, with a gap of 300 m between each reef and situated 200 - 300 m offshore (Halcrow 1991, NRA 1993, Gardner & Runcie 1995, King et al. 2000, Thomalla & Vincent 2003). At present, nine of the breakwaters are complete, four that are surface-piercing and five that are submerged breakwaters at high tide. These breakwaters are cheaper to construct than fish-tail groynes and will interfere less with longshore drift, so minimizing the risk of beach starvation downstream of the scheme. It is thought that the incident wave height will be reduced by 50%, and the net cost of LCS production is estimated at £30 million (King et al. 2000).

There are various other smaller schemes. A single detached breakwater and rock groyne system at Monk's Bay on the Isle of Wight, which protects the toe of a previous landslip and has also created a new amenity beach (Sir William Halcrow & Partners 1996). There is one detached offshore breakwater protecting an existing sea wall against flooding at Rhos-on-Sea, North Wales (Pilarczyk & Zeidler 1996). Two detached breakwaters have been built at King's Parade on the Wirral, which were constructed following the success of the Leasowe Bay fish-tailed groynes (Barber & Davies 1985, Pilarczyk & Zeidler 1996) and two oblique breakwaters have been constructed at Sidmouth in Devon (Andrews 1996).

1.6 Historical Review of the Study Area: Elmer

The coastline from Pagham to Shoreham on the South Coast of England (Figure 1.2b) is dominated by a well-defined intertidal beach with a predominantly steep and often narrow gravel backshore and low gradient wide sandy foreshore (South Downs Group 2003).

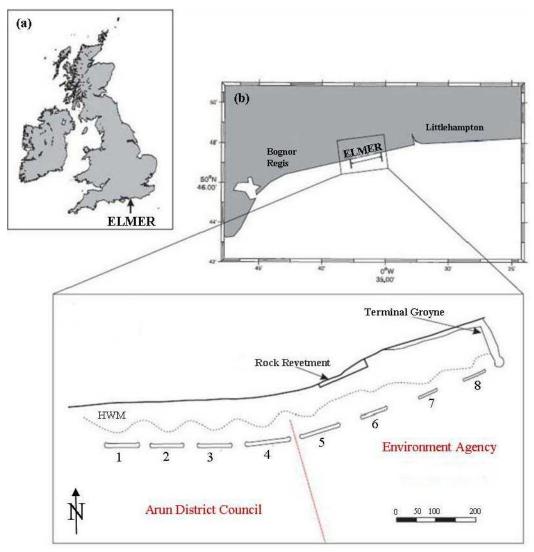


Figure 1.2 General location map of the study area showing: (a) regional setting; (b) coastline section; and (c) the breakwater scheme. The areas of responsibilities for Elmer beach by Arun District Council and the Environment Agency are given. Scale in metres.

This coastline has experienced long-term rapid coastal erosion throughout history (Harper 1985, Holland & Cooper 1994). Evidence of this erosive nature of the Elmer coastal system has been acknowledged in literature for nearly two centuries (Parry 1833). Analysis of the relative

movements of the positions of mean high and low water for the time period from 1875 to 1979, reveals long-term coastline retreating, intertidal narrowing and beach steepening for the majority of the coastline (Table 1.1, Robert West & Partners 1991). However, since the mid to late 1960s, the overall trend has been one of overall equilibrium or net accretion. This has been largely due to the substantially modified shoreline by the insertion of "hard" defence structures, such as seawalls, revetment and groynes, for some 100 to 150 years. On the other hand, the mean high water mark at Climping Beach, 1 mile east of Elmer Beach has advanced throughout much of the twentieth century. This is due largely to the obstruction to longshore transport by the West Pier training wall at Littlehampton, although in this case, there has been regular removal of sediment excess to compensate for net downdrift losses resulting (South Downs Group 2003).

1.6.1 Coastal Protection of Study Area

Engineering works started in 1813 (a review of a series of engineering works is provided in Table 1.1); by 1879 the coastline was heavily protected with timber groynes. In 1947, it was noted that the coastline had retreated about 20 m in comparison with 1913 (Robert West & Partners 1991). In 1963, defence works included concrete seawalls and timber breastwork constructions, in addition to maintaining the groynes. The groyne field, which had historically been adopted over the Elmer frontage, comprised of alternating long and short groynes. The long groynes (typically 100 m in length) were designed specifically to maintain or increase beach volumes by trapping shingle (Robert West & Partners 1991). In recent decades, these structures have been supplemented by gravel recharge and recycling (South Downs Group 2003).

Table 1.1 Summary of the historical development of the Elmer coastline (for more details see Robert West & Partners 1991)

Date	Major observations derived from the maps and plans of Elmer Beach
1813	 Groynes are built for the first time; their influence on the coastline can be
1013	observed in the downdrift area of the groynes.
	The coastline is heavily groyned.
1879	 A significant embayment had formed to the east of the groynes, probably due to
	the absence of groynes and the softer alluvial material.
1912	• The embayment is fronted by a breastwork structure.
1912	 Embankment in the area behind Elmer Beach.
1933	• Further straightening of the embayment is evident.
1755	 The timber breastwork appears to be much more regular in appearance

	The groyne alignment along the coastline is much more oblique, than the present
1947	day alignment.
	 The coastline has retreated 20 m in comparison with the 1913 map.

Since the early 19th Century, urbanisation has been on the increase; consequently the entire frontage between Selsey and Brighton is almost completely defended. Previous to shoreline management, beaches were subject to the impacts of extreme storm events. There was a 600 m breach at Widewater Lagoon in 1908 and 20 m of recession in less than 7 hours, at Lancing in 1877 (South Downs Group 2003). Although this type of catastrophic event has been largely protected by defences since the early decades of the twentieth century, several locations have continued to experience overtopping during surge events (Halcrow Maritime et al. 2001).

Despite these protection measures, the frontage at Elmer has long been affected by wave overtopping and the consequent flooding of the low-lying hinterland and nearby housing. The increasing flood risk was realised in the winter of 1989/90, when catastrophic flooding from severe storms during a spring tide period occurred on two separate occasions, causing large-scale damage to the existing defences (groynes and seawalls, Martin et al. 2005). Around this time, the Arun District Council's (ADC) groyne field was due for extensive renovation. Following these flooding events, there was reason for the implementation of a more comprehensive and dynamic management strategy, to combat the effects of wave overtopping and continued reduction in littoral drift material. Based upon the findings of Gifford Associates Consultancy (1997), groynes and inlet training structures were found to induce downdrift shingle deficits, reduce natural sources of shingle supply, and subsequently diminish many beaches over the 20th Century. The starvation of this part of the coastline from littoral material was considered to be one of the main reasons for the continued coastal problems. Consequently, an integrated management and protection strategy, over the entire joint ADC and Environment Agency (EA) frontage (Fig. 1.2c), was considered to be the way forward (Plomaritis 2006).

1.6.2 The Present Low Crested Breakwater Scheme

The defence scheme for Elmer was selected after a variety of options were considered and evaluated from both the engineering and socio-economic perspective. The stated purpose of the works was to reduce coastal erosion, prevent overtopping of seawalls by storm driven high tides and to reduce risk of a breach of the coastal defences on the Elmer frontage (Green 1992). The

works would also protect adjacent properties and highways from damage from flooding (Burcharth et al. 2007). The breakwater scheme was built jointly by ADC and the Southern Division of the National Rivers Authority (NRA; now the Environment Agency), and was designed by Robert West & Partners, following a consultation with HR Wallingford in the development of a physical modelling study (Hydraulic Research 1994).

An 'emergency works' plan was formed to overcome the immediate problems of the area and provide coastal protection over the impending winter periods. This plan included the construction of two emergent low crested rock breakwaters at approximately 120 m (close to low water mark) from the seawall face on the ADC frontage (to reduce incoming wave energy) and a rock revetment to the east on the NRA frontage (to provide storm protection) (King et al. 2000). The two 'emergency' breakwaters measured 90 m long, with a gap of 80 m between them, and were constructed of 6 - 8 tonnes of limestone blocks each. The side slopes of the breakwaters were 1:1.5 and the crest level was 4.5 m Above Ordnance Datum (AOD). The construction of this scheme, budgeted at £6.5 million, was only provisional and because of its success a permanent more extensive solution was adopted. Emergency work construction commenced in 1991, and the final scheme reached completion in August 1993, and actually cost £8.5 million (Burcharth et al. 2007). One year after commencement, more than 11,000 m³ of sand and single were placed in the salient areas to lee of the breakwaters, as part of a replenishment scheme (Plomaritis 2006).

1.6.2.1 Final low crested breakwater engineering design

In the final scheme, the initial emergency breakwater scheme (presently identified as breakwaters 3 and 4) was extended and a further 6 "rock islands" added, as well as a terminal rock groyne at the down drift end (eastern end; Fig. 1.2c) (King et al. 2000). The breakwater scheme extends along 1.75 km of coastline. The first 1.25 km from the west are under the responsibility of Arun District Council (structures 1-4) and 500 m under the responsibility of the Environment Agency (structures 5-8) (Fig. 1.2c, King et al. 2000). The design of the scheme was complex, with varying breakwaters lengths and gap widths between the structures; towards the east, the gaps were larger and the length of the breakwaters shorter (Table 1.2). This reduction in protection was intentional, in order to produce a smoother transition between the scheme and the open beach downdrift (King et al 2000) of the terminal (attached) rock groyne on beach volumes. The terminal rock groyne to the east of the system (downdrift end) acts as the beach level regulator. On the landward side of all of the structures tombolos have been formed, meaning the beach in the lee of the structures is higher in comparison with the seaward side. Subsequently, bays have been created between each of the structures (Sterlini 1997).

Table 1.2 Breakwater dimensions and design parameters of Elmer low crested breakwater scheme¹

Breakwater	Crest Elevation (m) AOD ²	Breakwater Length (m)	Gap length (m)	Distance Offshore (m)
1	4.5	90		85
			80	
2	4.5	90		79
			60	
3	4.5	140		75
_			60	
4	4.5	140		77
_	. ~	1.10	44	0.0
5	4.5	140	100	88
_	4.5	0.0	100	~ 4
6	4.5	80	1.40	54
_	2	0.0	140	60
7	3	80	0.0	68
	2	0.0	80	20
8	3	80		38

Data taken from hydrodynamic studies previously carried out at Elmer (Plomaritis 2006); ¹ for locations, see Figure 1.2; ² Above Ordnance Datum (AOD).

The breakwaters were round-headed with a slope of 1:2.5 at the head (Fig. 1.3), crest height was approximately 6 m, with a slope of 1:1.5 on the landward side and 1:2 on the seaward side and the top was 4 m wide; they were positioned 130 m from the shoreline (Martin et al. 2005). A 600 mm layer of graded bedstone was placed on the exposed bedrock, to provide the foundation of the breakwaters main rock armouring (Cooper et al. 1996a). The main breakwater body (ca. 95 %) was constructed with 33 000 tonnes of Norwegian syenite (an igneous rock) in the form of blocks of 6 - 10 tonnes (ca. 1 - 2 m³) each, in addition, some French quartzite was also used as a bedstone. Surrounding the base were smaller boulders (ca. 0.5 m³) scattered haphazardly (unlike the core).

There were difficulties in choosing the shore height location of the breakwaters because of it being in a macrotidal area, and it was essential to have scheme efficiency enabling protection during the whole of the tidal cycle. Compared to the original "ideal" design criteria, the embayments were wider and the tombolos narrower than originally anticipated, thereby giving

Elmer Beach a markedly sinuous beach planform (South Downs Group 2003). The breakwater structures are exposed completely at low tide and, during high water they do not become completely submerged. Since the completion of the breakwaters in 1993, no flooding events have been recorded in the area, causing a significant increase in the property values and a decrease in home insurance premiums (Burcharth et al. 2007).

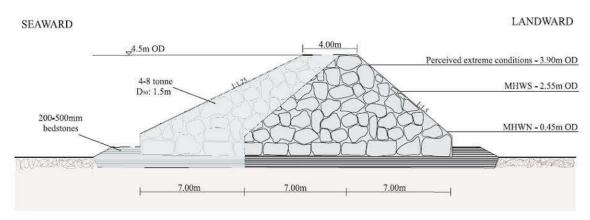


Figure 1.3 The positioning and size of the breakwaters at Elmer in relation to different water levels (Figure taken from Plomaritis 2006). MHWS = mean high water springs, MHWN = mean high water neaps, D_{50} = median grain size, AOD = Above Ordnance Datum.

1.7 Impacts of the Elmer Breakwater Scheme

1.7.1 Impacts on the Local Hydrodynamics

The construction of LCSs and other CDSs, result in considerable changes to the environmental parameters of the area, and consequently to the ecology. Prior to the breakwater scheme at Elmer there had been some research into the hydrodynamics and physical features of the beach and the surrounding coastline (Pingree 1980, Harper 1985, Jelliman et al. 1991, Robert West & Partners 1991). Following the completion of the final scheme in 1993, there has been an increase in both the quality and quantity of research and this has enhanced the knowledge and understanding of the coastal sediment transport process system on this frontage (Burcharth et al. 2007). Extensive beach surveys (e.g. beach profile and aerial surveys), and physical and numerical modelling studies have been undertaken by local authorities and research organisations (e.g. Green 1992, Holland & Cooper 1994, Cooper et al. 1996a, Gifford Associated Consultants 1997, King et al. 2000, Plomaritis 2006). The main focus of the studies was the investigation of hydrodynamic processes, sediment transport pathways and

morphological changes introduced by the scheme. For example, a study by Moody (1997) demonstrated the change in elevation on either side of the breakwater structures; this was due to the development of tombolos (i.e. sand accumulation) behind the breakwaters. King et al. (1996) carried out beach platform monitoring over the 32 months following scheme completion, they revealed that stability was achieved after rapid initial adjustments. Aluminium pebbles and fluorescent coated indigenous gravel sized particles were used to identify sediment transport pathways and rates of movement. These fluorescent pebble tracer studies revealed that sediment in the immediate lee of the breakwaters remained immobile during storm conditions, highlighting the degree of protection afforded by the structures; likewise, their ability to maintain the beach.

A later study by King et al. (2000), showed that the maximum rate of sediment transport in the lee of the breakwater was 57 m³/tide (for shingle) during a storm. This rate of transport was lower than that recorded on unprotected beaches under the same conditions, thus demonstrating the efficiency of the breakwaters in reducing wave energy reaching the beach. These tracer studies clearly identified a potential for sediments to drift through the scheme. Under calm conditions, movement from the west into the scheme was negligible but movement out of the scheme at the eastern end did occur (Cooper et al. 1996a, King et al. 1996). Loveless and Macleod (1999) examined the hydrodynamic and morphodynamic effects of building these submerged rubble mound breakwaters, but only partially understood the impacts on beach form from characteristic "set-up" currents generated from behind breakwaters. Plomaritis (2005) has since studied the scheme in considerable detail; highlighting the sediment transport pathways resulting from the complex tidal currents that exist within this coastal defence system.

1.7.2 Impacts on the Surrounding Ecology

The EU Funded project "Environmental design of low-crested coastal defence structures" (DELOS EVK3-CT-2000-00041) studied the beach at Elmer and its structures, along with other macro- and microtidal shores in Europe in quite some detail from 2001-2004 (Airoldi et al. 2005, Lamberti et al. 2005, Martin et al. 2005, Moschella et al. 2005, Bertasi et al. 2007). There has been no other known published work on the effects this low crested breakwater scheme has on the ecology of the surrounding area, nor on any other LCS scheme in the UK.

The construction of the LCSs at Elmer has produced a series of changes to the surrounding environment (Burcharth et al. 2007). Environmental impacts include aesthetic effects on the landscape, recreational value, ecological effects on soft- and rocky bottoms, fish assemblages and other mobile fauna and birds (Burcharth et al. 2007). These impacts, as a result of the structures, were documented by the DELOS programme (2001-2003) (Burcharth et al. 2007). Qualitative observations were made about the effect on birds and the effect of the accumulation of seaweed detritus on the beach. Quantitative research was carried out on the effects on the surrounding sediment infauna, the provision of rocky habitats and the effects on fish and mobile fauna, excluding birds. This section briefly states the findings of the DELOS research, followed by the areas that require further study.

The LCSs at Elmer have changed the local communities in a number of ways (Burcharth et al. 2007). In place of the structures there is the immediate loss of the natural sedimentary habitats and associated assemblages of animals and plants, with the introduction of new rocky shore species; thereby changing the diversity of species. Furthermore, the reduction of wave energy to the area changes the local hydrodynamics, which in turn affects the remaining surrounding sedimentary habitats (Burcharth et al. 2007). It has been suggested that the creation of new habitats through urbanisation not only increases habitat diversity, but also causes an increase in species diversity (Rebel 1994). CDSs are often explicitly or implicitly considered a local benefit to coastal sandy area for their potential to increase local species diversity by allowing settlement of new species that usually live on rocky reefs (Airoldi et al. 2005, Airoldi & Beck 2007, Burcharth et al. 2007). In recent years, CDSs have been regarded as important resource enhancement tools for the productivity of commercial species and mitigate habitat losses (Bohnsack & Sutherland 1985, Pickering et al. 1998).

1.7.2.1 Effect of decaying macroalgae deposits on the beach

The stretch of coast where the Elmer defence scheme is located is periodically affected by large amounts of macroalgae that are detached from the offshore reefs and washed onto the shore after stormy weather (Burcharth et al. 2007). This phenomenon was observed by researchers to be particularly evident around the LCSs (Hawkins & Moschella unpub. obs.) Burcharth et al. (2007) suggested that the algae were probably pushed inshore by waves and inshore winds, and eventually got trapped by the LCSs. Periods of calm weather conditions that may lead to

stagnant water and degradation of bathing water quality, may be enhanced by these deposits. The deposition and accumulation of seaweed may cause recreational and ecological problems as strong unpleasant smells develop as a consequence of the seaweed decaying; this can be detrimental for beach users and several complaints have been made by the local community (author's pers. comms). Decaying macroalgae deposits can also have ecological consequences: the sediment covered by the detrital material may become anoxic as a consequence of changes in the redox potential. This is likely to have an impact on the infaunal assemblages, especially for the more sensitive species. At high tide however, some of the algae float and seem to provide an attractive habitat for juvenile fish, thus potentially enhancing the local fish populations. As seaweed deposition on beaches may be an environmental and amenity problem, there is a clear need for integrated applied research.

1.7.2.2 Effect on sediment fauna

The deployment of artificial rocky substrata along sandy shores to prevent coastal erosion can cause changes in the composition, abundance and trophic structure of benthic assemblages inhabiting the marine sediment. This can be due to modification of wave regime and sediment depositional processes (Bacchiocchi & Airoldi 2003, Martin et al. 2005). Two studies were carried out in the summer of 2001 and 2002 looking at the effect of the LCSs at Elmer on the surrounding sediment-dwelling biota (Burcharth et al. 2007). The first study was restricted to the effects of LCSs on infauna and sediment characteristics, whilst the second investigated the extent of these effects along the shore and the effect of tidal level. The sampling regime chosen was to look at the difference between the landward and seaward sides of the structures, in addition, compare this to two control sites, east and west of the structures. A brief overview of the DELOS research is given below (Burcharth et al. 2007). More in depth discussion of their findings and other studies will be given in Chapter 5 (also see Burcharth et al. 2007).

Results from the DELOS research project (Burcharth et al. 2007) showed consistency between the two years, with no significant differences detected. There was, however, a high degree of spatial variability for both the sediment descriptors and biotic features, making it difficult to explain any patterns in the community as the changes were too small. Nevertheless, it was noted that the sediment descriptors, chlorophyll and organic matter, showed some differences between the landward and seaward sides of the structures. These observations were attributed to the

location of the structures and their context; i.e. a moderately exposed beach and their porosity. The LCSs had apparent effects on the composition and abundance of the infaunal communities; patterns were seen between the landward and the seaward sides, and the control sites. Crustaceans dominated the infaunal communities at all the locations. On the landward side of the structure, the average abundance of amphipods was approximately ten times higher than that of polychaetes, such as the lugworm *Arenicola marina* (Linnaeus, 1758). The effect of LCSs on the soft-bottom community appeared to be evident only on the landward side, as the seaward side and the other control areas along the coast were very similar in diversity and abundance of organisms and sediment characteristics. Furthermore, the effect appeared localised within 100 m or so around the structures, as no effect was detected at increasing distances. The DELOS studies showed that the environmental setting was extremely important in determining the magnitude of impacts on the soft-bottom habitat and communities. On relatively reflective and exposed beaches such as Elmer, LCSs seem to have a minor but significant impact on sediments and infaunal communities.

1.7.2.3 Provision of rocky habitats

Elmer is located on a stretch of coastline that lacks extensive natural rocky shores, with only patchy boulder fields and small rocky outcrops. A major effect of the LCSs at Elmer was the creation of artificial habitats for species living naturally on rocky shores. New substratum is rapidly colonised by fauna and flora common to hard substrata (Anderson & Underwood 1994), thereby potentially supplementing natural habitats by supporting natural assemblages, in terms of species composition and relative abundances. Alternatively the structures may support only a subset of natural assemblages, providing habitat for additional species not found on nearby rocky shores, or providing habitat in which some species are consistently missing and additional species found (Chapman & Bulleri 2003). In addition, they can have large scale effects, by acting as stepping stones that facilitate the dispersal of rocky shore species across habitats that would naturally be unconnected (Burcharth et al. 2007).

The abundance and composition of assemblages on the face of the large blocks and in the rock pools amongst the small boulders and blocks at the base of the structures were examined by the DELOS project (see Burcharth et al. 2007). In light of previous studies on CDSs, DELOS researchers found that typically, the epibiotic assemblages consisted of similar species, but that

they were less diverse than natural rocky shore communities (Moschella et al. 2005). The epibiota found colonising the boulder faces of the breakwaters was relatively poor in terms of diversity (21 species). The most common organisms observed were fucoids, ephemeral algae, limpets, littorinid snails and barnacles. Distinct differences between landward and seaward sides of the LCSs were observed on all structures. On the seaward side of the LCSs limpets and barnacles were dominant, whilst on the landward side permanent patches of fucoid and ephemeral algae were present. The absence of algae on the seaward side was thought to be because of the combined result of physical factors (strong exposure to waves, higher dislodgement forces) and biological interactions (higher grazing pressure) (Jonsson et al. 2006).

Rock pools were also present at the base of the structures on the seaward side. These had extremely high diversity (72 species), with numerous species typically found on the lower intertidal and subtidal zone. One of the reasons stated for the notably lower diversity on the structures than in the rock pools, was probably the low complexity of the blocks and their freely draining nature, lacking the micro-habitat diversity that would be found on a natural rocky shore. Experiments that were carried out on the structures showed that more complex surfaces with holes and pits had increased species diversity, particularly for species that were more sensitive to desiccation and insulation stresses occurring at low tide. Several south-western species that reach their limits in the English Channel were noted to have colonised further east than previously recorded (Crisp & Southward 1958), by using the breakwater at Elmer. These included the purple topshell *Gibbula umbilicalis* (de Costa 1778) and *Melaraphe neritoides* (Montagu 1803) (Hawkins, Frost & Moschella, unpub. obs.).

1.7.2.4 Effect on fish and mobile fauna, including birds

Surveys of fish and mobile fauna were carried out over the three years of the DELOS project (2001-2003). The LCSs appeared to have had some effects on fish and mobile fauna. In a similar way to the results obtained for the soft-bottoms, effects were more evident on the landward side of the structures. The composition of fish and mobile fauna consisted of species typical of both rocky and soft-bottoms. It was suggested that LCSs, especially when built in coastal areas dominated by soft bottoms, can have a strong influence on the structure of fish communities, attracting species typical of rocky shore therefore increasing local diversity (Burcharth et al. 2007). Several of these species were of commercial importance such as sea

bass *Dicentrarchus labrax* (Linnaeus 1758), mullet *Chelon labrosus* (Risso 1827) and *Liza ramada* (Risso 1826), sole *Solea solea* (Linnaeus 1758), plaice *Pleuronectes platessa* Linnaeus 1758 and other flat fish. More importantly LCSs may provide a nursery ground for fish, particularly for commercially and recreationally important species, the sea bass *D. labrax* and several flat fish (e.g. *S. solea, P. platessa*). So, potentially LCSs could have an enhancement effect on local fisheries. The landward side of the structure appears to have provided a better habitat for juvenile fish, as well as the deposition and accumulation of drift algae, which also provided a suitable habitat for juveniles and several species (Burcharth et al. 2007).

Crustaceans, such as shrimps and crabs were particularly abundant in the structures and represented further potential food resources for fish and birds. There was evidence that the breakwaters attract birds that are generally found on rocky shores, such as cormorants and oystercatchers; these use the structures as resting sites and for feeding resources (e.g. limpets). In contrast, the LCSs could negatively affect other species of birds by modifying the species composition of infaunal assemblages on which these birds feed.

1.8 Further Research Requirements

As can been seen from Section 1.7, there has been some extensive work done on how the LCSs at Elmer effect the ecology of the structures and surrounding areas. There are, however, still significant areas that lack understanding and research.

1.8.1 Decaying Macroalgae Deposits

The phenomenon of decaying macroalgae deposits at Elmer was only assessed qualitatively in the DELOS project. For this reason, the frequency of occurrence, abundance, distribution and composition of the seaweed in and around the structures needs to be assessed quantitatively (see Chapter 3). Secondly, in order to decide if these structures enhance the problem or not, comparisons are needed with different types of defence structures on adjacent stretches of the coastline. Another issue that is important to consider, is how these decaying deposits affect the underlying benthic communities and the communities that have colonised the LCSs, with investigations into how important this organic resource to the food web is (see Chapters 4 & 7).

1.8.3.1 Seaweed detritus – detrimental or beneficial?

The supply of oxygen to infauna is one of the most important chemical influences on the biology of sediments (Little 2000). Deposited seaweed can stress infaunal populations by inducing hypoxic conditions at the sediment algal interface (Norkko and Bonsdorff, 1996) and by inflicting a physical cover over the sediment. Paradoxically, this can also offer refuge from predation by epibenthic predators (Norkko, 1998). Where there are intermediate amounts of algal deposits, there can be an increase in habitat heterogeneity with patches occurring, where the uncovered areas are exposed to predation and the covered areas offer refuge. The quantity of macroalgal cover will affect how the sediment structure and composition of infaunal communities are affected. It can therefore be hypothesised that decaying algae could cause two effects of opposite extremes; either that it may amplify diversity in the soft sediment assemblages due to increased carbon and nitrogen, nutrients and available shelter, or that it creates a highly anoxic environment that becomes less inhabitable and therefore reduces diversity.

1.8.3.2 Seaweed detritus as a food source?

Macroalgae can enter the coastal food web through different pathways. It is probable that a low percentage of macroalgae is consumed while these algae are still living (Fenton & Ritz 1988, Mann 1988), and that macroalgae is mostly related to detritic food chains (Pomeroy 1980, Adin & Riera 2003), however these detrital trophic pathways still remain incompletely understood. In coastal ecosystems a significant fraction of the macroalgal biomass is generally deposited ashore after being dislodged by currents and waves (Branch & Griffiths 1988, Riera & Hubas 2003). After decomposition by microbes and abiotic fragmentation, the decaying algae becomes an important energy source for invertebrates (Bustamante et al. 1995). Nutrients bound in the organic material are returned to the sediment (Gartner & Cardon 2004) and consequentially into the interstitial trophic chains of these environments (Inglis 1989). Seaweed detritus represents the most important food for many marine species such as polychaetes (e.g. Magnum & Cox 1971), limpets (e.g. Bustamante et al. 1995) and amphipods (e.g. Inglis 1989). One example of decaying macroalgae consumption is reported from a sandy beach off the west coast of the Cape Peninsula, South Africa; Griffiths et al. (1983) reported that 53 % of the annual seaweed

deposition was consumed by talitrid amphipods. However, Rodriguez (2003) stated that despite the fact that decaying macrophytes seem to play such an important role in the trophic food web, the consequences of consumption of this resource for populations and/or communities has been little explored. The significance of the role of macrophyte-derived detritus as a source of organic carbon and nitrogen for subtidal consumers (Stuart et al. 1982, Mann 1988, Fielding & Davis 1989, Bonsdorff 1992, Wilson 2002) and rocky-intertidal consumers (Backlund 1945, Soulsby et al. 1982, Bustamante & Branch 1996) has been well documented. There have also been studies on the decomposition of macrophyte strandline debris on sandy beaches (Koop et al. 1982). At present, however, the importance of macrophyte detritus in and around CDSs has not been documented and remains allusive.

1.8.2 Sandy Beach Assemblages

The DELOS project (Burcharth et al. 2007) carried out a preliminary sampling programme of the soft sediment communities surrounding the LCSs. There are still, however, questions to be addressed (see Chapter 4), for example, only the tombolos were sampled on the landward and seaward sides of the structures. The bays between the structures were not investigated, and as reported by Plomaritis (2006), these areas undergo complicated tidal circulation patterns which differ throughout the breakwater scheme, due to varying structure and gap lengths. Therefore, it would be expected that the community composition and abundances would be influenced by this hydrodynamic regime; this may also influence the distribution and quantity of decaying macroalgae deposits, which in turn may influence the benthic community. It would also be expected that these ecological patterns would vary temporally; the DELOS project only addressed the summer seasons on two occasions and found no significant differences in the sediment communities on the tombolos. In reality, it is necessary to gain an insight into how the soft sediment communities vary in other seasons.

1.8.3 LCS Rocky Shore Assemblages

The study of the faunal assemblages on the LCSs was extensive. However, because the coastline in this region has no natural rocky shores no comparison has been made with other hard CDSs nearby (< 10 miles); this was carried out and discussed in Chapter 5. Furthermore, the seasonal changes in the epifaunal communities of CDSs were studied, as it had not previously.

1.9 Study Aims and Objectives

1.9.1 Study Aims

The overall aim was to study the role of CDSs in modifying community structure and ecological processes in coastal ecosystems. In particular, to focus on the importance of the decaying macroalgae deposits around low crested breakwater structures. The research aimed to describe the interactions between the decaying macroalgae deposits and the hydrodynamic regime around sea defence structures, both spatially and temporally. The study then explored the consequences for the community composition and abundance of the sediment infauna and rocky shore epifauna both spatially and temporally. The work showed the importance of subtidal seaweed cycling within intertidal communities, through decay experiments and foodweb studies using stable isotope analysis. The low crested breakwaters at Elmer, West Sussex were used as a test system.

The specific objectives were to:

- 1. Describe the environmental setting (e.g. wave climate, hydrodynamic and sediment environments) of the research area and the reasons for the study locations used (Chapter 2).
- 2. Assess the species composition, frequency of occurrence and distribution of the decaying macroalgae deposits around the LCSs at Elmer (the main study site) and two other nearby CDSs (comparative sites), and establish the driving environmental factors. (Chapter 3);
- 3. Assess the ecological effects LCSs and decaying macroalgae deposits may have on the surrounding benthic assemblages both temporally and spatially. The composition, abundance and diversity of sediment infaunal communities surrounding the LCSs at Elmer were quantified on varying temporal scales, as well as for two nearby comparative sites with groyne structures. Hydrodynamic regime and decaying macroalgae data were used to attempt to explain the community structure and spatial distribution of the sediment infaunal communities (Chapter 4);
- 4. Describe the spatial and temporal changes in epifaunal assemblages (composition, abundance and diversity of the motile and sessile assemblages) of the Elmer LCSs and

- nearby groynes in relation to CDS design (e.g. different sides of the structures and vertical shore levels) and environmental parameters (Chapter 5);
- 5. Examine the processes of decay in a selection of macroalgae species, both aerobically (in the field) and anaerobically (in the laboratory), and the change in δ^{13} C and δ^{15} N isotope values of a variety decaying macroalgae species during decay over time (Chapter 6); and
- 6. Examine whether decaying macroalgae deposits are utilized by sediment infauna, rocky shore epifauna and mobile fauna within the Elmer LCS and Felpham groyne ecosystems by means of stable isotope analyses, and to determine the level of importance of these deposits (Chapter 7).

Concluding remarks, a synthesis of the results from each chapter and the background information obtained throughout the present investigation, and recommendations for further research are presented in Chapter 8.

Chapter 2: Environmental Setting of Research Area

2.1 Introduction

Elmer is a low-lying residential seaside village located on the South Coast of England, between Bognor Regis and Littlehampton, on the West Sussex coastline (Fig. 2.1b). This approximately 12 km straight section of coastline faces south east. The shoreline bulges slightly beyond the average coastal alignment, forming a small headland (Green 1992). The coastline between Pagham and Brighton is heavily-protected, with a long history of defence schemes. This particular stretch of coastline has been associated with an increasing amount of residential development. This has created the need for effective flood control works through coastal protection schemes, inevitably resulting in local small scale environmental changes (Green 1992, Holland & Cooper 1994, Cooper et al. 1996a). The area is now protected by a segmented emergent low crested breakwater scheme. The differences in the design parameters of the LCSs (i.e. length, gap size and distance from the shore; Table 1.2), together with environmental parameters (i.e. water depth, tidal flow direction, angle of structure sides and wave direction relative to the coastline) has generated distinct processes over different parts of the scheme.

In this chapter the reasoning for choosing this study area, with details of the three different study sites used are explained. An overview of the environmental characteristics and data analysis of available hydrodynamic information (Channel Coastal Observatory & Plomaritis 2006) is presented for the period of study in this area, in terms of: the wind and wave characteristics, tides and currents, sedimentology and sediment transport and sea temperatures. Finally, the ecology of the area is briefly described.

2.2 Choice of Study Sites

The main study site was the low crested breakwater scheme at Elmer (WGS84: $50^{\circ}47'23.72 \text{ N}$ $0^{\circ}36'40.63 \text{ W} - 50^{\circ}47'34.78 \text{ N}$ $0^{\circ}35'21.81 \text{ W}$) (Fig. 2.1c), which is approximately 5 km to the east of Bognor Regis, on the West Sussex coastline.

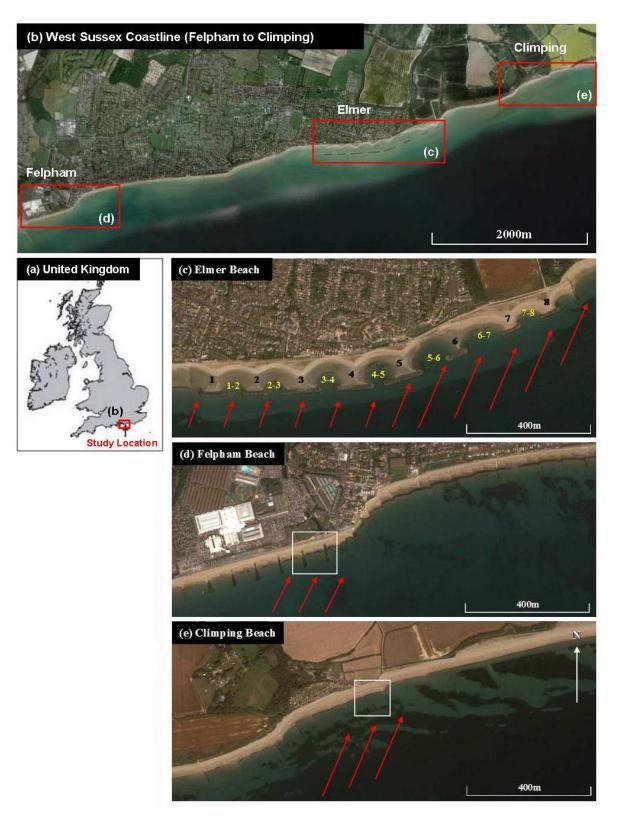


Figure 2.1 Location of the study location in relation to (a) the United Kingdom and (b) the south coast of England for (c) Elmer Breakwater Scheme, (d) Felpham Beach, and (e) Climping Beach. Photos taken from Google Earth: Image ©2007 DigitalGlobe. Red arrows denote the average predominant wave direction. White boxes (b & c) show study area within the beach. Yellow number in (a) are the names for each of the bays, and the black numbers the breakwater/tombolo number. Photos relative to north.

Two further sites were chosen; the first was on the Felpham frontage (WGS84: 50°47'01.95 N, 0°39'32.14 W - 50°47'02.70 N, 0°39'27.30 W) (Fig. 2.1d), approximately 3 km west of Elmer, which consisted of a series of seven rock groynes (~ 75 m long) in the order of 100 m apart and built in 1998. The second at Climping Beach (WGS84: 50°47'51.50 N 0°34'18.85 W - 50°47'52.23 N 0°34'14.40 W) (Fig. 2.1e), approximately 1 km east of Elmer, consisted of a series of sporadic small wooden groynes with large expanses of sand (50 m to > 200 m) between each one. High wave energy and a large tidal range (6m, Plomaritis 2006) were common features at all three study sites in this area.

Elmer was chosen as the focal study site as it was the only LCS scheme of its kind and magnitude along the south coast and one of only a few in the UK. From a logistical perspective, the location of the scheme in the intertidal zone allowed easy access to the structures for the study as they were completely uncovered at low tide. The relative proximity of Elmer to the University of Southampton also allowed frequent field visits to the breakwaters. Felpham was chosen as a comparative site, as being so close in proximity (within 2 km); it was subject to the similar large scale environmental conditions, such as wave climate, geology, sedimentology, bathymetry and tidal regime. Like Elmer, the groynes were made of Norwegian granite; this allowed comparisons to be made because of similarity in structure material. The CDSs differed from those at Elmer, in that the groynes lay almost perpendicular to the land, with a southeasterly aspect and were younger in age (by 4 yrs). The beach consisted of sandy sediment below the mid tidal level and was superseded with shingle, whilst above this there was a concrete and tarmac walkway. The second comparative site was at Climping, which also experienced similar large scale environmental conditions to Elmer and Felpham, but with wooden groynes instead of granite. On the south coast of England there are no undefended beaches (that could have been used at control sites) in close proximity to Elmer beach (within a 30 km radius) that are exposed to similar environmental conditions (e.g. wave exposure, tidal currents, hydrodynamics, etc).

2.3 Beach Morphology

Lidar data (metres Ordnance Datum Newlyn (ODN \pm 0.05 m)) for Elmer Beach (recorded on 12th June 2006) were obtained from the CCO (no data was available for Felpham and Climping. ArcMap® (version 9.1) was used to model the cross-shore beach morphology (Fig. 2.2).

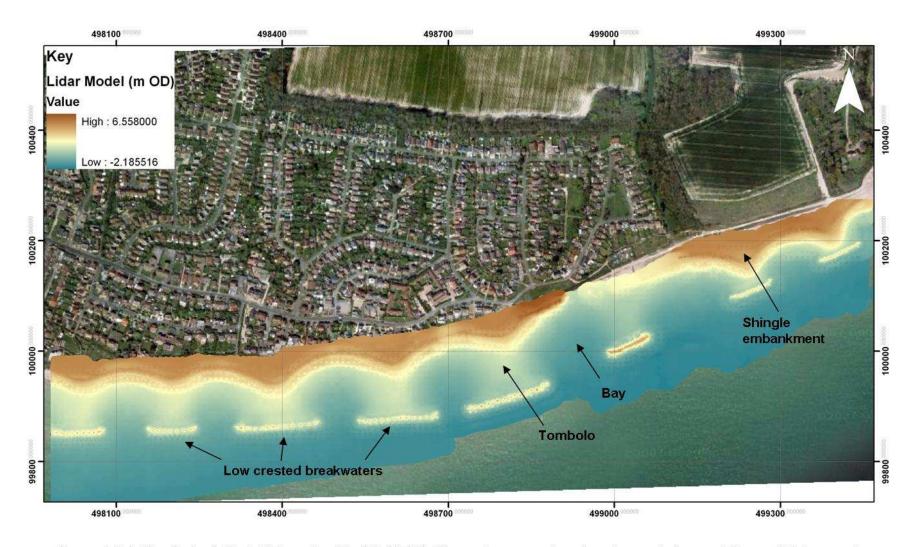


Figure 2.2 Lidar-derived Digital Elevation Model (DEM) illustrating cross-shore beach morphology at Elmer. DEM created in ArcGis and is in British Grid.

It can be seen from the DEM (Fig. 2.2) that the shore elevation was higher behind the low crested breakwaters than between the breakwaters. The elevated areas behind the breakwaters are known as tombolos. Tombolos are a build up of sediments that have been created artificially during construction of the breakwater scheme and maintained by the localised currents within the scheme (see Chapter 1, Section 1.6.2.1). The areas between the breakwaters are semi-circled bays with lower beach elevations than the tombolos (Fig. 2.2).

In this thesis, the spatial variation in decaying macroalgae deposits (Chapter 3) and benthic macrofaunal communities (Chapter 5) were investigated; this was done by randomly choosing four bays and four tombolos (for their location see Fig. 2.3) because of the their differences in horizontal shore beach morphology. The shore profiles down the bays adjacent to the granite breakwaters were clearly concave (Fig. 2.4). Bays 4-5 and 6-7 had the most concave profiles; the beach height just behind the breakwaters on the landward side was approximately -1.0 and -1.5 m Ordnance Datum Newlyn (ODN), respectively higher than the same vertical position in bays 2-3 and 3-4. The shore profile of the tombolos showed a gradual decline in elevation with a slight convex nature (Fig. 2.4). Tombolos 2 and 4 were similar in profile; the beach elevation was approximately 4 m ODN at the upper shore (before the shingle embankement) and 1m ODN just behind the breakwater on the landward side. Tombolo 6 exhibited the lowest shore elevation from the upper shore (2 m ODN) to the breakwater (0.2 m ODN), whilst tombolo 8 was the steepest and highest, as the breakwater was closer to the shingle embankment than the other structures (Fig. 2.2). On the seaward sides of the breakwaters the elevation was lowest in front of structures 4, 6 and (Fig. 2.4 f and g), with a shore height of approximately -2 m ODN. Whereas, on the seaward side of structure 2 the elevation approximately –1 m ODN.

The field survey design employed to investigate the macroalgal deposits and benthic communities also assessed three vertical shore levels: two on the landward side (upper and lower) of the breakwaters and one on the seaward (see Fig. 2.5 for their location). The cross-shore beach profiles for each vertical shore level are shown in Figure 2.6. It is clearly illustrated that the shore height oscillates on the landward sides of the breakwaters, between the tombolos and bays (Fig. 2.6). The lower landward demonstrated the largest fluctuations in shore elevation over the shortest distances, for example the top of tombolo 4 had a shore height of approximately 1.25 m ODN, whilst the centre of bay 4-5 had a shore height of –0.75 m ODN, a difference of 2 m over a distance of approximately 50 m (see area (b) in Fig. 2.6).

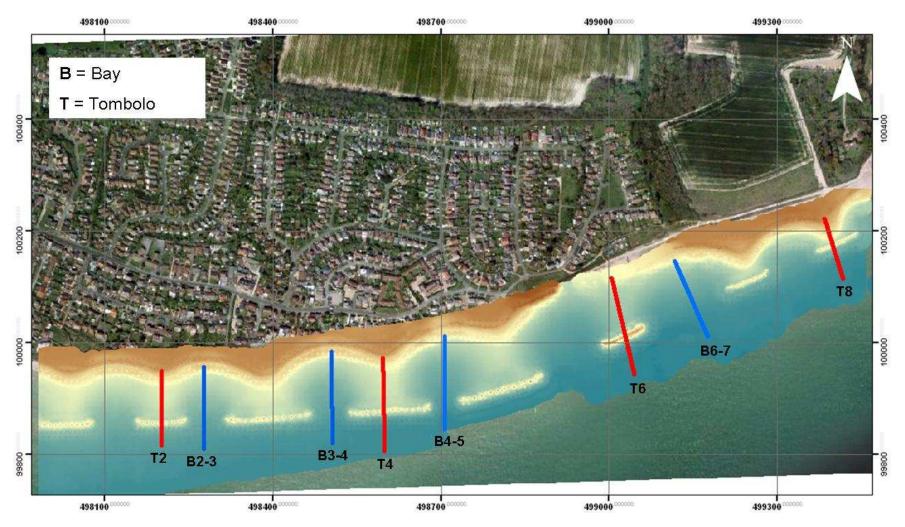


Figure 2.3 Lidar-derived Digital Elevation Model (DEM) illustrating cross-shore beach morphology at Elmer. Vertical shore transects (Red = Tombolos; Blue = Bays) for the areas sampled during field surveys for decaying macroalgae (Chapter 3) and sediment faunal communities (Chapter 4). Model in British Grid.

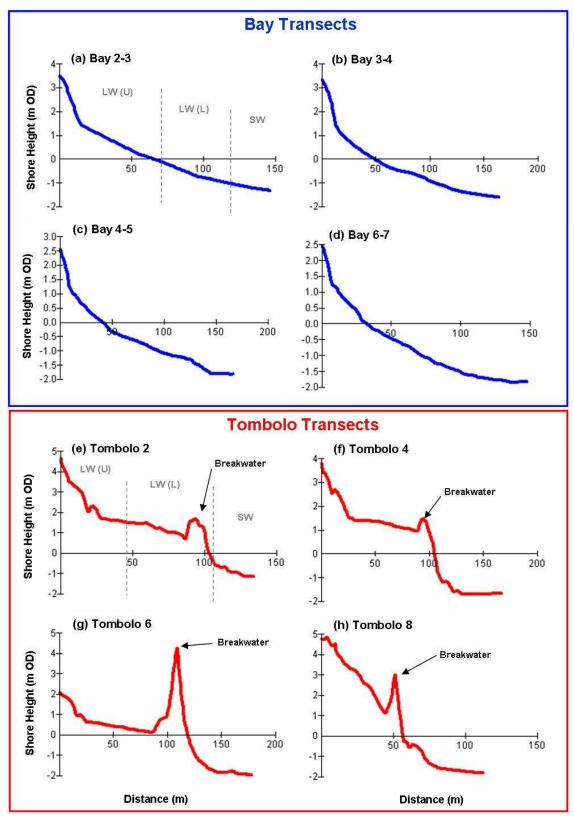


Figure 2.4 Figures (a) – (e) illustrate the vertical (up shore) beach profiles for the four bays and four tombolos that were surveyed for the spatial patterns in decaying macroalgae deposits (Chapter 3) and benthic macrofaunal communities (Chapter 4) at Elmer. The beach morphologies are derived from the lidar-derived DEM in **Figure 2.3** using ArcGIS. X axes (distance, m) and Y axes (shore height, m OD) scales are different.

In the upper landward level of the beach, the difference in shore height between tombolo 4 and bay 4-5 is acute (approximately 3.5 m over 100 m distance), though not as much as in the lower landward shore level of the same bay and tombolo (Fig. 2.6). A notable difference between the tombolos, is the shore elevation of tombolo 6 in the upper landward shore level that was sampled was less than the lower landward elevation, which was not the case for any of the other tombolos (see area (c) in Fig. 2.6). Tombolo 8 had the greatest shore elevation in the lower landward shore level, with an estimated height of 2.5 m ODN; this was approximately 1 to 2 m higher than the other tombolos (see area (d) in Fig. 2.6).

The shore height on the seaward sides of the breakwaters did not illustrate the prominat oscillating pattern of the landward sides. The general trend observed is that the shore was more elevated on the western end of the scheme becoming deeper by the eastern end, before rising on the eastern side of breakwater 8 (Fig. 2.6). Very small oscillations can be seen in the profiles for the seaward side, this is not the shore, but since the lidar data points are recorded in grid format with 10 m spacing between sample points, the data expresses this.

2.4 Wind and Wave Climate

2.4.1 General Wind and Wave Climate

Shoreline wave exposure increases gradually eastward from Pagham to Shoreham (Mouchel Consulting Ltd 1997). The study area has high energy beaches and is predominately exposed to southwesterly winds. The sheltering effect of the Isle of Wight limits waves arriving from the south-west. In response to the gently sloping bathymetry at Elmer, the waves reach the coastline with very small angles of approach; this is especially characteristic of waves arriving from the southeast direction, which are more normally aligned to the shore (Burcharth et al. 2007). The area experiences substantial wave focusing and this, together with other environmental factors, produces a regime of increased wave height and potential for flooding (Green 1992). Jelliman et al. (1991) examined wave conditions at Littlehampton as part of a national study, attempting to predict future wave climates in the context of relative sea-level rise and climate change. They found that 40 % of waves (1974 - 1990) came from the west or south west, with a mean significant wave height (H_s) of 1.8 m.

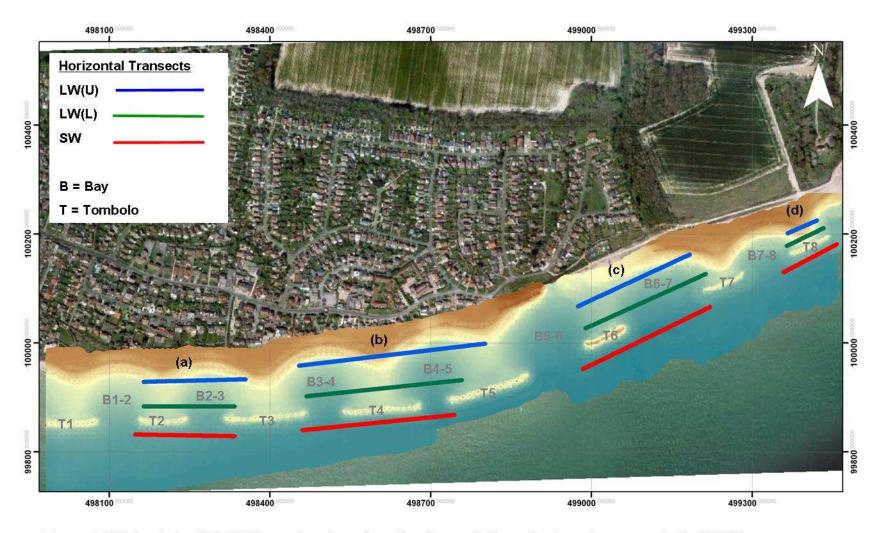


Figure 2.5 Lidar-derived DEM illustrating along shore beach morphology. Horizontal transects in the LW(U) - upper landward; LW(L) - lower landward; and SW – seaward levels of the beach. Transects (a) cross Tombolo 2 and Bay 2-3, (b) crosses Bay 3-4, Tombolo 4 and Bay 4-5, (c) crosses Tombolo 6 and Bay 6-7, and (d) crosses Tombolo 8. See **Figure 2.6** for the cross-section shore profiles. Tombolo and Bay numbers in grey. Model shown in British Grid.

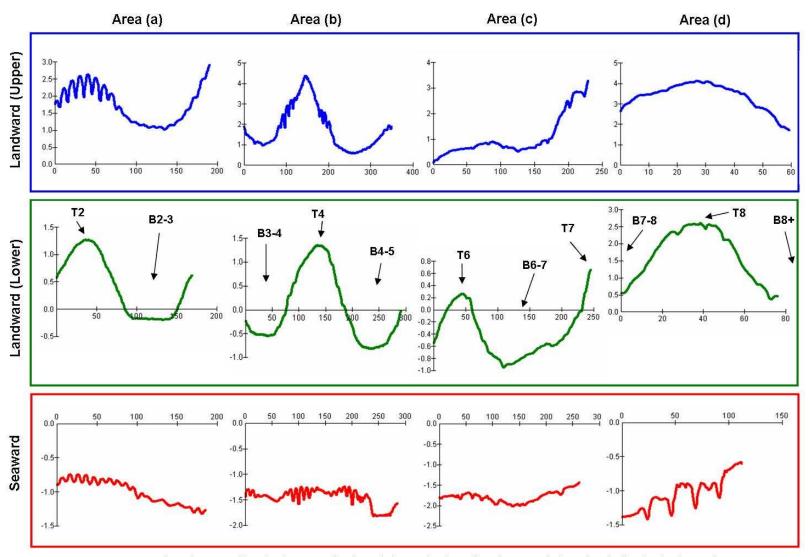


Figure 2.6 Cross-section shore profiles in the upper landward, lower landward and seaward shore levels for the horizontal transects (for areas (a), (b), (c) and (d) shown on the lidar-derived DEM **Figure 2.5**. The locations of the relative Tombolos (T) and Bays (B) are illustrated. X axes (distance, m) and Y axes (shore height, m OD) are different scales. Data derived from the DEM in ArcGis.

The wave climate over the study area contributes considerably to the prevailing hydrodynamics, especially for the coastal regions; as such, it has formed the main focus of the studies undertaken, prior to the construction of the low crested breakwater scheme (Burcharth et al. 2007).

2.4.2 Measuring Wave Climate

Exposure to wave attack can be defined on the basis of three simply-defined exposure categories (Channel Coastal Observatory 2003): low, medium, and high exposure. Low exposure areas have wave conditions that are generally very small and significant wave heights are unlikely to exceed 1 m; medium exposure tend to be fetch limited; high exposure areas are where nearshore conditions (H_s) regularly exceed 2 m. The predominant angle of wave attack also determines exposure levels.

Wave measurements were obtained from the Channel Coastal Observatory (CCO), Southampton for the period 1st January 2005 to 22nd December 2006 for comparison with all the ecological surveys carried out. They were recorded from a Datawell Directional WaveRider Buoy Mk II (Depth 9.9 m) off Rustington (7.7 km off the coast and some 7 km east of Elmer) at 30 minute intervals (WGS84 50°44.0365' N 00°29.6765' W). For all parameters the 30 minute data recordings over the course of each day were averaged in order to have a more manageable data set.

The parameters recorded were: significant wave height (H_s) , maximum wave height (H_{max}) , peak wave period (T_p) , zero up crossing period (T_z) and wave direction (Dir). The definitions for these parameters are as stated by the Channel Coastal Observatory: " H_s " (m) is the average height of the highest one-third of waves at a location during a wave measurement period and equates to wave height. Storm events are defined as significant wave heights (H_s) that exceed 3m (Fig. 2.7). " H_{max} " (m) is the highest wave (crest to trough) in metres recorded during a wave measurement period; " T_p " (s) is the peak wave period in seconds, being the wave period at which the highest wave energy is centred; " T_z " is the zero up crossing period. "Dir" (degrees) is the direction of waves with the highest energy (i.e. the direction of the waves of period T_p); it defines the direction from where waves come from and is measured clockwise from magnetic

north (e.g. 270° means waves are approaching from the west). In addition to calculating the mean values of H_{max} and H_{s} , the maximum, minimum and range were also calculated.

2.4.3 Wave Climate Measurements

The average significant wave height (H_s) at Elmer and Felpham from January 2005 to December 2006 was 0.75 m, reaching 4.81 m in the winter 2006. Wave attack was the least in both summers 2005 and 2006 (Table 2.2 & Fig. 2.7), and were recorded as being around 2 m (H_s) ; the coastline can be classified as being highly exposed (according to the CCO). There were no storms in the spring 2005 and both summers 2005 and 2006 (Table 2.2, Fig. 2.7). Seven storm events occurred over the two year period; the most severe storm was in December 2006 with a maximum significant wave height (H_s) of 4.81 m. Autumn 2005 and winter 2006 had significant wave heights greater than winter 2005 (Table 2.2).

Table 2.2 Seasonal mean and maximum wave data measurements. H_s = Significant wave height, H_{max} = Maximum wave height, T_p = Wave length, T_z = zero crossing period, SST = Sea surface temperature. Data recorded by Rustington WaveRider Buoy from 2005 – 2006 and provided by the Channel Coastal Observatory.

	$H_{\rm s}$	$\mathbf{H}_{\mathbf{s}}$	H _{max}	H _{max}	T _p	Tz	Direction	SST
Season	(mean)	(max)	(mean)	(max)	(mean)	(mean)	(mean)	(mean)
Season	(m)	(m)	(m)	(m)	(s)	(s)	(°)	(°C)
Winter 05	0.89	3.37	1.35	6.07	6.23	3.69	197	8.0
Spring 05	0.59	2.09	0.91	3.81	6.70	3.68	194	8.6
Summer 05	0.55	2.42	0.86	4.13	5.21	3.36	200	17.8
Autumn 05	0.82	3.64	1.27	5.90	6.34	3.68	193	15.9
Winter 06	0.87	3.84	1.34	6.63	7.54	3.90	185	7.7
Spring 06	0.80	3.18	1.23	5.22	6.36	3.76	195	8.9
Summer 06	0.50	1.94	0.78	3.59	4.83	3.25	195	18.1
Autumn 06	1.00	3.19	1.56	5.97	6.61	3.86	196	16.2

The dominance of waves in 2005 were from the south west with 77.2 % of the annual waves approaching from between 180° to 240° (Fig. 2.8); these waves also represented the highest wave heights, reaching up to 4.8 m. Some 20 % of the waves approached from a south-easterly direction (100° to 180°), with maximum wave heights of 2.2 m. The direction which corresponded to the greatest wave heights (H_s) was the sector 200° to 220° , with a maximum significant wave height of 4.9 m and a wave period of 9.2 sec in December 2006 (Fig. 2.8a-c).

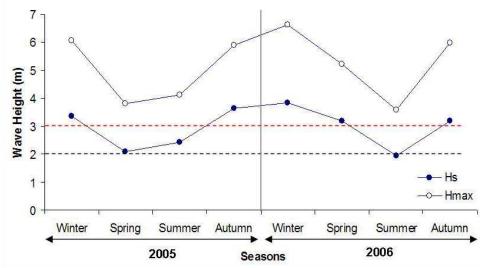


Figure 2.7 Seasonal exposure to wave attack (max H_s) and maximum storm wave heights (H_{max}) at Elmer, Felpham and Climping. Data recorded from Rustington WaveRider Buoy. *Black dotted line* (2 m) = high exposure threshold (H_s); *red dotted line* (3 m) = storm threshold (H_s).

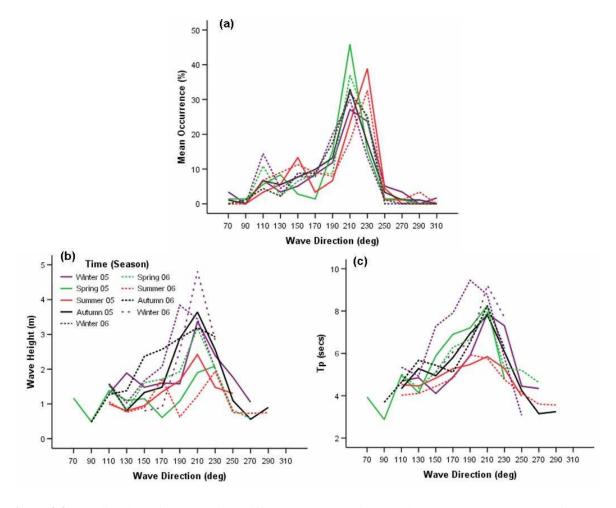


Figure 2.8 The direction of waves during different seasons against (a) the percentage occurrence of waves approaching from different directions; (b) the maximum significant wave height (H_s) of waves; and (c) the wave period (T_p) . Data collected from Rustington WaveRider Buoy, CCO. Key (b) applies for (a) & (c).

There were differences between seasons in both wave direction data and maximum significant wave height (Table 2.2), with consistent seasonality between the two years (2005 and 2006) in wave direction (Fig. 2.8a). The average wave direction was 195° (\pm 0.44). Spring had the least variability in wave direction with the highest percentage occurrence of waves from 180° to 220° , 18 % higher than the annual average (Fig. 2.8). There was a shift in the summer from the principal wave direction in the summer months of both years (Fig. 2.8a), with the waves predominantly arriving from a more south-westerly direction (220 to 240°) than other times of the year (200° - 220°).

The average maximum wave heights in the spring and summers were diminished in comparison to the winters and autumns (Table 2.2). Whilst, larger maximum wave heights were recorded in winter 2007 compared to winters 2006 and 2007 (Fig. 2.8b). The wave period (T_p) together with the wave height, dictates the strength of the waves. The wave period also changed over the course of a year, with shortest wave periods in the summers and the longest in winters (Table 2.2). The sector from which the longest wave periods came was 140° to 220° .

2.5 Hydrodynamic Environment

2.5.1 Tide and Current Characteristics

Tidal data were obtained from the British Oceanographic Data Centre (BODC) as part of the function of the National Tidal and Sea Level Facility, hosted by the Proudman Oceanographic Laboratory (POL) and funded by DEFRA and the Natural Environment Research Council (NERC). Data were obtained from the nearest recording tide gauge (National Network gauge in Newhaven). Current characteristics could only be obtained for the low crested breakwater scheme at Elmer from a previous study, which recently carried out on the sediment dynamic processes in the vicinity of the scheme (Plomaritis 2006).

Elmer is located within a macrotidal environment, with a semidiurnal tide. During spring tides there is a tidal range of 6.01 m, whilst during neap tides, there is a tidal range of 4.17 m (Plomaritis 2006). The tidal excursion (~ 600 m, during springs) extended beyond the structures at both Elmer and Felpham; as a result, the structures are exposed completely at low water. During high water, they are not completely submerged and have a freeboard of 0.45 m at mean

high water springs (MHWS) and 1.45 m at mean high water neaps (MHWN).

The offshore currents in the eastern English Channel rotate anti-clockwise, (in contrast to the western part, which rotate clockwise), with speeds not exceeding 1 m/s during spring tides (Pingree 1980). Near bottom (ca. 30 cm above the bed) tidal current velocities close to the coastline are much lower (ca. 0.3 m/s during spring tides) running in a general east-west direction in the offshore areas. In the intertidal zone in this coastal cell, currents almost always flowing in a westerly direction, increasing speed from east to west (Plomaritis 2006). However, the flow direction appears to reverse under strong superimposed wind energy conditions (Pingree 1980), and similar results have been observed in the close vicinity of the structures (Pope 1997). This flow reversal is an important factor controlling the net sediment transport (i.e. longshore drift) close to the breakwaters (Plomaritis 2006). Sterlini (1997) observed the general water circulation pattern inshore of the breakwaters to be characterised by an east-west orientation. Through further investigation, Plomaritis (2006) found tidal currents accelerated as they flowed over the salient features (tombolos) enhancing the sediment mobility; this mechanism is thought to control the salient growth behind the structures. Peak tidal currents coincide with high water and the beginning of the ebb (Plomaritis 2006). The magnitude of these currents depends upon the direction of wave approach and their characteristics; the maximum speed is 0.45 m/s during spring tides.

It is important to understand the tidal current regime within the scheme at Elmer, as these may have strong influences on any relationships between sediment infaunal communities and deposition of decaying algae. The breakwaters are located in the lower intertidal (see Table 1.2 for position), where submersion of the intertidal zone occurs on average from 3 hours before, to 3 hours after high water. The speed and direction of currents change across the scheme throughout this tidal period (Plomaritis 2006). The anticlockwise rotation and the progressive nature of the tide over the area, produce a westerly peak flow at high water (Plomaritis 2006). Tidal flow and flow acceleration over the tombolos and through the gaps of the scheme were modelled (based on field data) by Plomaritis (2006). The findings are summarised for spring tides in the following two sections (also see Fig. 2.9). During neap tides the patterns are generally similar to the spring tides, with similar flow direction but reduced peak intensity (35 - 40 %); the flow maximum (0.3 m/s) occurs in the area just offshore of the breakwater.

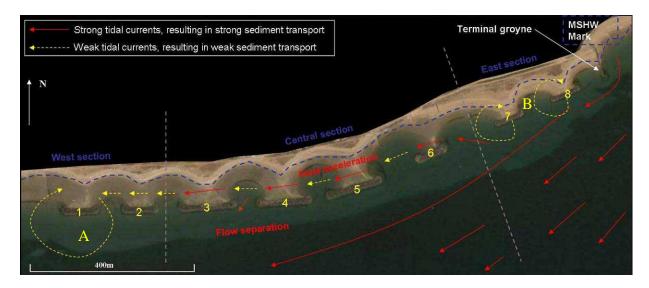


Figure 2.9 Illustration of Plomaritis's (2006) conceptual model of the local tidal currents during high water and their resultant sediment transport (i.e. longshore drift) for the entire scheme at Elmer (identified on the basis of numerical modelling).

2.5.2.1 Flow over tombolos

During the flood phase of the tidal cycle (high water (HW) –3 h/–2 h) of the tidal cycle, currents flow north-easterly, with current speeds of less than 0.25 m/s. One hour before high water, the current speed increases (ca. 0.35 m/s) and the flow direction changes rapidly to generally westwards, although the breakwaters influence the exact direction. Flow speeds are particularly strong around the tip of the terminal groyne, behind structure 5 and on the west end of structure 6, reaching speeds of 0.45 m/s (Fig. 2.10). During this time-period (HW –1h), the water level is greater than the tombolo elevation and all the breakwaters are detached from the coastline. The increased gap lengths and water depths over the eastern part of the scheme (e.g. between breakwaters 6 and 7), combined with the coastal configuration, allow the tide to enter and flow between the breakwaters and the coastline (Fig. 2.9). The presence of the breakwaters, together with the decrease in water depth caused by the tombolo in comparison with the bays, forces flow acceleration over the tombolos. This phenomenon is more intense over the central part of the scheme (structures 4 and 5, Fig. 2.10), where the offshore distance of the breakwater is greater and there are smaller gaps between the structures (Table 2.1).

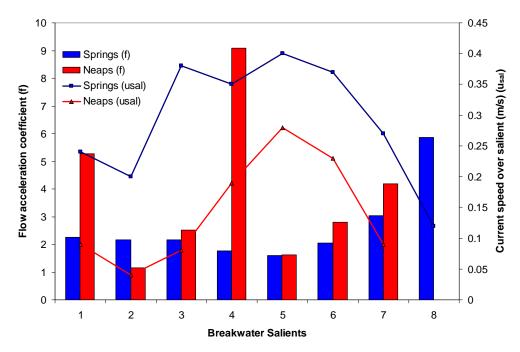


Figure 2.10 The acceleration factor (f) of the tidal current with the current speed over the salient (u_{sal}) for all the breakwaters at high water (HW) during spring (blue) and neap (red) tidal conditions (for breakwater location see Fig. 2.4). Data from Plomaritis (2006).

During the hour of high water and one hour after, the flow magnitude increases further still, however, the flow direction remains constant and the patterns described above are maintained. Speeds reach > 0.5 m/s on the leeward side of the structures, as well as on the landward side of structure 5; speeds of between 0.38 and 0.42 m/s on the landward side of structures 4 and 6 are reached. The gaps between the structures, with the exception of between 6 and 7, experience reduced currents (< 0.2 m/s) throughout the cycle. Over this part of the tidal cycle there is a distinct deceleration of the flow from the east to the west of the scheme.

The acceleration of the tidal currents was more intense around high water spring tides over the central part of the scheme (breakwaters 3 - 6), with the exception of over breakwater 4. The flow accelerates and decelerates rapidly with its peak located at the top of the tombolo; as a result the maximum velocities are confined to a small area behind the breakwaters. The magnitude of the acceleration follows the trend of the offshore tidal flow, decreasing from east to west. The bays are not influenced substantially by the accelerated tidal flow; this is related to the deceleration after the salient. The turbulence, however, generated by these unsteady flows can be significant. As a result of these conditions, there is a weak secondary clockwise flow in the central part of the bay during high water.

2.5.2.2 Flow through breakwater gaps

During spring tides, there are differences in the magnitude of the flux between the central (3-4 and 4-5) and the western gaps (1-2 and 2-3) (Fig. 2.11a). The central gaps (3-4 and 4-5) experience strong onshore flush, around 0.3 m³/s/m of water two hours prior to HW; resulting in weaker flow acceleration farther westwards down the scheme. During neaps, although the flux through the gap 4-5 follows the same pattern, this is not the case for gap 3-4; this behaved in a similar way to the westerly gaps (1-2 and 2-3). Plomaritis (2006) stated that this was due to the fluxes through the gaps being related to tidal range, particularly with the gap between breakwaters 3 and 4; the flux volumes change significantly when the tidal range decreases. The flux pattern through the gaps provides an indication of the tidal current speeds over the salients. During spring tides, together with the limited width of the gap between breakwaters 4 and 5 (the smallest throughout the scheme, at 30m) the flow was forced to accelerate over the salient (breakwater 4); likewise, to exit the scheme through the next gap (3-4).

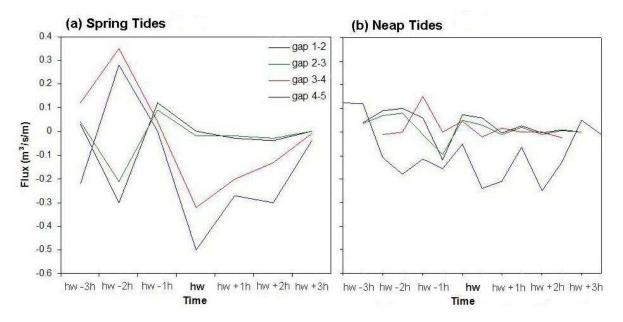


Figure 2.11 Water fluxes through the breakwater gap for the western and central part of the scheme, during (a) spring and (b) neap tidal conditions. Positive flux values represent onshore, whilst, negative values represent offshore fluxes (for gap location see Fig. 2.9). Data from Plomaritis (2006).

The construction specifications play an important role in the morphological evolution of the beach at Elmer (King et al. 1996). In particular, the acceleration in the tidal currents results in a significant increase in the local sediment transport, which effectively regulates the growth of the tombolos. At the same time, a weak clockwise circulation is observed within the inner central

part of the bays (Fig. 2.9); however this does not produce any sediment transport. The terminal groyne at the eastern end of the scheme obstructs the tidal currents, forcing them to change direction; resulting in low tidal current speeds. Where there are large gaps between breakwaters (5-6 & 6-7) and the breakwaters are located farther from the coastline, a large volume of the tidally-induced flow is retained behind the breakwaters. Flow within the landward part of the scheme is channelled by the breakwaters and, at the same time, accelerates over the tombolos. This process takes place mainly over the central part of the scheme. This further restriction of the flow is not translated into a further flow acceleration; in contrast, there is weakening of the flow over the salient. This reduction is the result of a significant loss of water, through flushing at the gaps. The intensity and area of influence of the tidal flow over the tombolos, is controlled by the tidal prism and the gap widths. Plomaritis (2006) stated that the bays are influenced by wave activity, whereas, the protected areas (tombolos) are dominated by tidal currents. The system appears to be in a dynamic equilibrium, whereby the build-up of the tombolos by wave activity in the bays is being regulated by the tidal currents.

2.6 Sediment Environment

2.6.1 *Geology and Sedimentology*

The regional geological substratum of the beaches in the study area consists mainly of bedded Upper Cretaceous chalk. The in-situ chalk is generally in a highly weathered condition. Patches of reconstituted chalk can be found over the eastern end of the site, as well as coarse-sized gravel and cobble layers of black flint (Robert West & Partners 1991). The upper beach is relatively steep and flat-crested and has a noticeable upper storm berm. This is composed predominantly of poorly-sorted shingle and coarse flint gravel with a median diameter of 20 mm (Cooper et al. 1996a, King et al. 2000). In many areas of the coast the storm berm is mainly replenishment material e.g. Climping Beach. The lower beach is less steep forming a low gradient foreshore extending for several hundred metres seaward to low water; this generally consists of a poorly-consolidated layer of sand, with a 115 µm median grain size, with chalk pebbles and boulders (Mouchel Consulting Ltd 1997). Overall, the beach profiles are convexoconcave in form (Cooper et al. 1996a). In the extreme lower intertidal zone (seaward of the breakwaters), the lack of sedimentary material is demonstrated by the presence of a chalk outcrop running parallel to the coastline. Intensive management involving the holding of a

largely fixed line of coastal defence for the past 100 - 150 years has inhibited the natural tendency for landward migration of the shoreline. It has greatly reduced the supply of fresh sediments from coastal retreat and extensive groyne fields have intercepted much of the drift of gravels and coarse sand on the upper beaches. In addition, gravel recharge, re-cycling and bypassing supported by carefully designed and maintained control structures now largely control sediment transport and attempt to maintain beach stability.

2.6.2 Sediment Transport

Sediment transport pathways in the close vicinity of the breakwater scheme at Elmer are related directly to the prevailing hydrodynamics, which affects the morphological development of the area (Plomaritis 2006). Such processes include wave diffraction in the gap and between the breakwaters, leading to a reduction of wave action on the lee side of the breakwaters. This results in a water circulation system (Fig. 2.9), whose strength depends mainly upon the magnitude of the incident wave energy (Plomaritis 2006). As a result of the above hydrodynamic processes, there is a reduction in sediment transport on the lee side of the breakwaters and enhanced sediment transport in the gap. In addition, the combination of the asymmetrical tombolo flanks (where the upstream (easterly) slopes are steeper than the downstream) and the direction of the littoral drift results in sediment accumulation on the western side of the tombolos (Plomaritis 2006). The movement of sediments is substantially wave-induced, with tidal currents being insufficiently strong to move coarser sands and gravels independently. Rates of transport across the lower foreshore are likely to be higher than the upper shore because of lack of interruption by groynes and the finer grades of sediment leading to greater mobility.

Beach profile analysis, undertaken following the completion of the Elmer scheme (King et al. 1996) revealed an overall accretion to both the west (an increase in beach volume of around $5000 \text{ m}^3/\text{yr}$) and central parts of the scheme (ca. $9000 \text{ m}^3/\text{yr}$) (Fig. 2.1). Throughout the remainder of the scheme (under the Environment Agency) the beach volume was reduced by $3500 \text{ m}^3/\text{yr}$.

Plomaritis (2006) identified permanent flow features within the scheme (Fig. 2.9), these are likely to be of importance to the ecology of the system. There are low velocities to the landward

of the breakwaters; flow acceleration in the area of the salients; and flow acceleration and eddy formation at the tip of the terminal groyne. A larger-scale feature is the flow separation at the Elmer headland in the final stages of the ebb; this influences tidal flow only in the area of the two western breakwaters (1 and 2). The widths of the gaps between the structures are extremely important controlling mechanisms, since they regulate the water flushing; this, in turn, is related to the magnitude of the flow acceleration. The processes described above separates the scheme into three sections (Fig. 2.9): (i) a western part (breakwater 1 and 2), influenced by the large headland eddy (A); (ii) a central part (breakwaters 3 to 6), with increased tidal acceleration over the salients; and (iii) an eastern part (breakwater 7 and 8) influenced by the presence of the terminal groyne, associated with an eddy (B).

2.7 Sea Surface Temperature

The sea surface temperature (SST) in Celsius (°) was measured by the same Datawell WaveRider Buoy off the coastline at Rustington that the wave measurements were recorded by. The data was treated as with the wave data, where 30-minute interval data was averaged for each day (Fig. 2.12). The SST showed seasonality as expected, but importantly there were annual variances, for example the mean temperature in winter 2006 was lower than in winter 2005 (Table 2.2). The coldest period was in March 2005 at 5° C (Fig. 2.12), followed by a gradual increase until it flattened out between July and September at around 18° C, before dropping rapidly from November (15.5° C) to December 2005 (7.5° C). An important annual difference in temperature can be seen at the end of July (Fig. 2.7), with the SST being 2° C warmer in 2006 than it was in 2005.

2.8 Ecology of the Surrounding Area

The intertidal zone is typical of moderately exposed sandy shores. Polychaetes and amphipods dominate the infaunal assemblages. In particular, the most common species are the lugworm *Arenicola marina* and amphipods such as *Bathyporeia* spp. In the extreme lower intertidal natural boulder fields and rocky outcrops are colonised by ephemeral algae (*Ulva* spp. and *Enteromorpha* spp.), gastropods (slipper limpets, *Gibbula cineraria* (Linnaeus 1758)), crustaceans such as amphipods, shrimps and crabs, and benthic fish (gobids). The subtidal

sediments are a mixture of sand, shingle and rocky areas. There is no known published literature on the ecology of the subtidal communities off Elmer Beach.

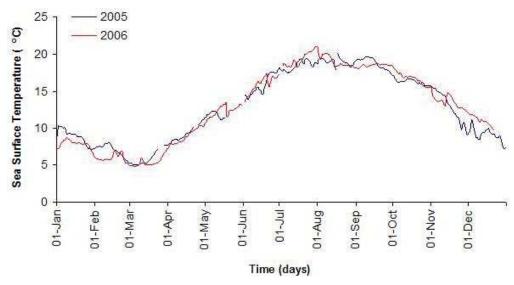


Figure 2.12 Sea-surface temperatures from Channel Coastal Observatory archive time series data recorded off Worthing for 2005 and 2006.

Chapter 3: Temporal and Spatial Patterns of Decaying Macroalgae Deposits

3.1 Introduction

Macroalgal production plays a key role in coastal ecosystems (Van der Merwe & McLachlan 1987, Everett 1994, Norkko & Bonsdorff 1996a, Polis & Hurd 1996, Raffaelli & Hawkins 1996, Adin & Riera 2003), being consumed in situ and exported as detritus. Macrophytes may be detached and transported as a result of a range of coastal processes, including tidal currents, waves and storms (Ochieng & Erftemeijer 1999, Orr et al. 2005). This detrital material may be washed into the surf zone and deposited in varying quantities throughout the entire range of intertidal habitats including sandy beaches, salt-marshes, sandflats, and rocky shores with important ecological consequences. Patches and banks can be formed and are subsequently exposed to wind, sun, fragmentation, leaching and decomposition (Lenanton et al. 1982), and end up as an important nutrient source (Hanisak 1993). Compared with rocky and estuarine mud-flats, exposed sandy beaches have very little in situ primary production (Inglis 1989, Brown & McLachlan 1990); their major sources of allochthonous organic material are phytoplankton and stranded marine macrophytes (macroalgae and seagrasses, e.g. Brown & McLachlan 1990, Dugan et al. 2003). The availability of intertidal detrital input depends on the amount and type of source intertidal and subtidal reefs. Changes in the input of algal detritus could shift infaunal community structure and alter energy flow to consumers and prey availability to higher trophic levels (Dugan et al. 2003).

Several studies have investigated the occurrence of macroalgae detritus (e.g. Van der Merwe & McLachlan 1987, Ochieng & Erftemeijer 1999, Piriz et al. 2003, Table 3.1), for example, on mobile surf-zone communities (e.g. Robertson & Lenanton 1984, Van der Merwe & McLachlan 1987) and in particular, the 'strandline' on the upper shore (e.g. Dugan et al. 2003, Olabarria et al. 2007). Both these communities depend upon oceanographically transported allochthonous inputs to deliver nutrients (Dugan et al. 2003). For example, it has been shown that macroalgae deposits alter community structure by providing food (Pennings et al. 2000) and refuge habitats (Norkko et al. 2000) to a diverse and abundant component of the macrofaunal communities (Inglis 1989, Colombini et al. 2000, Dugan et al. 2003). Furthermore, the release of nutrients

following bacterial decomposition alters the sediment chemistry (Rice & Tenore 1981, Pellikaan 1984, Tenore et al. 1984). The spatio-temporal variability in the supply of this algal detritus affects the distribution and zonation of the communities inhabiting the upper shore levels of exposed sandy beaches (Koop & Griffiths 1982, Stenton-Dozey & Griffiths 1983, McGwynne et al. 1988a, Dugan et al. 2003). The degree to which this 'spatial subsidy' has consequences for intertidal and supralittoral macrofauna depends on the species composition and the quantity of beach-cast detrital material (Mews et al. 2006), as well as the frequency with which it is deposited.

The composition of detrital macrophyte (e.g. macroalgae, seagrasses) material is extremely variable and dependent on the supply from nearby rocky intertidal and subtidal macroalgal reefs and seagrass meadows. There have been several studies on the effect of the composition of detrital material on surrounding faunal species (e.g. Tenore et al. 1984, Marsden 1991a). For example, Crawley et al. (2006) found that changes in detrital macrophyte composition may influence fish abundances in the surf zone, as they may provide different habitat structures because of differences in plant structures. In the same manner that different macrophyte species will provide varied nutritional properties for feeding macrofauna such as amphipods (Crawley & Hyndes 2007).

To date studies investigating detrital macrophyte deposits on temperate beaches have mostly been in the southern hemisphere (Koop & Field 1980, Griffiths et al. 1983, Ochieng & Erftemeijer 1999, Piriz et al. 2003), with studies in the northern hemisphere (Malm et al. 2004, Orr et al. 2005) only occurring recently (Table 3.1). Whilst most studies have concentrated on relatively exposed sandy beaches (e.g. McLachlan & McGwynne 1986, Olabarria et al. 2007), a few have investigated the affects of these decaying macroalgal deposits on sheltered beaches (Malm et al. 2004, Orr et al. 2005). The input, turnover, and standing crop of macroalgae detritus on a sandy beach can be affected by many factors (Dugan et al. 2003).

Spatio-temporal patterns are highly variable and are highly dependent on the climate, hydrodynamics and the proximity of beaches to sources of drift macrophytes, such as rocky habitat and marine macrophyte beds (Ochieng & Erftemeijer 1999, Colombini & Chelazzi 2003). For example, an estimated 1,200 – 2,179 kg/m/yr of kelp wrack is stranded on beaches on the west coast of South Africa (Griffiths et al. 1983) and 1,900 kg/m/yr in Western Australia

(Hansen 1985, quoted in, McLachlan 1985). Far smaller quantities were found by comparison on beaches studied by Hayes (1974) in southern California, and Marsden (1991a) in southern New Zealand, with estimated inputs of 473 and < 400 kg/m/yr, respectively (Table 3.1).

An important question to consider is when do the greatest detrital algal depositions occur on beaches? Our understanding of the timings of macrophyte deposition will enhance our understanding of the ecological impacts on the surrounding ecosystems, as well as the implications of amenity management such as beach cleaning.

There is some disagreement in the literature, with conflicting results from those few published studies (Table 3.1); this results in a diversity of opinions on the subject. Most studies have only sampled detrital macrophyte depositions on one temporal scale, whether this is daily (e.g. Orr et al. 2005), monthly (e.g. Malm et al. 2004), seasonally (e.g. Crawley et al. 2006) or annually (Piriz et al. 2003, Malm et al. 2004) with a few sampling more than one temporal scale (Ochieng & Erftemeijer 1999, Piriz et al. 2003, Malm et al. 2004, Orr et al. 2005). The majority of these studies have made coincidental statements about the temporal distribution of this detritus, some as a result of studying other aspects such as macrophyte decomposition rates or harvesting effects (e.g. Lavery et al. 1999, Dugan et al. 2003), rather than to specifically study the variation in quantity and composition of decaying macrophyte deposition over a range of temporal scales (e.g. Piriz et al. 2003, see Table 3.1).

Algal material is prone to the dynamic removal from nearby subtidal reefs through tidal events (Orr et al. 2005). Tidal influence has had some attention in the literature, but remains incompletely understood. Tides could potentially have an effect at a range of temporal scales: daily (semidiurnal differences), weekly (semi-lunar), and monthly (lunar). Orr et al. (2005) found deposition rates differed according to the stage of the ebb tide, with the highest deposition in the first 90 min. Having also studied the daily variation within one tidal cycle, they concluded that decaying macrophyte deposition did not follow a predictable, daily pattern of deposition. With regards to the semi-lunar cycle, there is agreement that spring tides coincide with the greatest deposition in comparison with neaps (Ochieng & Erftemeijer 1999, Orr et al. 2005). Caution is needed, as many of these published statements are unsupported; there is often a lack of analysis to correlate tidal data with depositions, or insufficient sampling intensity (e.g. Lavery et al. 1999).

Table 3.1 Studies on measurements of decaying macroalgae deposits in the nearshore and intertidal zone. NS = not stated; N/A = not applicable.

Author	Date	Hemi- sphere	Country	Main focus of study	Temporal Scales: Biomass/Cover	Spatial Scale: Biomass/Cover	Tidal state	Exposure to wave action	Dominating Macrophyte	Max. Quantity Deposition	Temporal patterns
Koop & Field	1980	S	Kommetjie, South Africa	Population dynamics of <i>Ligia dilatata</i>	Monthly (<i>n</i> = 17)	HWS to LWS	NS	NS	Kelp	NS	Seasonal cyclicity: winter > summer
Marsden	1991	S	Canterbury, New Zealand	Decaying macroalgae composition and distribution related to sandhoppers	Neap tide, monthly (n = 12)	max high to low neap tide mark (n = 5 transects)	NS	Moderately exposed	Wood, grass, Macrocystis pyrifera & Durvillaea antarctica	Monthly average: 11.25 kg/ 5 m	Seasonal cyclicity: winter > summer
Ochieng & Erftemeijer	1999	S	Kenya	Seagrass Deposition - Spatial & Temporal Patterns	Weekly (n = 52) (semi-lunar cycle), included seasonality	high to low tide marks. 9.5 km beach	Semi- diurnal: Max 4m range	NS	Seagrass	93,000 kg dry weight over 9.5 km beach	Lunar cyclicity: Springs > Neaps
Lavery et al.	1999	S	W. Australia (estuarine)	Effect of Beach Cleaning	Monthly (n = 2) (before & after harvesting)	high to low tide marks	NS	NS	Green algae	NS	
Dugan et al.	2003	N	California, USA	Response of macrofauna and birds to decaying macroalgae deposits on beaches	Monthly (n = 2) Spring low tides	high to low tide marks: n = 3 transects, each beach (n = 15)	NS	Varying from sheltered to exposed	Macrcystis pyrifera (giant kelp) & Phyllospadix torreyi (surfgrass)	5.03 m ² /m (mean cover)	
Piriz et al.	2003	S	S. Patagonia, Argentina	Changes in biomass & composition of decaying macroalgae deposits for beach cleaning	Monthly & Annually (1992-1994)	Strandline 4.5 km beach	NS	NS	Assorted macroalgae, changes temporally	2500-12000 t/year/beach (wet weight)	Seasonal cyclicity: summer > winter
Malm et al.	2004	N	Sweden, Baltic Sea	Effect of Beach Cleaning	Monthly (n = 28) & Annually	Upper shore	None		Red algae	NS	Seasonal cyclicity: summer/autumn > winter/spring
Orr et al.	2005	N	Vancouver Island, Canada	Decaying macroalgae deposits - Spatial & Temporal Patterns	Daily (<i>n</i> = 11) Monthly (<i>n</i> = 2)	high to low tide marks (n = 3 transects, each beach)	NS	6 beaches: ranging from sheltered to exposed	Macroalgae: Variable depending on beach substratum	NS	Lunar cyclicity: Springs > Neaps
Crawley et al.	2006	S	SW Australia	Volumes & types of macrophytes in surf zones	Seasonal $(n = 2)$ autumn & winter	Surf zone	NS	2 beaches: moderately & fully exposed	Seagrass & macroalgae	944-1070 litres/ 100 m ²	

The temporal scale that has been most studied is seasonal; however, there are contrasts in the causes and hence time of these seasonal peaks in deposition occur. Ochieng and Erftemeijer (1999) found, after a year-round quantitative assessment along the Kenyan coast that larger amounts of deposited macroalgae were recorded during the rainy season, dominated by the South-East Monsoon (Mar - Oct) and minimal amounts during the dry season, dominated by North-East Monsoons (Nov - Mar). The rainy season produces the greatest magnitude of downwelling, wind speed, wind run/force, wave heights and water column. Seasonal deposition of beach cast material has also been reported for kelp detritus in South Africa (Griffiths et al. 1983) and detached macrophytes in Australia (Lenanton et al. 1982, Robertson & Hansen 1982, Crawley et al. 2006) and New Zealand (Marsden 1991a, b), where again deposition was highest during seasons when frequent storms increased the intensity and frequency of seas and heavy swells (i.e. autumn and winter) (Crawley et al. 2006). In contrast, Piriz et al. (2003) found after a two year (monthly samples) study in Argentina, that the greatest deposition of decaying macroalgae occurred in spring and summer, stating that this may have been related to the increase of nutrient inputs in the area. These findings concurred with those of Merwe and McLachlan (1987) elsewhere in South Africa.

The studies by Piriz et al. (2003) and Malm et al. (2004) have been the only investigations to date that have been long-term enough to investigate any annual differences in decaying macroalgae biomass. Piriz et al. (2003) found great variation in decaying macroalgae deposit biomass among years, ranging from 2500 - 12,000 t/yr/4.5 km beach (wet weight). This annual variability was also found by Malm et al. (2004), variations with three times more material during the autumns of 1999 compared with 2000 and 2001 were found. Potential reasons for these annual differences where not explored; although Malm et al. (2004) stated that the study needed to be repeated over a period of several years and correlated with temperature data to gain further understanding. Many authors have stated that large macrophyte deposits are related to storms and heavy swells (Lenanton et al. 1982, Griffiths et al. 1983, Inglis 1989, Kirkman & Kendrick 1997, Colombini & Chelazzi 2003), but none of these have provided correlating evidence of these deposits with wave or wind data for storms. All the studies apart from the recent study by Orr et al. (2005) have been qualitative statements based on coinciding storm seasons. In addition, the sampling frequency of these studies have not been frequent enough, or spatially replicated enough to properly establish which particular temporal scales have the greatest influence.

Few studies have investigated the temporal variation in decaying macroalgae deposit composition, which inherently may have implications for the receiving ecosystems. Ochieng and Erftemeijer (1999) found that the contribution of some seaweed species (i.e. *Sargassum* sp. and *Ulva* spp.) in the beach cast detrital material became prominent only during the beginning of the SE monsoon (March to May), when rains coincided with short periods of macroalgal blooming. In concurrence, Piriz et al. (2003) reported a succession in dominance over a period of seven years, potentially correlated with waste waters. The most comprehensive study to date is by Orr et al. (2005). They found that during the different stages of an outgoing ebb tide there were differences in the species composition deposited, which they believed was as a result of differing buoyancy properties between species. In addition, they found that there were differences in decaying macroalgae species composition depending on beach substratum type.

The temporal cyclicity of detrital algae depositions in the intertidal zone may not only have relationships with the tidal currents, winds and waves, but also with the composition of available macrophytes. Many seaweeds exhibit distinctive seasonal growth cycles (Luning 1993), which may be influenced by storms (Kain 1989). If the macrophytes are ephemerals, such as the green algae *Enteromorpha* sp., *Ulva* sp., and *Cladophora* sp. (Raffaelli et al. 1998), and also filamentous brown algae such as *Ectocarpus* sp. and *Pilayella* sp., then there are likely to be higher quantities in the spring and summer seasons, particularly in cold temperate areas when water movements are reduced and nutrient loads are increased (Kolbe et al. 1995, Kiirikki & Blomster 1996). Whereas, in areas dominated by large kelp species, senescence occurs in the autumn and winter periods (Dominik & Zimmerman 2006), so that there would be large deposits on beaches following strong swell and storms. Dugan et al. (2003) proposed that considering the depositional patterns of detrital macrophytes and other drift material (e.g. wood), together with other physical factors, such as hydrodynamics and sediment pathways, will allow a more complete understanding of the influence on the benthic infaunal community and trophic structure on exposed sandy beaches.

Little work has been done on how CDSs influence the spatial distribution and biomass of decaying macroalgae deposition. These structures could have strong influences on the spatial distribution of detritus, with subsequent consequences for the fauna that inhabit or utilise the deposited algae and underlying sediments.

Dugan et al. (2003) suggested that human activities and engineered structures, such as beach grooming and rock groynes and jetties, may affect beaches by cutting off longshore transport of drift littoral materials, thereby influencing the infauna associated with decaying macroalgae. Similarly, Ochieng & Erftemeijer (1999) suggested that the irregular spatial distribution of decaying macroalgae found along a 9.5 km stretch of Kenyan Coast indicated that coastal morphology (e.g. rocky protrusions) changes the hydrodynamics and therefore determines the distribution and deposition of sediments and drift macroalgae. Following both these studies, Orr et al. (2005) carried out a series of studies relating wave action and beach substratum to the amount and composition of deposited decaying macroalgae on beaches in Canada. They stated that both wave exposure patterns and beach substratum type govern algal deposition patterns, as well as decaying macroalgae species composition; they concluded that further understanding of this important aspect of marine-terrestrial nutrient and energy fluxes is warranted. Recent studies on the benthic communities surrounding LCSs (Airoldi et al. 2005, Martin et al. 2005, Moschella et al. 2005) have shown that the differences occurred within the beach communities, for example, exposure to wave action influenced communities differently between the landward and seaward sides of the breakwaters. The above findings (by Ochieng & Erftemeijer 1999, Orr et al. 2005), together with observations that there were larger quantities of decaying macroalgae at sites with LCSs in comparison with adjacent beaches (Martin et al. 2005 and Burcharth et al. 2007), brings attention that the depositional processes and spatial distribution of this detritus could be influenced by these artificial structures, with potential impacts for benthic infaunal communities. There could potentially be complex relationships between the arrays of environmental factors influencing the deposition and the influence this deposition has on the sediment fauna.

Despite substantial deposits of decaying macroalgae material on the beaches along the West Sussex coast near Bognor Regis, and the economic importance of these beaches for tourism, there have been no previous detailed studies of this phenomenon. Thus, the overall aim of this study was to compare the spatial and temporal variation in the amount of deposited algal detritus around three types of CDSs (granite offshore breakwaters, granite groynes and wooden groynes), thus, addressing whether the spatial and temporal patterns observed in other studies on exposed and sheltered beaches was displayed on artificially protected coastlines.

The three specific objectives were:

- 1. First, to investigate whether there were any seasonal or annual differences in the species composition of the macroalgae deposits around the LCSs at Elmer.
- 2. Second, to undertake a detailed study of the patterns of decaying macroalgae deposition at different temporal scales (diurnal, daily, weekly, monthly, seasonal and annual) between two of the breakwaters at Elmer, in order, to determine what environmental factors (waves and/or tide) may be causing the variations in these deposits.
- 3. Third, to describe quantitatively the spatial patterns of decaying macroalgal depositions around the low crested breakwaters on Elmer Beach, the main study site. The spatial patterns of macroalgal deposits on two nearby beaches with different types of CDSs were also studied. A detailed survey analysing monthly spatial distribution and quantity of deposited detrital macroalgae material on the West Sussex coastline was undertaken in order to test two null hypotheses:
 - **a.** Firstly, that there were no differences in the amount of decaying macroalgae deposited down the vertical shore (between the landward and seaward sides of the breakwaters) or horizontally across Elmer beach (between and within the bays and tombolos within the breakwater scheme) over time (seasonally and monthly); and
 - **b.** Secondly, that there were no differences in the quantity of decaying macroalgae deposited at different shore levels around the three different types of CDSs.

3.2 Materials and Methods

3.2.1 Study Location

The study area is a 3.5 km stretch of coastline located on the south coast of England, between Bognor Regis and Littlehampton (Fig. 2.1); it is protected from sediment erosion with three different types of CDSs (see Chapters 1 and 2 for detailed area description). Three beaches adjacent to three different types of coastal defence structures were compared: granite groynes at Felpham Beach, granite low crested structures within the breakwater scheme at Elmer Beach, and wooden groynes at Climping Beach. This area of coastline has a history of decaying macroalgae (all algae terms referred to hereon in is 'decaying macroalgae', as no seagrasses were present) being deposited on the beaches.

The area is macrotidal, with a semidiurnal subequal tide reaching up to 6 m at spring tides and a dominant west to east longshore drift (Pingree 1980, Plomaritis 2006). The beaches are predominately exposed to southwesterly winds and are often subjected to elevated wave energy (Cooper et al. 1996a, Plomaritis 2006) resulting in convexo-concave beach profiles with relatively steep and flat-crested upper beaches (King et al. 1996). The three beaches are all predominantly of poorly-sorted shingle and coarse flint gravel with a median diameter of 20 mm (Cooper et al. 1996b). The lower beaches have a low gradient foreshore extending for several hundred metres seaward to low water, generally consisting of a poorly-consolidated layer of sand (115 µm median grain size), with chalk pebbles and boulders (Cooper et al. 1996b). The subtidal substratum is a mixture of sand, shingle and rocky areas; with a rocky reef consisting of a variety of macroalgal species, referred to as 'Bognor Rocks' (Cooper et al. 1996b).

3.2.2 Sampling Programmes of the Decaying Macroalgae Deposits

3.2.2.1 Measurement of physical variables

Breakwater scheme engineering design

The engineering design of the breakwater scheme was not homogeneous across the scheme; the differences in breakwater length, distance from the mean high water spring (MHWS) mark, and gap width between breakwaters could potentially influence decaying macroalgal deposits. The design measurements (see Table 2.2) of the scheme (already discussed in Chapter 2) were used in the discussion in interpretation of the spatial patterns of decaying macroalgae deposits.

Beach elevation

Lidar data were obtained from the CCO for Elmer Beach and ArcMap (v.9) was used to illustrate the cross-shore beach elevation in the form of a Digital Elevation Map (DEM; see Section 4.2 for more details of the beach morphology). Global Positioning System (WGS 84 \pm 10 cm) points were recorded for each of the quadrats sampled during the spatio-temporal survey (see Section 3.2.2.5). These GPS points were overlaid on the DEM to illustrate the location relative to beach elevation.

Wave climate

Wave climate variables of significant wave height (H_s), maximum wave height (H_{max}), wave direction (Dir) and wave period (T_p), as well as sea surface temperature (SST) were obtained from the Channel Coastal Observatory (CCO), Southampton (for detailed analysis see Section 2.2.3); data were recorded in 30 minute periods by a Datawell Directional WaveRider Buoy Mk II (Depth 9.9 m) at Rustington (WGS84 50°44.0365' N 00°29.6765' W), the closest recorder to the study area. These variables were used in analysis with the species compositional and spatiotemporal surveys of decaying macroalgae deposits around the different CDSs. To do this, the average for H_s, Dir, T_p, and SST and maximum recordings of H_{max} and SST were calculated for the necessary temporal scale required. In addition, the frequency of storm events, defined as significant wave heights (H_s) exceeding 3 m (as defined by the CCO), was calculated. Average and maximum wave climate variables were calculated monthly and seasonally for the period 1st March 2005 to 31st March 2006, and daily, monthly and seasonally for the period 23 June 2005 to 22 December 2006 for comparison with macroalgae deposition.

Tidal data

Tidal data were obtained from the British Oceanographic Data Centre (BODC) (see Section 2.2.1 for more detail) for the nearest recording tide gauge (National Network gauge at Newhaven, Longitude N 50.78, Latitude W 00.06). The diurnal tidal range was calculated from the sea level (m) data recorded in 15 minute intervals for the period 1st March 2005 to 22nd December 2006.

3.2.2.2 Seasonal species composition of deposited macroalgae deposits

Composition of seasonal detrital macroalgae deposits within the study area were determined by random sampling of the material from autumn 2004 to autumn 2006 (n = 7). Approximately 500 g (wet weight) samples of detrital algae (n = 3) were randomly taken for each of the chosen time periods from around the LCSs at Elmer, in order to assess the species/taxa composition and rank abundance. Samples were collected and stored on ice for transport back to the laboratory. In the laboratory the samples were rinsed of sediment, and sorted according to species where possible (some were grouped at family level, due to missing important structural material). The ten most dominant species that contributed to the total decaying macroalgae load (according to wet mass)

were individually measured, and then the dry weight (oven dry at 60° C to constant weight) determined to establish the water content of each species.

3.2.2.3 Multi-scale temporal study of decaying macroalgae deposits

Detrital macroalgae deposits were measured daily in a bay location of the beach between two of the breakwaters (4 and 5) at Elmer from 23 June 2005 to 22 December 2006 (no data available for 20 Sept - 7 Nov 2005). A remote time-lapse photography technique was used to monitor changes in the amount of macroalgae covering the beach at low tides, due to the impracticality of daily sampling.

The time-lapse system was configured to capture still images (from the landward perspective; Fig. 3.1) of the bay every 2 hrs during daylight hours. The system consisted of a 5.8 mega pixel Praktica DC440 camera with a PICAXE-18 microcontroller circuit board and light dependent resistor in Basic. The camera was DC mains powered and mounted on a tripod, with a memory card large enough to store over a month's data. This system provided a cheap, effective method to assess the depositional patterns of decaying macroalgae at a range of temporal scales from semidiurnal tides to annual differences in seasons.



Figure 3.1 Daily camera survey photographs using the time-lapse still camera of Bay 4-5 at Elmer Beach. Photographs illustrate the different percentage cover of macroalgae detritus calculated by image analysis.

Daily image collection was based on selecting the appropriate photographs for each daily low tide. During winter months, only one diurnal tide was captured due to lack of daylight. Nevertheless, when daylight hours were longer during the summer months, two images were captured, enabling the assessment of semi-diurnal algal deposits. The photographs were processed and analysed using Image Pro-Plus image analysis package (Version 4.5.0.29 for Windows 98/NT/2000; Media Cybernetics). The variation in algal cover was analysed in terms of relative image area (total pixels) occupied by the detritus in each image. A segmentation process followed to differentiate between algal deposits and bare substratum using a pixel dropper to create a mask, which was then converted to a greyscale image. Following this, a pseudo-colour filter with 256 colour divisions was applied, this image equates to a binary (black-and-white) bitmap. The number of pixels for each colour division was reported for the entire picture; only the extreme end divisions were relevant (1 and 256; where 1 is decaying macroalgae cover and 256 is bare substratum). Percentage cover of the algae was then calculated. Where there were images for both diurnal tides in the summer months (May-Sept), mean percentage cover was used, as there were no significant differences (p > 0.05) in amount of decaying macroalgae cover between the lowest and highest low tides (F $_{(1, 118)} = 0.00$, p =0.998, n = 120), nor was there a correlation between the diurnal tidal height and amount of macroalgae recorded.

Potential human error that could occur during the segmentation stage was corrected for by applying a correction factor. The correction factor was calculated by analysing photos with distinctly different amounts of algal cover (e.g. ~ 25 %, 50 %, and 75 %); this was replicated randomly (each of the photos was assigned ten run numbers and a random run number order was generated using the 'RANDBETWEEN' function in Microsoft Excel®) ten times to produce an estimate of error. Mean percentage algal cover (± Standard Error (SE)) was calculated for all the images; the calculated S.E. was then applied as a correction factor to the results of all the images over the time-lapse sampling period.

3.2.2.4 Spatio-temporal survey of decaying macroalgae deposits

Field measurement technique of decaying macroalgae deposits

The quantity of total algal deposits was determined monthly for one randomly chosen spring tide over a thirteen month period (March 2005 to March 2006) by measuring the biomass and

cover of samples taken. The biomass: cover ratio was subsequently calculated in order to give a description of the 'deposition pattern'; where, high ratio values denote thin, light coverings of detritus with high spread, whilst low ratio values denote thick, heavy coverings of algal deposits in relation to percentage cover (i.e. dense patches). A quadrat (1 m², split into 4 % sectors) was randomly thrown and the amount of decaying macroalgae material within the frame was estimated to the nearest 1 % and total wet biomass measured and weighed in a fine meshed net bag using digital scales (accurate to within 1g; any excess water was drained first). Photographs of these quadrats were taken for use as a source reference.

Field Survey

The distribution of detrital algae deposits on the beach at Elmer (granite breakwaters), as well as on two nearby beaches, Felpham and Climping, with different CDSs (granite and wooden groynes, respectively), was determined monthly for the period March 2005 to March 2006 (Climping surveyed started in April 2005) by surveying the amount of detached macroalgae using the field measurement technique (Section 3.2.2.4). Each stretch of beach adjacent to the three CDSs was divided vertically into levels down the shore, referred to as 'landward' and 'seaward'; this was according to the position of the breakwaters at Elmer (Fig. 3.2a). The 'landward' level (~ 50 m long) was sub-divided into two further sections: 'upper' (below the shingle bank on the upper foreshore) and 'lower' (directly behind the breakwaters) (each ~ 25 m wide) on the landward side of the structures, and for the 'seaward' there was one level (~ 25 m wide) on the seaward side of the breakwaters (Fig. 3.2a).

At Elmer, the horizontal shore profile differed with the presence of bays and tombolos because of the breakwaters; two types of horizontal shore were therefore chosen: 'bays' and 'tombolos' (Fig. 3.2a). There were eight horizontal shore locations at Elmer in total: four replicate bay (2-3 (the bay between structures 2 and 3), 3-4, 4-5, and 6-7) and four replicate tombolo (behind and in front of structures 2, 4, 6 and 8) locations, these were chosen at random (see Figure 3.3 for all quadrat locations). Only one horizontal shore location was sampled on the beaches with granite groynes (Felpham) (Fig. 3.2b) and wooden groynes (Climping), both bays (Fig. 3.2c) because of the lack of tombolos. In each vertical shore level, for each horizontal shore location, the quadrat was thrown four times at random and measurements of the decaying macroalgae were made (Fig. 3.2 and see Section 3.2.2.4).

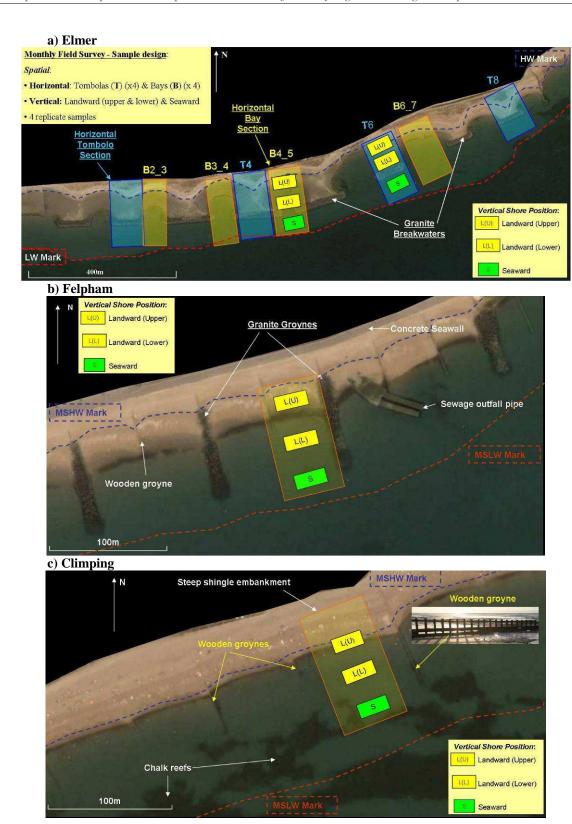


Figure 3.2: Illustration of the sampling design for the monthly survey of decaying macroalgae distribution around the a) granite breakwaters at Elmer Beach, b) granite groynes at Felpham, and c) wooden groynes at Climping. Four random quadrats of the macroalgae were recorded on a low spring tide for each vertical shore level in each horizontal shore location over a 13 month period (March 2005-March 2006).



Figure 3.3 Lidar-derived Digital Elevation Model (DEM) illustrating cross-shore beach morphology at Elmer, with the GPS-derived location of all the quadrats used to survey the spatio-temporal deposition of decaying macroalgae.

3.2.3 Statistical Analysis

3.2.3.1 Variances in seasonal macroalgae composition

Differences in the species and major group composition of decaying macroalgae deposits were assessed for seasonal variation by analysis of similarities (Clarke & Warwick 2001) and multi dimensional scaling (MDS, Clarke 1993).

First, a ranked triangular matrix of similarities was calculated between each replicate (n = 3) for each season (n = 7) using the Bray Curtis similarity matrices (Bray & Curtis 1957), following square root transformations. After which, MDS was then used to generate two-dimensional ordination plots to visually evaluate variation in the seasonal macroalgae deposits. The differences between the samples were formally tested using a one-way analysis of similarities (ANOSIM) permutation test (Clarke & Green 1988), with season (autumn 2004 - autumn 2006; excluding spring 2006) as the factor. ANOSIM is a non-parametric procedure, which uses the difference between average ranked Bray-Curtis dissimilarity values among replicates, between samples and within samples, to calculate the R statistic. If R was significantly different from 0 at the 0.05 probability level, pairwise comparisons (ANOSIM, Clarke 1993) were used to identify which factors levels differed. Finally, the algal species contributing to the differences in seasons were investigated using the similarities percentage procedure SIMPER (Clarke 1993). All multivariate analysis was carried out using PRIMER software for non-parametric multivariate techniques (PRIMER software package, version 6; Plymouth Marine Laboratory, U.K.).

3.2.3.2 Effect of temporal scale on decaying macroalgae deposits

Univariate analysis of time-lapse data

The comparison of decaying macroalgae quantities at different temporal scales was statistically tested with a series of ANOVAs. A one-way ANOVA was used to test the null hypothesis that there was no difference between the lower and higher diurnal low tides. A further series of one-way ANOVAs (unequal sample sizes) were used to test several null hypotheses: the first was that there were no differences in decaying macroalgae cover between neap and spring low tides

over the period of a year (1st Dec 2005 – 30th Nov 2006; n = 56). The days on which the lowest spring and neap tides within the tidal cycle fell on were used in the analysis. Secondly, the differences in detrital algae deposits between different months (n = 11) and seasons (n = 4) were tested using one-way ANOVAs (unequal sample sizes) for the period of one year (1st Dec 2005 – 30th Nov 2006). Finally, the null hypothesis that there were no annual differences in decaying macroalgae deposition was tested using a two-way ANOVA. Factor one (month) had five levels (June, July, August, September, November, and December) and factor two (year) had two levels (2005 and 2006); both factors were random and orthogonal. Detrital algae cover data were transformed using arcsine percentage square root transformation to meet assumptions of homogeneity of variance (tested using Levene's Test) and p was set to 0.01 to compensate for the increased likelihood of Type 1 error (Underwood 1981). *Post hoc* comparisons to determine the significant differences between group means were carried out using Games-Howell test. All parametric ANOVAs were carried out using SPSS (SPSS 2005).

Bivariate correlation analysis was used to assess the influence of wave parameters on the variability of detrital algae deposits. Pearson's correlation coefficient was used as the data were normally distributed (one-tailed test). The influence of the tidal cycle was assessed by calculating the number of days since the last lowest low spring tide (TmS), then plotting this against detrital algae cover and calculating a polynomial line of best fit. The expected outcome was one of a quadratic best fit, with either a peak at the spring tides or neap tides. The r value was used as a measure of how well the tide influenced the decaying macroalgae cover.

3.2.3.3 Spatio-temporal effects on decaying macroalgae deposits

Annual biomass of decaying macroalgae deposits

The daily camera survey only assessed the percentage cover of decaying macroalgal deposits on the beach for Bay 4-5, whilst, the monthly field survey recorded both the percentage cover and biomass of the deposits of the whole beach. An estimate of the annual deposition across the 1.75km breakwater scheme at Elmer was calculated.

First, the correlation between the cover (%) and biomass (kg/ m^2 wet) of field recorded deposits of decaying macroalgae was obtained by plotting a scatter graph (Figure 3.4). Then the biomass (kg/ m^2 wet) of the decaying macroalgae deposits at Elmer beach was calculated for every day

over one year (1st December 2005 to 30th November 2006); this was done by using the polynomial order 3 correlation equation ($y = 0.000029857x^3 - 0.001828673x^2 + 0.095078560x^1 - 0.102943726$; Figure 3.4) from the best fit trend line to extrapolate the average daily biomass from the time-lapse percentage cover results (see Section 3.2.2.3). The annual average biomass (kg / m^2) was calculated from the daily extrapolated data (n = 365) for the period December 2005 to November 2006; this was then used to estimate the annual average biomass deposited along the 1.75 km stretch of shore at Elmer. The upper and lower standard error margins were then used to get the range of estimated biomass as well as the average.

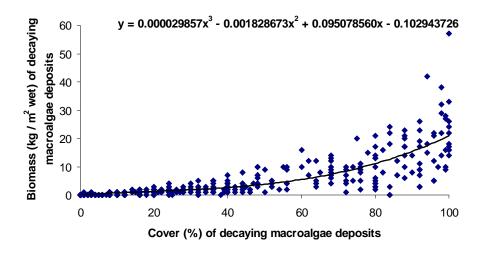


Figure 3.4 The relationship between the percentage cover and biomass (kg / m^2) of decaying macroalgae deposits measured during the spatio-temporal field survey at Elmer beach over a year (March 2005 – March 2006; n = 1149; see Section 3.2.2.5 for sampling strategy). An order 3 polynomial curve was the trend line of best fit that was used to extrapolate the biomass from the daily time-lapse recorded cover of macroalgae.

Univariate analysis of spatio-temporal field data

Hypotheses about the spatio-temporal patterns in the cover and biomass of decaying macroalgae deposited on beaches around different CDSs were tested using analysis of variance (ANOVA). To verify a number of null hypotheses a series of three-factor ANOVAs were carried out on the decaying macroalgae measure of cover and biomass.

The first null hypothesis was to test that there were no significant differences in algal deposits between the horizontal shore locations and vertical shore levels within the breakwater scheme at Elmer Beach, over a twelve month period. Factor one (horizontal) had two levels (bay and tombolo), factor two (vertical) had three levels (upper landward (LW (U)), lower landward (LW (L)), and seaward (SW)), and factor three (time) had twelve levels (March 2005 - March 2006;

excluding October 2005 as no sampling occurred). Factors one and two were fixed and orthogonal, whilst factor three was random and orthogonal.

The second null hypothesis tested that there were no significant differences between and within (vertically) different bays, nor between and within different tombolos over time, this was done with two separate three-way ANOVAs. The first with the following design: Factor one (bays) had four levels (bays 2-3, 3-4, 4-5 and 6-7), factor two (vertical) had three levels (LW (U), LW (L), and SW) and factor three (time) had twelve levels (March 2005 – March 2006; excluding October 2005). The second was the same design but factor one was instead 'tombolos' and also had four levels (tombolo 2, 4, 6, and 8). Factors one and two were fixed and orthogonal, whilst factor three was random and orthogonal.

The third null hypotheses tested that there were no significant differences between the detrital algae deposits in the bays adjacent to different types of CDSs and that there were no differences in the vertical shore deposits at each type of CDS over time. There were no significant differences (p > 0.05) between the upper and lower landward shores across the three beaches for the biomass or cover of decaying macroalgae (p > 0.05). Therefore only the upper landward section of beach was used in this ANOVA model for between different structure types. Factor one (CDS type) had three levels (granite breakwaters (Elmer), granite groynes (Felpham), and wooden groynes (Climping)), factor two (vertical) had two levels (LW (U) and SW) and factor three (time) had ten levels (April 2005 - Feb 2006; excluding October 2005). Factors one and two were fixed and orthogonal, whilst factor three was random and orthogonal. To make the design balanced, four separate three-way ANOVAs were performed, using a different bay adjacent to the granite breakwaters at Elmer (Bay 2-3, 3-4, 4-5 and 6-7) each time to compare against the other CDS types, as there were significant differences (p < 0.01) between the bays at Elmer.

All the analyses were done on $\log (x + 1)$ transformed data, apart from percentage and ratio data, which were transformed using arcsine percentage square root transformation. Prior to analysis, data were tested for homogeneity of variances using Kolmogorov-Smirnov normality tests. The majority of data remained non-normal following transformations. Therefore the more stringent criterion of p > 0.01 was used to reject null hypotheses, since ANOVA is robust for the departure from this assumption when there are many independent replicates and sizes of

samples are equal (Underwood 1997). Significant results were, however, interpreted with caution. When ANOVA indicated significant differences among means, Tukey's HSD and Games-Howell *post hoc* tests were used to distinguish between them (p < 0.01). Tukey's HSD was chosen as it controls type I error rate very well, although a little conservative it is powerful when testing large numbers of means. Games-Howell *post hoc* was chosen in addition because the data were not normally distributed and is a particularly powerful test in this situation. All parametric ANOVAs were carried out using SPSS (SPSS 2005).

3.2.4 *Caveats of the field survey*

There were several caveats in the field survey that investigated the decaying macroalgae deposits at the three beaches of Elmer, Felpham and Climping. The primary aim of the study was to investigate how the algae deposits varied spatially and temporally around the low crested breakwaters at Elmer. It was observed in preliminary site visits that this beach received greater amounts of algae deposits than along the adjacent coastlines (10km either side). It was therefore decided that it was necessary to provide some context to the amount of algae within the breakwater scheme at Elmer in comparison to control sites: to investigate whether the breakwaters were trapping the algae to greater extent than if they were not present. Ideally, control sites would have consisted of beaches without any coastal defence structures. However, this was not possible as the south coast of England is heavily protected by CDSs and no unprotected sites that experienced similar environmental conditions could be found. Therefore, it was decided to use two beaches either side of Elmer beach as comparisons as they would experience the same exposure to wave action; these beaches were Felpham with granite groynes and Climping with wooden groynes. These beaches cannot therefore be treated as control beaches, as one, they were protected and two, they were protected with different types of coastal defence structures. Instead they should be observed as comparative beaches that give some idea of the amount of algae deposited within the same geographical cell.

Another limitation with the design of the field survey was the number of replicates that were carried out at Felpham and Climping. As the main focus of the study was on the beach at Elmer, there were shortcomings with the amount of time that was available to both sample and work up results for the two additional sites. At Elmer, the cover and biomass of the algae was measured with 96 replicates, so the spatial extent (both horizontal shore locations and vertical shore

levels) of the scheme was very thorough, whereas at Felpham and Climping only 12 replicates at each were taken (only vertical shore levels). Ideally the design should have been balanced with the same replication at all three sites, therefore it should be noted that when comparisons are made between the three sites in this study that there may be some variation around this, though the author observed clear differences when out in the field. Any future studies of Elmer, should emcompass a better replicated design for any comparative sites.

The temporal sampling strategy of the field survey design was to sample monthly on one spring low tide over a year period. The results from the survey were analysed monthly, this complicated the patterns observed, it would have been more simplified to have pooled the summer and winter samples, since the time-lapse survey clearly showed there were differences in these time periods.

3.3 Results

3.3.1 Environmental Conditions

For the period when all surveys took place (March 2005 to December 2006), there were no storms in the summer months, nor in the spring and autumn of 2005 (see Chapter 2, section 2.3.3 for more details). The spring and autumn months in 2006 experienced more storms than in 2005, with three storms in both seasons. Both winters had frequent storms, four in 2005 and five in 2006. The greatest storm occurred in the spring 2006 with a maximum significant wave height of 5.84 m and an average wave direction for the period was 195°, from the south-west. At times there were severe changes in wave direction, for example, in the August 2006, the wave direction shifted by 100° from the average to a maximum of 294° from the west-north-west, and in summer 2005 and autumns 2005 and 2006 waves came from the east (90°).

The seasonal changes in sea surface temperature (SST) for the above period showed summer and autumn months were the warmest seasons; average temperatures ranged from 18° C to 15° C (see Chapter 2, section 2.6.1). The SST in summer 2006 was greater than in 2005, reaching 21° C in July 2006, but only 19° C in July 2005. Winter and spring were the coldest, reaching a minimum daily average of 4.8° C in March 2006.

3.3.2 Monthly Decaying Macroalgae Composition

Thirty six macroalgal species occurred amongst the top ten dominant species in monthly (October 2004 to October 2006) sampled algal deposits at Elmer (Table 3.2). Rhodophyta was the dominant group, followed by Phaeophyta, then Chlorophyta. The dominant species was the red alga Chondrus crispus (Linnaeus) in both abundance (38% \pm 5) and frequency of occurrence in samples (92 %). Several red algae were consistently present (Table 3.2) but low in biomass (< 12 %) (due to their frondose or filamentous morphology), these were *Calliblepharis* sp. (79 % occurrence), Plocamium cartilagineum (Linnaeus) Dixon (79%), Griffithsia sp. (63 %), Ceramium spp. (54%) and Polysiphonia spp. (50%); the latter three only occurred in the spring and summer months. The dominant brown alga in abundance was *Ectocarpus* sp. (31 $\% \pm 7$), although not in frequency of occurrence (29 %). The most frequently occurring brown algal species did not contribute largely (< 10 %) to the biomass of the decaying macroalgae deposit; these were *Halopteris* spp. (88 % occurrence) *Cladostephus spongiosus* (H. C Agardh) (83 %), Laminaria spp. (75 %; probably mostly Laminaria saccharina (L. Lamouroux), as too difficult to tell from fragments), and Fucus spp. (58 %; probably mostly Fucus spiralis (Linnaeus) and Fucus vesiculosus (Linnaeus). The former two species are small in physical form, and the latter two although large in form and biomass, occurred most frequently in fragments. The most dominant green macroalgae in both abundance and frequency was Ulva spp. (13 \% \pm 4), with Cladophera sp. also occurring in almost 30 % of the samples.

Table 3.2 Average abundance (percent of total biomass) of different algal species and taxa \pm SE, and frequency of occurrence (out of n=24), in the algal deposits at Elmer, West Sussex; October 2004 - October 2006. **Bold data** are the most abundant and/or frequently occurring. Table sorted by frequency of occurrence within each algal major grouping.

Species/taxa	Abundance (%)	SE	Occurrence (%)	
Chlorophyceae	11.14	3.95	10	
<i>Ulva</i> sp.	13.15	4.19	79	
Cladophera sp.	5.46	2.47	29	
Chaetomorpha linum	0.30	0.13	13	
Spongonema tomentosun	0.78	0.00	4	
Phaeophyceae	31.39	3.19	40	
Halopteris sp.	3.06	0.75	88	
Cladostephus spongiosus	3.69	0.74	83	
Laminaria sp.	9.39	2.32	75	
Fucus sp.	2.83	0.44	58	
Halidrys siliquosa	11.74	4.50	50	
Chorda filum	7.98	3.01	38	
Halurus sp.	1.46	0.44	33	
Ectocarpus sp.	31.10	6.49	29	
Furcellaria lumbricalis	2.18	0.90	17	
Desmerestia aculeata	4.29	4.18	13	
Sargassum muticum	1.22	0.42	8	
Dictyota dichotoma	1.12	0.00	4	
Himanthalia elongata	2.17	0.00	4	
Rhodophyceae	57.46	3.48	50	
Chondrus crispus	37.69	4.88	92	
Calliblepharis sp.	5.77	1.79	79	
Plocamium cartilagineum	1.32	0.34	79	
Griffithsia sp.	1.40	0.42	63	
Ceramium sp.	11.76	3.63	54	
Polysiphonia sp.	9.67	2.46	50	
Phyllophora crispa	3.74	1.39	38	
Chylocladia verticillata	1.58	0.41	33	
Porphyra sp.	1.40	0.47	29	
Polyides rotundus	10.45	5.02	25	
Cryptopleura ramosa	1.76	0.74	21	
Apoglossum ruscifolium	1.74	0.96	13	
Naccaria wiggii	1.61	0.51	13	
Petalonia fascia	5.69	2.18	13	
Chondria dasyphylla	34.84	34.18	8	
Lomentaria clavellosa	6.16	4.60	8	
Dasya sp.	1.28	0.00	4	
Heterosiphonia plumosa	0.08	0.00	4	
Palmaria palmata	1.98	0.00	4	

The dominant species in both summers were made up of filamentous green (*Cladophora* sp. and *Ulva* spp.) and red algal species (*Ceramium* spp. and *Polysiphonia* spp.). In 2005 abundance

was dominated by red species (53 %) and by green algal species (63 %) in 2006. *Ceramium* spp. and *Polysiphonia* spp. were only present in the summer seasons (> 5 % occurrence), whereas green algae were present in small quantities in all seasons except winter 2005. In spring 2005, when brown algal species accounted for 55 % of the decaying macroalgae, *Laminaria* spp. (18% \pm 1; probably mostly *L. saccharina*) and *Ectocarpus* sp. (21 % \pm 1) were the most abundant genera. The latter species was only present on one other occasion (where it was equally abundant), in autumn 2006. *Laminaria* spp. were only present from spring to autumn 2005, in decreasing proportion from 18 % to 7 % of the total genera recorded.

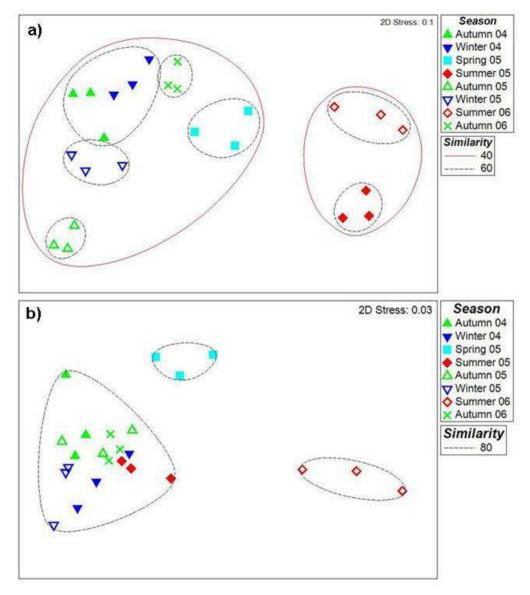


Figure 3.5 Seasonal differences in the composition of decaying macroalgae using a) species and b) major groups (Chlorophyta, Phaeophyta, Rhodophyta) from Elmer Beach from Autumn 2004 to Autumn 2006 (no samples for Spring 2006). MDS is based on Bray-Curtis similarity matrix of square root transformed macroalgae deposit occurrence data, with similarity lines from cluster analysis.

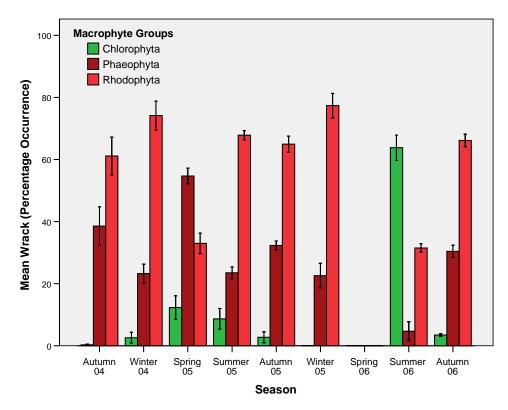


Figure 3.6 Seasonal composition of decaying macroalgae showing the percentage occurrence of macroalgal groups (Chlorophyta, Phaeophyta, and Rhodophyta). Data are means with S.E. bars (n = 3).

3.3.3 Multi-Scale Temporal Study of Decaying Macroalgae Deposits

3.3.3.1 Decaying macroalgae deposition at different temporal scales

The amount of decaying macroalgae cover was recorded daily for a period of 18 months (June – Sept 2005; Nov 2005 – Dec 2006) (Fig. 3.7); this enabled the analysis of different temporal scales (diurnal, neap and spring tidal cycle, monthly, seasonal, and annual), to investigate what, if any, temporal cycles existed.

There was no significant difference in the amount of seaweed deposited between the two low tides within one day (lower and higher diurnal low tides) (p > 0.05). There, were, however significant tidal differences between neaps and springs (F _{1, 49} = 5.652, p = 0.021) for the period 1st December 2005 to 30th November 2006. On average there was 42 % greater macroalgal cover deposited during a spring tide compared to a neap tide.

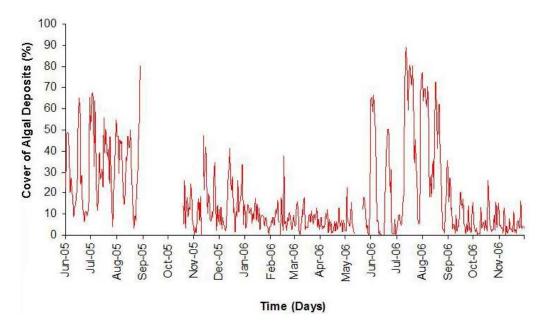


Figure 3.7 The daily decaying macroalgae cover from 22 June 2005 to 19 December 2006 at Elmer Beach (Bay 4-5) recorded by the daily camera survey.

Data collected daily for one continuous annual period (1st December 2005 to 30th November 2006) showed that seasonal (F $_{3, 364} = 14.742$, p < 0.001) and monthly (F $_{11, 364} = 23.842$, p < 0.001) significant differences occurred in the amount of decaying macroalgae deposited on the beach. The largest average deposition occurred in the summer (33 % \pm 3), the least cover occurred in the spring (7 % \pm 1), whilst, in winter 2005 and autumn 2006 similar quantities of deposition occurred. There was some within season variability; this was greatest for the summer and autumn months. In the summer, the greatest average cover was in August 2006 (57 % \pm 5), this was four times greater than in July and two times than seen in June (Fig. 3.8), whilst in the autumn, September (27 % \pm 4) had four times the amount of cover measured in October and November, but was similar to that in June. In the winter months, December and January showed two times the cover seen in February (8 % \pm 1), and in the spring, when there was the least cover there was no significant variability (6 - 9 % \pm 1) (p > 0.05).

Data collected from the months June, July, August, September, November and December in two consecutive years, 2005 and 2006, were used to investigate annual variability (Fig. 3.9). There was no significant difference in the decaying macroalgae cover between the two years (p > 0.05). In total the extrapolated biomass amounted to approximately 3.6 t/m² in 2005 and 3.5 t/m² in 2006. There were, however, significant differences in the monthly depositions ($F_{5, 267} = 34.360$, p < 0.001), as well as when interactions between years and months ($F_{5, 267} = 9.773$, p < 0.001)

0.001), i.e. the amount remained the same for the different years but the months in which the algae were deposited in changed greatest.

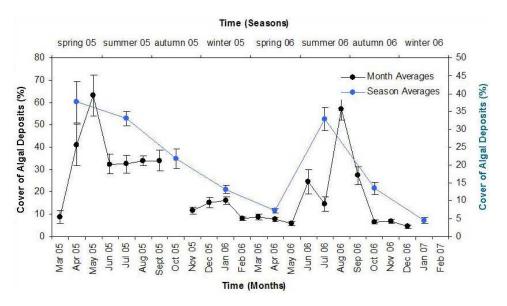


Figure 3.8 The monthly and seasonal cover of decaying macroalgae deposition from March 2005 to December 2006 at Elmer Beach (Bay 4-5) from the daily camera survey (Mar – May 05 decaying macroalgae data from monthly field survey). Data are means \pm SE.

In 2005, the amount of deposited macroalgae was consistently the same for June, July, August and September. In July 2006, however, there was 56% less decaying macroalgae than in 2005, and then in August there was 32% greater cover in 2006 than 2005. In December 2005, there was almost 5 times the amount of decaying macroalgae than in 2006 (4 % \pm 1), and no significant difference between either year for November (7 - 12 % \pm 2).

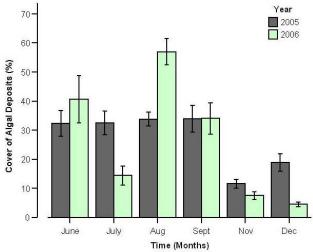


Figure 3.9 The annual variation in quantity of decaying macroalgae cover for between for six different months using daily camera survey data at Elmer beach. Data are means \pm SE.

3.3.3.2 Environmental influences affecting temporal patterns of macroalgae deposition

There are several measurable environmental variables that could influence the quantity of decaying macroalgae deposited on the beach: tidal influences, wave parameters, such as wave height, wave length, and direction, and sea surface temperature. The tide changes daily, with neaps and springs, whilst wave parameters have been shown to experience daily, monthly, seasonal and annual variation (see Section 2.3). Pearson's correlation analysis showed that there were strong negative correlations between the seasonal decaying macroalgae depositions and the frequency of storms (r = -0.89, p < 0.001), maximum significant wave height (r = -0.95, p < 0.001), and wave length (r = -0.68, p < 0.05). Maximum wave height was the best environmental predictor (Fig. 3.10). All the chosen wave predictors were not entirely independent of each other, as they showed multicollinearity, and therefore multiple regression analysis was not used. Storms are measured by wave height (significant wave height >3m), correlation shows that the greater the frequency of storms the higher the waves (r = 0.90, p < 0.001), furthermore when the wave height increases so does the wave length (r = 0.76, p < 0.05).

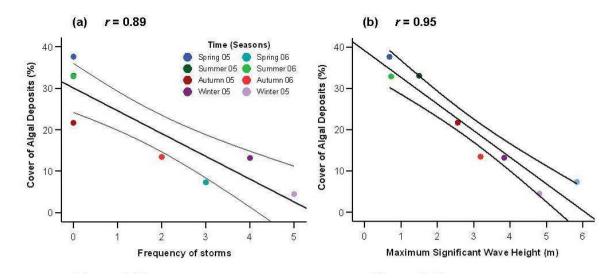


Figure 3.10 Linear regression with 95 % confidence intervals for average seasonal deposits of decaying macroalgae versus (a) frequency of storms, and (b) maximum significant wave height for the period 1 Mar 2005 to 21 Dec 2006. Significane values (p) are given in the text.

When the frequency of storms and severity were high, particularly in the winter months, the decaying macroalgae deposits were low (Fig. 3.10). When there were high algal deposits in the summer there were no storms for either year. Slightly different trends were observed for each

season (Fig. 3.10). In spring 2006, there was very little decaying macroalgae (7 % cover) in comparison with spring 2005 (38 %). This can be explained by the unusual storm severity (largest in 18 months) for this time of year; there was increased maximum wave height (5.84 m), and shorter mean wave lengths (6.36 m), this resulted in low decaying macroalgae deposits. The difference between autumn 2005 and 2006 could also be explained by the wave climate, as although the maximum wave height and wave length were similar between the two years, the frequency of storms was not. There were two storms in the 2006 and three in 2005, this correlated to the reduced decaying macroalgae deposits in 2005. Again, the difference in algal deposits between the two winters was because of a greater frequency of storms in winter 2006. The storms in 2006 were more severe, which resulted in less decaying macroalgae than in winter 2005.

On a monthly scale, maximum significant wave height (max H_s) was negatively correlated (Pearson's correlation, r = -0.69, p < 0.01) with the quantity of algal cover, explaining 48 % of the variation in detrital macroalgae deposits (Fig. 3.11a). The greater the wave height, the less detrital algae there was on the beach. Of particular interest, were May 2005 and August 2006, when the algal deposits were greatest (> 50 % cover), this was when the maximum significant wave height (max H_s) was very low (< 1 m). In contrast, when the wave height (max H_s) was at its greatest in April and December 2006 (5.84 and 4.81 m, respectively) the algal cover was at its lowest (8 and 4 %, respectively). There were some discrepancies that did not fit this explanation, which was why the linear correlation was not stronger; for example, when the significant wave height (mean H_s) was low in March and April 2005 (0.63 and 0.56 m, respectively), similar to that in May (0.59 m), the amount of decaying macroalgae was very variable between the three months (Fig. 3.11). This difference may be explained by the marked changes in wave length and direction for this period, even though there were no overall significant correlations between algal cover with either wave length or direction (at p > 0.05). The wave direction was relatively consistent, with an average direction of 194° (± 0.2 , i.e. from the south-west-south). On several occasions there were marked changes in wave direction (e.g. May 2005 and August 2006, Fig. 3.11c). When there were strong changes in wave direction, as well as an extreme elevated or reduced wave height the quantity of macroalgae cover was affected. For example, in May 2005, the maximum wave height was low (0.48 m) and the wave direction shifted by 68° from the average to the east-south-east (Fig. 3.11c), perhaps explaining the high decaying macroalgae cover (> 60 %).

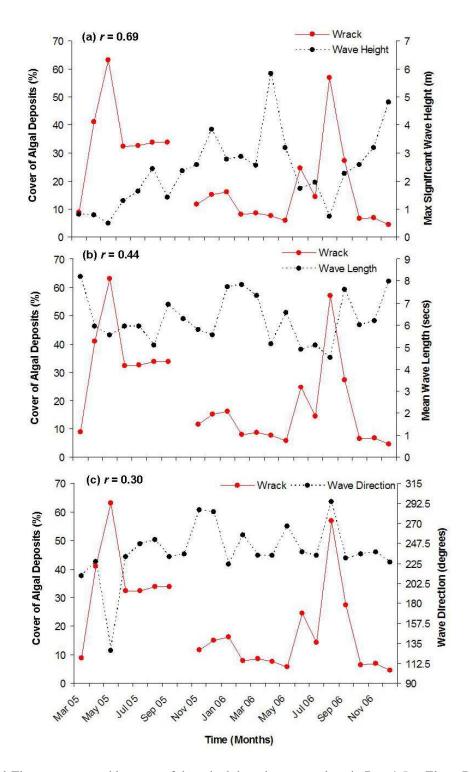


Figure 3.11 The average monthly cover of deposited decaying macroalgae in Bay 4-5 at Elmer Beach for the period March 2005 to Dec 2006 with the monthly wave variables: (a) maximum significant wave height, (b) average wave length, and (c) maximum wave direction. Linear regression r values are given for the correlation between each of the wave variables and the decaying macroalgae cover on a monthly temporal scale. Significane values (p) are given in the text.

Furthermore, a similar event happened in August 2006; there was a strong shift in wave direction by 100° from the average to a west-north-westerly direction, together with a reduced maximum wave height (0.73 m) and very short wave lengths (4.5 seconds), this resulted in an elevated deposition of decaying macroalgae on the beach (> 50 % cover). On a finer scale, there were also weekly and daily fluctuations in decaying macroalgae cover (Fig. 3.7); this may have been as a result of changing tidal cycles, as well as the wave environment. A one-way ANOVA showed a significant difference between neap and spring tides (F $_{1,49} = 5.652$, p = 0.021) in the amount of decaying macroalgae deposited. The tidal influence of neaps and springs was further measured by correlating the algal cover to the number of days since the last low spring tide (TmS), resulting in a quadratic regression relationship (Fig. 3.12, Table 3.3).

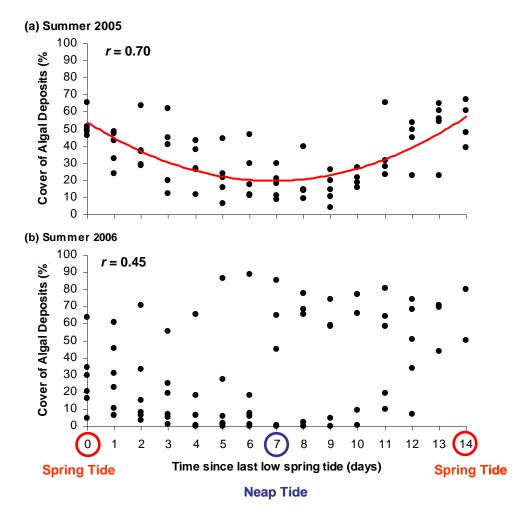


Figure 3.12 Quadratic regression scatterplots for the amount of decaying macroalgae cover in relation to the time it was deposited since the last low spring tide for the period 22 June to 19 September for the years 2005 and 2006 at Elmer Beach (Bay 4-5).

Table 3.3 R values from scatterplots of tidal influence (quadratic correlations) and wave variables (linear correlations) on the amount of decaying macroalgae cover deposited at Elmer Beach (Bay 4-5) on both seasonal (n = 7) and monthly (n = 18) scales. Negative signs indicate a negative correlations; NR = no correlation. The significant variables (p < 0.05) is given in bold

		TmS	Wave Height	Wave Direction	Wave Length		•	TmS	Wave Height	Wave Direction	Wave Length
Season	n (days)	Quadratic R^2	Linear R^2	Linear R^2	Linear R^2	Month	n (days)	Quadratic R^2	Linear R^2	Linear R^2	Linear R^2
C						Jun-05	9	0.786	-0.122	0.000	-0.456
Summer 70 2005	70	0.484	0.006	0.03	NR	Jul-05	31	0.548	0.011	-0.018	0.004
2003						Aug-05	30	0.394	0.014	0.296	0.085
A				-0.013	0.002	Sep-05	19	0.556	-0.029	-0.029	0.228
Autumn 42 2005	42	0.292	-0.026			Oct-05 ^a					
2003						Nov-05	23	0.123	0.05	0.000	-0.006
Winter 2005 89		0.256	0.008	0.047	NR	Dec-05	30	0.484	0.015	0.293	-0.002
	89					Jan-06	31	0.468	-0.011	-0.012	0.035
						Feb-06	28	NR	-0.116	-0.023	-0.001
Spring 92 2006		0.015	0.013	0.013	0.002	Mar-06	31	0.011	0.005	0.037	0.036
	92					Apr-06	30	0.172	0.015	0.078	-0.002
		0.012				May- 06	31	0.014	0.015	-0.006	0.038
Summer 2006 80					_	Jun-06	20	NR	0.142	-0.012	0.005
	80	0.1	0.162	0.168	NR	Jul-06	29	0.367	0.385	0.050	0.056
						Aug-06	31	NR	-0.002	0.096	0.177
Autumn 91		0.114		-0.01	0.008	Sep-06	30	0.428	-0.033	0.068	0.213
	91		-0.047			Oct-06	31	0.334	0.116	-0.031	0.044
2000						Nov-06	31	0.107	0.00004	-0.011	0.000
Winter 2006	21	0.05	-0.124	0.046	0.006	Dec-06	21	0.05	-0.124	-0.046	-0.006

^a No samples for recorded.

There was tidal cyclicity in the decaying macroalgae deposits for summer 2005 (Fig. 3.12a); high algal cover (> 40 %) occurred 0 - 3 and 12 - 15 days after the last spring tide (i.e. on or around a spring tide) and low cover (< 40 %) occurred 5 - 9 days after the last spring tide, which was during the neap tides. Table 3.3 shows the seasonal and monthly quadratic correlation values for the influence of different periods of the tidal cycle on algal cover, as well as linear correlation results with wave parameters. The algal deposits in summer 2005 showed the strongest correlations with spring and neap tides (Quadratic r = 0.70) and they were not affected by the wave environment (Fig. 3.12, Table 3.3). In contrast, summer 2006 algal deposits were not influenced by the tidal cycle, instead a slight correlation with wave direction was seen, but this only accounted for 16 % of the variation. The tidal cycle was the strongest variable to predict the amount of macroalgae deposits for 11 out of the 18 months, with wave height having the strongest influence in July 2006 (explaining 39 % of the algal cover variation).

A strong negative correlation can be seen between the influence of the tidal cycle and maximum significant wave height (Fig. 3.13). When wave height was low (e.g. summer months), the tidal cycle had the greatest influence on the fluctuations of algal deposits, and when the wave height was high and storms occurred (predominantly in the autumn and winter months), little decaying macroalgae was deposited on the beach.

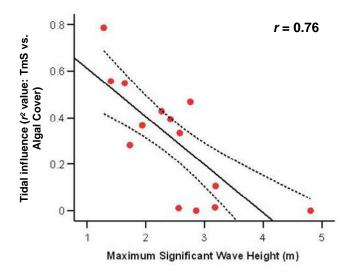


Fig. 3.13 Correlation with 95% confidence intervals of the relationship between tidal cycle influence (Time since last spring (TmS)) and maximum wave height influences on the amount of decaying macroalgae cover deposited monthly at Elmer Beach (Bay 4-5) for the period June 2005 to December 2006. (Severe outliers removed: Nov & Dec 2005; Apr & Aug 2006; discussed in text). Tidal influence is the measure of R^2 values from monthly quadratic regressions of the effect of the 'time since the last spring tide (TmS)' and the amount of decaying macroalgae cover.

The influence of the tidal cycle on the depositions of decaying macroalgae was particularly strong over the summer period of 2005 (June to the beginning of September). The peaks and troughs in algal cover correlated with neap and spring tides (Fig. 3.14a). The same pattern could not be seen for the same period in 2006 (Fig. 3.14b), as there were periods when there were large quantities (> 80 % cover) of algal detritus during the neap tides instead of spring tides (e.g. 1st to 10th August 2006).

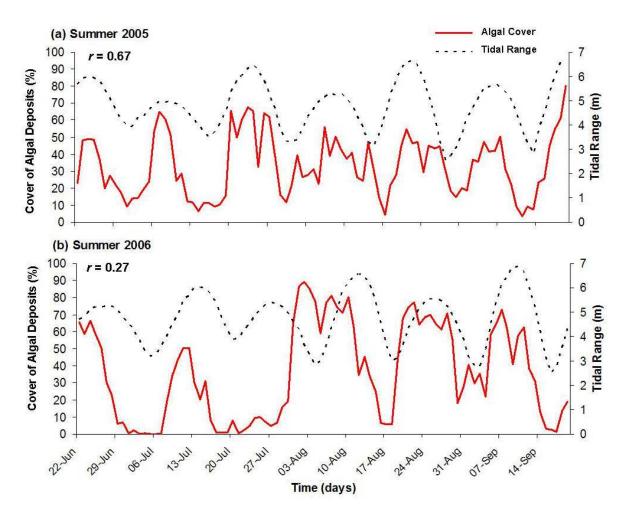


Fig. 3.14 The daily cover of decaying macroalgae deposits and tidal range at Elmer Beach (Bay 4-5) for the period 22 June to 19 September 2005 and 2006 (referred to as 'summers'). Linear regression r values are given.

The large amount of decaying macroalgae deposits seen between the 1st and 10th of August could not be explained by the wave parameters alone. The sea surface temperature, however, helped in understanding this unexplained pattern in algal deposits (Fig. 3.15). The temperature of the sea in the summer periods of 2005 and 2006 differed between the two years. Although the average temperature was same for both years (18.7° C), the daily pattern was very different. In

June 2005, the temperature steadily rose from 17.3° C to 19.4° C by the middle of July, and did not exceed 19.5° C until the middle of August, when it reached a maximum of 20.1° C.

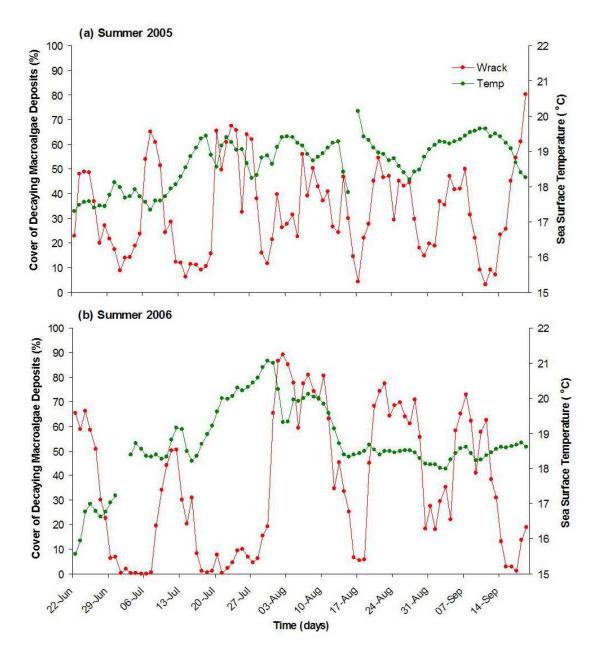


Figure 3.15 The daily cover of decaying macroalgae deposits and sea surface temperature at Elmer Beach (Bay 4-5) for the period 22 June to 19 September 2005 and 2006 (referred to as 'summers').

In contrast, the temperature was almost two degrees cooler (15.6° C) in June 2006; this was followed by almost a six degree rise over a month, reaching a maximum of 21.1° C on the 31st July. A 6° C rise in temperature in such a short space of time is unusually rapid for coastal seas; this temperature peak occurred simultaneously with the unexplained peak in algal cover in

August 2006. On closer inspection, all rapid increases and decreases in sea surface temperature for both years correlated to quick changes in decaying macroalgal cover with a 2 - 3 day lag (Fig. 3.15), e.g. the rapid decrease in temperature of 2° C from 31st July to 2nd August 2006, showed a three-day lag in a decrease in decaying macroalgae cover, followed by an increase in both temperature and decaying macroalgae cover.

3.3.4 Overall biomass of decaying macroalgae deposits

The total biomass of wet decaying macroalgae surveyed for the period March 2005 to March 2006 within the granite offshore breakwater scheme at Elmer Beach was 1,940 kg, with an average biomass (\pm SE) of 1.69 \pm 0.14 kg/m². Extrapolation from these monitoring results indicated that the total biomass of decaying macroalgae on the 1.75 km stretch at Elmer beach, in and around the breakwater system, would have been approximately 518,000 kg wet weight over 12 months. In comparison, the average biomass (\pm SE) adjacent to granite groynes at Felpham and wooden groynes at Climping was 3 times less, 0.56 \pm 0.14 and 0.52 \pm 0.11 kg/m², respectively. The greatest amount of decaying macroalgae deposits recorded varied both in amount and with time between the three types of CDS, with a maximum of 57 kg/m² recorded in May 2005 at Elmer. This was 5 times more than the maximum at Felpham (October 2005) and 6 times that at Climping (June 2005).

3.3.5 Spatio-Temporal Survey of Decaying Macroalgae Deposits

3.3.5.1 Spatial differences in horizontal and vertical shore deposits at Elmer

The spatial distribution of decaying macroalgae around the granite low crested breakwaters at Elmer beach was patchy and complex. There were significant differences in the vertical and horizontal distribution with strong interactions between them. The quantity of macroalgae deposited around the breakwaters at Elmer differed between tombolo and bay horizontal shore sections. ANOVA indicated that this difference was highly significant for both cover and biomass (p < 0.001, Table 3.4). There was almost three times the cover and biomass of decaying macroalgae within bay sections of the beach in comparison with tombolos (Fig. 3.16a).

Table 3.4 A three-factor analysis of variance testing for the spatio-temporal effects of low crested breakwater structures on the percentage cover and biomass (kg) of decaying macroalgae deposited within Elmer

breakwater system. Variables were factor 1, 'horizontal shore type' with 2 fixed levels (bay or tombolo; n = 576), factor 2, 'vertical shore levels' with 3 fixed levels (Landward upper & lower or Seaward; n = 384), and factor 3, 'time' with 12 fixed levels (month; n = 96). p set to 0.01; *p < 0.05, **p < 0.01, ***p < 0.001.

		Cover		Biomass		
Variable	df	MS	F	MS	F	
HS	1	10.03	171.56***	17.49	157.76***	
VS	2	1.02	17.42***	0.37	3.33*	
T	11	2.02	34.51***	4.02	36.22***	
HS x VS	2	0.52	8.81***	0.97	8.72***	
VS x T	11	0.84	14.38***	1.77	15.98***	
HS x T	22	0.41	7.02***	0.62	5.60***	
HS x VS x T	22	0.12	2.00***	0.23	2.04***	

HS = horizontal shore; VS = vertical shore; T = Time

Additionally, there were significant (p < 0.0001) differences in the amount of macroalgal cover deposited vertically on the landward (upper and lower) and seaward sides of the breakwaters, whilst the differences in decaying macroalgae biomass was not as significant (p = 0.036, see Table 3.4).

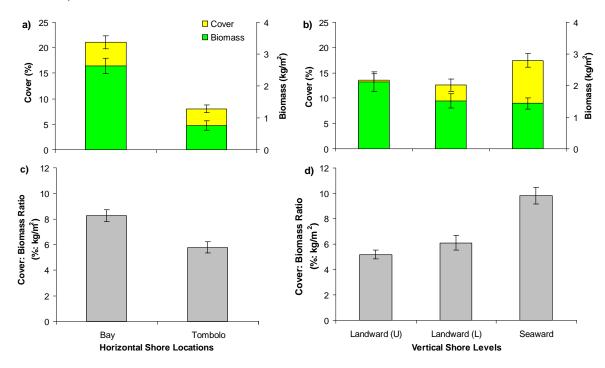


Figure 3.16 The cover (a & b), biomass (a & b) and cover to biomass ratio (c, d) of decaying macroalgae deposits in different horizontal shore types and up vertical shore levels around the breakwaters at Elmer for March 2005 - 2006. (c & d: Y Scale: low values = low cover, high biomass; high values = high cover, low biomass). Data are mean \pm SE values (n = 384).

The patterns observed in the detrital algae deposits on the landward and seaward sides of the CDS were relatively complex. Greater biomasses of algae were deposited on the upper landward sides of the structures than just behind (lower landward) and in front (seaward) (Fig. 3.16b). In contrast, there was more algal cover on the seaward side than either landward area.

The cover: biomass ratio explained the vertical shore depositional pattern best (Fig. 3.16c,d); whereby, decaying macroalgae is laid down in large thinly covered deposits on the seaward side and smaller thickly covered deposits on the landward side of the breakwaters. This deposition pattern can also be seen when correlating the biomass and cover of decaying macroalgae, as seen in Figure 3.17. The strongest correlation was seen for the upper landward shore level (r = 0.856) and the least, which is still very good for the seaward side (r = 0.797) of the breakwaters. For example, for 80 % decaying macroalgae cover, the biomass on the upper landward shore would have been 16.5 kg/m² wet, the lower landward shore 12.5 kg/m² wet, and the seaward shore level 8 kg/m² wet, i.e. the biomass is twice that on the upper landward than on the seaward sides of the structures for the given algal cover (Fig. 3.17).

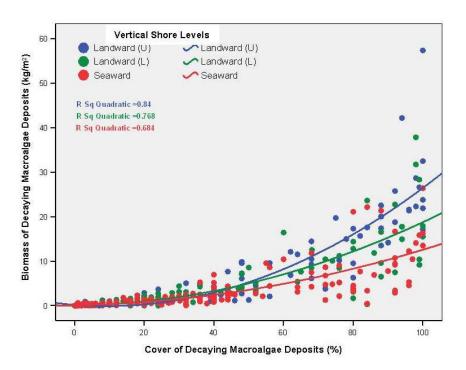


Figure 3.17 Relationship of cover and biomass measurements of the decaying macroalgae deposits at Elmer Beach adjacent to the breakwaters for the three different vertical shore positions for the period March 2005-2005 (n = 1148).

Highly significant spatial interactions occurred in the amount of decaying macroalgae deposited vertically and horizontally within the breakwater system (HS x VS, p < 0.001; Table 3.4, Fig. 3.18).

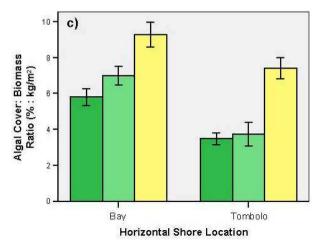


Figure 3.18 The cover to biomass ratio of decaying macroalgae deposited for interacting vertical and horizontal beach sections around breakwaters at Elmer Beach for March 2005-2006. Data are means \pm SE values.

Tombolos received reduced quantities of macroalgae to that in bays, with thinly covered low biomass depositions on the seaward sides of the structures for both bays and tombolos, and patches of greater biomass and marginally less cover on the landward sides (Fig. 3.19). Immediately behind the breakwaters on the tombolos there was less deposition, in both cover and biomass, than either higher up the shore on the landward or seaward sides.

3.3.5.2 Temporal differences in horizontal and vertical shore deposits at Elmer

There were significant temporal differences in the quantity of macroalgae deposits surveyed on a monthly scale from March 2005 to March 2006 at Elmer beach (p < 0.0001; Table 3.3). In March 2005, the biomass (ca. 0.25 kg/m²) and cover (ca. 8 %) of decaying macroalgae deposits was small (Fig. 3.19). Following this, there was an increase in accumulations, peaking in May 2005 with a biomass of 7 kg/m² and cover of 39 % (Fig. 3.19). The accumulations gradually decreased until in August they were similar levels to March. There then followed a flux of macroalgae deposited in September, but 50 % less than in May. No data were recorded for October, but by November the deposits were very low again ($< 1 \text{ kg/m}^2 \text{ and } < 5 \% \text{ cover}$), followed by another flux of decaying macroalgae deposition in December and January similar to that in September. February and March 2006 experienced the lowest levels of macroalgae deposits sampled (Fig. 3.19).

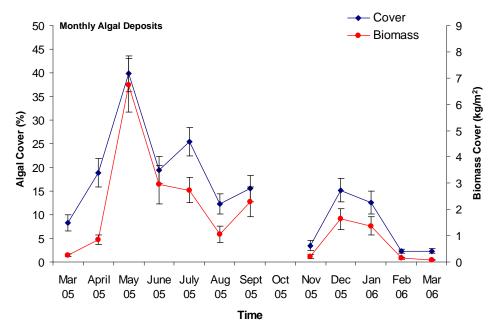


Figure 3.19 The monthly changes in the amount of cover and biomass (wet weight) of decaying macroalgae deposits around the offshore breakwater at Elmer Beach. Data are mean values \pm SE.

There were significant differences in the seasonal quantities of detrital algae deposited around the breakwaters at Elmer (p < 0.001). Tukey's HSD post hoc tests showed that spring and summer, and autumn and winter were grouped together respectively, because of similar amounts of macroalgae deposits, with significant differences between these two groupings (Fig. 3.20). In the spring and summer the biomass (ca. 2 kg/m^2) and cover (ca. 17 %) of macroalgae deposits was greater than the autumn and winter (ca. 1 kg/m^2 and 10 %, respectively).

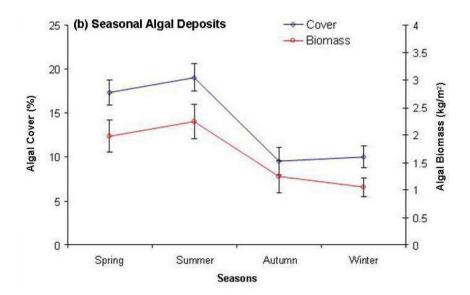


Figure 3.20 The seasonal changes in the amount of cover and biomass (wet weight) of decaying macroalgae deposits around the offshore breakwater at Elmer Beach. Data are mean values \pm SE.

3.3.5.3 Spatial differences in deposits between different bays and tombolos

The amount of macroalgae deposited within each of the four bays sampled differed significantly (p < 0.001, Table 3.5a) for the biomass of decaying algae deposits. Tukey's HSD *post hoc* test revealed that bay 6-7 received the least deposits and bay 2-3 the most (Fig. 3.21a). Overall, there was no difference in the quantity biomass of decaying macroalgae deposits between landward and seaward areas within the bays (p > 0.05, Table 3.5a).

Table 3.5 Two three-factor ANOVAs testing for the spatio-temporal effects of different a) bays and b) tombolos at Elmer on the biomass (kg) of decaying macroalgae deposits within the Elmer breakwater scheme. Variables for a) were factor 1, 'bays' with 4 fixed levels (2-3, 3-4, 4-5 and 6-7; n = 96), factor 2, 'vertical shore level' with 2 fixed levels (landward and seaward, n = 192; upper and lower landward combined as no difference shown in earlier analysis), and factor 3, 'time' with 12 fixed levels (month; n = 32). Variables for b) were factor 1, 'tombolos' with 4 fixed levels (2, 4, 6 and 8; n = 144), factor 2, 'vertical shore level' with 3 fixed levels (landward (upper), landward (lower) and Seaward; n = 192), and factor 3, 'time' with 12 fixed levels (month; n = 48). p = 100 set to 100 set

	a) Bays			b) Tombolos			
Variable	df	MS	F	df	MS	F	
B/To	3	1.18	16.27***	3	0.07	1.43 NS	
VS	1	0.11	1.55 NS	2	1.34	28.90***	
T	11	2.74	37.69***	11	0.94	20.38***	
VS x T	11	1.04	14.29***	6	0.18	3.92***	
VS x B/To	3	0.79	10.83***	33	0.33	7.19***	
T x B/To	33	0.46	6.35***	22	0.15	3.32***	
VS x T x B/To	33	0.41	5.69***	66	0.14	3.01***	

B = bays, VS = vertical shore, T = time, To = tombolos

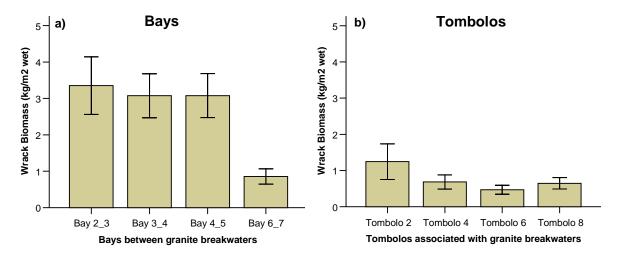


Figure 3.21 Detrital algae deposits associated within different (a) bays and (b) tombolos within the breakwater scheme at Elmer for March 2005-2006. Data are means \pm SE values.

The biomass of decaying macroalgae deposited on each of the four tombolos sampled did not significantly differ overall (p < 0.01, Table 3.5b). There were complex patterns in the biomass of macroalgae deposits up the vertical shore levels, with the biomass of deposits on the lower landward and seaward levels being significantly (p < 0.01) different; the latter had greater quantities (Fig. 3.22b). There were no differences between the upper landward and seaward shore levels.

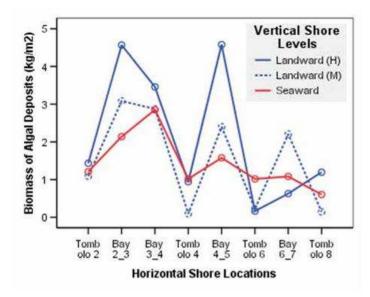


Figure 3.22 The (a) cover and (b) biomass of decaying macroalgae deposits within the offshore breakwater system at Elmer Beach for March 2005-2006; shows horizontal beach profile of different bays and tombolos on the landward and seaward sides of the breakwaters. Values are means data.

The lack of homogeneity in macroalgal deposits around the breakwaters may better be explained by examining the strong spatial interactions found between the different bays and tombolos with the vertical shore levels (Table 3.5). The greatest mean biomasses accumulated on the upper landward shore of bays 2-3 and 4-5 (4.57 kg/m² and 4.58 kg/m², respectively; Fig. 3.22b), whilst the least occurred on the upper landward and seaward shore levels of bay 6-7 (0.63 kg/m² and 1.08 kg/m², respectively). The upper landward end of each bay and tombolo received heavier patches than the seaward sides of the breakwaters, where it was thinly distributed. Deposition on the lower landward levels showed similar patterns as the upper landward levels but had marginally thinner and lighter cover.

3.3.5.4 Spatio-temporal interactions at Elmer

There were very strong significant interactions in the spatial and temporal deposition of decayed macroalgae on a monthly scale (p < 0.001; Table 3.3), with the deposition varying spatially with time. Tukey's HSD *post hoc* tests illustrated that tombolos had significantly less macroalgae for all months except August and November 2005. This was during months that had low quantities of cover (< 12 %) and biomass ($< 2 \text{ kg/m}^2$). When there was high cover (> 20 %) and biomass ($> 3 \text{ kg/m}^2$) there were significant differences between bays and tombolos; the greatest differences occurring in June and September 2005, with more than 80 % more macroalgal cover on the bays than tombolos. The spatio-temporal pattern for the vertical shore is more complex than horizontally for between the bays and tombolos (Fig. 3.22). Deposits on the seaward side of the breakwaters were different from the upper landward shore, but had overlaps with the lower landward sides of the structures. The greatest biomass occurred in May for both the seaward and lower landward areas, whereas this was in June for the upper landward section of the beach. In September there was a reasonably large deposit of macroalgae but only on the landward sides of the structures.

The seasonal trend in spatial macroalgae deposition showed clear differences between the bays and tombolos on the landward sides of the structures, while similar quantities occurred on the seaward side throughout time (Fig. 3.23). The seaward and lower landward sections showed the same seasonal trends as stated above, whilst the upper landward showed a marked difference in the summer, with an average biomass of more than 6 kg/m², and no difference to the amount of decaying macroalgae in the autumn.

3.3.5.5 Decaying macroalgae deposits around different types of CDSs

The biomass of detrital algae deposited adjacent to the different types of CDSs was different (p < 0.001, Table 3.6). The four bay sections adjacent to the granite breakwaters were analysed separately with each of the other two structure types because there were significant differences between each of these (Table 3.4). The amount of biomass was significantly greater adjacent to granite breakwaters (GB) at Elmer than both wooden and granite groynes, which were not significantly different from each other (Table 3.6 and Fig. 3.23). This pattern was true of all the

bays at Elmer except bay 6-7, where there was similar biomass to that found at Climping Beach (WG), but both still greater than at Felpham Beach (GG).

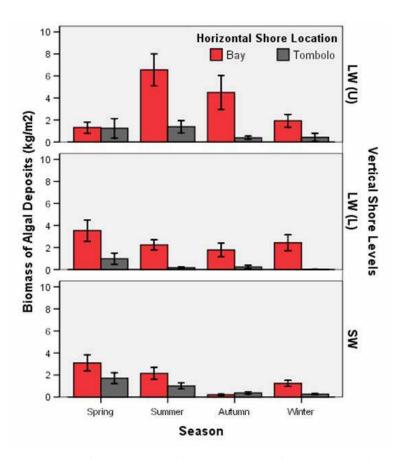


Figure 3.23 The seasonal changes in the amount of (a) cover and (b) biomass of decaying macroalgae deposits on the horizontal (bays and tombolos) and vertical (SW = seaward; LW (L) = landward (lower); LW (U) = landward (upper)) shore positions around the offshore breakwater at Elmer Beach. Data are mean values \pm SE.

When there were no significant differences in vertical shore level between the CDSs when Bay3-4 and Bay 6-7 were compared to Climping and Felpham; this was because there were neither significant differences between the upper (landward) and lower (seaward) shore deposits at Felpham, nor at Climping (p < 0.05) for both the biomass and cover (Table 3.6). There were however, significant differences in the quantity of detrital material between the landward and seaward sides of the granite breakwaters at Elmer; this has already been discussed in detail in sections 3.3.4.1 and 3.3.4.2.

Table 3.6 Results from a three-factor analysis of variance testing for spatio-temporal effects of different structure types on the biomass (kg) of decaying macroalgae deposited within beaches (bays) adjacent to CDS. Variables were factor 1, 'structure type' with 3 fixed levels (granite groynes, granite breakwaters (each bay tested separately) and wooden groynes, n = 80), factor 2, 'vertical shore' with 2 fixed levels (landward and seaward; n = 120), and factor 3, 'time' with 10 fixed levels (month; n = 24). p set to 0.01; *p <0.05, **p<0.01, ***p<0.001 and **NS** = not significant (p > 0.05).

Variable	df	MS	F	Variable	df	MS	F
Elmer Bay 2_3				Elmer Bay 4_5			
S	2	2.76	79.47 ***	S	2	3.6	77.55***
VS	1	0.73	21.17***	VS	1	1.33	28.62***
T	9	0.84	24.11***	T	9	0.77	16.50***
VS x T	2	0.35	10.04***	VS x T	2	0.55	11.93***
VS x S	18	0.66	19.15***	VS x S	18	0.49	10.59***
TxS	9	0.61	17.69***	TxS	9	0.59	12.61***
VS x T x S	18	0.43	12.47***	VS x T x S	18	0.35	7.60***
Elmer Bay 3_4				Elmer Bay 6_7			
S	2	4.5	83.61***	S	2	0.26	9.15***
VS	1	0.01	0.15 NS	VS	1	0.01	0.48 NS
T	9	0.75	14.01***	T	9	0.52	17.86***
VS x T	2	0.63	11.71***	VS x T	2	0.6	20.71***
VS x S	18	0.56	10.41***	VS x S	18	0.37	12.67***
TxS	9	0.59	11.00***	T x S	9	0.4	13.72***
VS x T x S	18	0.35	6.57***	VS x T x S	18	0.21	7.40***

S =structure type, VS =vertical shore level, T =time.

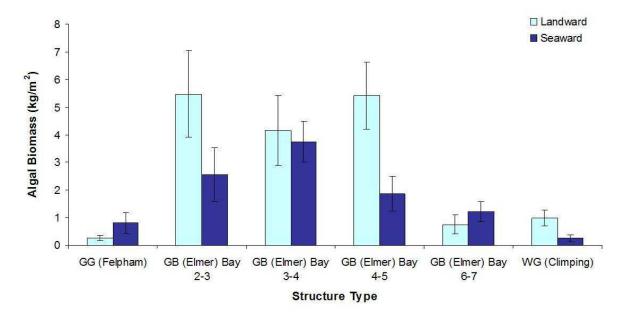


Figure 3.24 The differences in the biomass (wet weight) of decaying macroalgae deposits on beaches adjacent to three different types of CDSs (GG = Granite Groynes; GB = Granite Breakwaters; WG = Wooden Groynes). Vertical shore positions: landward and seaward are relative to the granite breakwaters. Data are mean values \pm SE (n = 144).

3.3.5.6 Temporal macroalgae deposits around different types of CDSs

There were differences in the seasonal deposits of decaying macroalgae between the three structure types (Fig. 3.25), with only the breakwaters experiencing a peak in the summer. In contrast, Felpham experienced the lowest quantity of macroalgal deposits of the year at this time, whilst Climping experienced no difference between the summer and spring seasons.

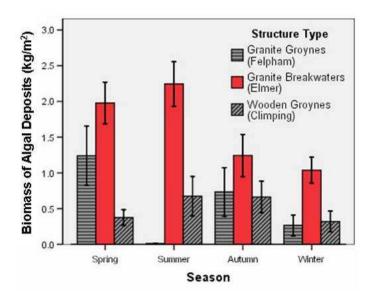


Figure 3.25 The seasonal changes in the amount of biomass of decaying macroalgae deposits deposited on the beaches adjacent to the three different coastal defence structure types (granite breakwaters, granite groynes and wooden groynes). Data are mean values \pm SE. Data from Elmer are for bays only.

No obvious patterns were seen for the monthly differences in deposits of decayed macroalgae adjacent to the different structures (Fig. 3.26). Overall for the majority of the year (March 2005 - 2006) the macroalgae deposits were significantly the greatest adjacent to the breakwaters at Elmer. April was the exception, as Felpham beach received the greatest algal deposits of all three beaches, as well as being the greatest for Felpham alone. The biomass of algal deposits on Climping beach was consistently low in comparison with that on Elmer beach (Fig 3.26), but similar to Felpham on most occasions. The survey showed that the biomass of macroalgae deposits left within the breakwater scheme in comparison with that of both types of groynes was often far greater, for example, in May the deposits were over 4 times as great at the other beaches.

Tukey's *post hoc* tests showed that Climping and Felpham generally experienced greater quantities of decaying macroalgae in the upper shore. It can be seen at Elmer that differences

occurred in the amount of macroalgae deposits between the landward and seaward sections of the shore in the spring and summer months, whereas from November to March 2006 there was no difference in vertical pattern of deposition.

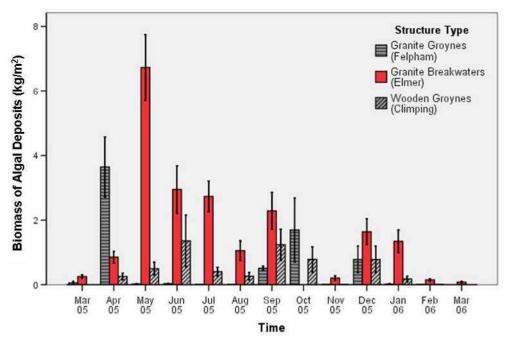


Figure 3.26 The monthly changes in the amount of biomass of decaying macroalgae deposits deposited on the beaches adjacent to the three different coastal defence structure types (granite breakwaters, granite groynes and wooden groynes). Data are mean values \pm SE. Data from Elmer are for bays only.

3.4 Discussion

Large quantities of decaying macroalgae have been deposited on a regular basis along the beaches of the south west coast of Sussex, England. Such a phenomenon has been recorded and quantified on many occasions worldwide (e.g. Griffiths et al. 1983, Lenanton et al. 1985, Ochieng & Erftemeijer 1999, Dugan et al. 2003, Mews et al. 2006), although this study differed from these in a number of ways. Firstly, this study quantified decaying macroalgae depositions on an intertidal beach with low crested breakwaters over a range of temporal scales from daily to annually; most previous studies had only focused on one or two scales. In addition, the main potential environmental drivers of decaying macroalgae deposition and removal (such as winds and nearshore currents) were investigated, as well as their interactions. Previously these processes were not well understood (Kirkman & Kendrick 1997). This study showed that there were complex interacting temporal cycles in decaying macroalgae deposits with wave parameters, sea surface temperature, and tidal and lunar cycles. Secondy, it assessed the spatio-

temporal deposition of decaying macroalgae within a low crested breakwater scheme, as well as two other nearby beaches with groyne structures, which had not been done before.

Over a one year period (March 2005 – 2006), considerably greater quantities of decaying macroalgae were found to be associated with the LCSs at Elmer than with the groynes at Felpham and Climping, with an estimated deposition margin of 600 - 2,300 kg/m²/yr of stranded macroalgae at Elmer. This was overall three times greater than the stranded macroalgae around the granite groynes at Felpham Beach (200 - 800 kg/m²/yr) or the wooden groynes at Climping Beach (200 - 600 kg/m²/yr). The detrital algae at Elmer showed most variability both spatially and temporally, which gave rise to the large estimated range. The findings of this chapter suggest that the relatively closed breakwater scheme can affect the amount of decaying macroalgae trapped on the beaches to a greater degree than more open defence schemes such as groyne fields. Dugan et al. (2003) had also previously suggested this, but from observations rather than directed studies.

3.4.1 Temporal Depositions of Decaying Macroalgae

The macroalgae composition was dominated overall by Chondrus crispus, but mainly in the autumn and winter months and opportunistic ephemerals (Ulva spp. and Ectocarpus sp.) and filamentous red algae (*Polysiphonia* spp. and *Ceramium* spp.) dominated in the summer months. This composition differed from that reported by Olabarria et al. (2007), who found detrital algae deposits on an exposed sandy beach in Spain were composed of brown algae (e.g. Laminariales and Sargassum muticum (Yendo) Fensholt). My results were, however, similar to the Ulva sp. and macroalgal blooms found by Ochieng and Erftemeijer (1999) on a Kenyan beach, and the red filamentous algal cast walls on Baltic beaches studied by Malm et al. (2004). Comparisons with other studies show that the quantity of decaying macroalgae deposits at Elmer was comparable to the decaying macroalgae stranded on beaches in South Africa (Griffiths et al. 1983) and Western Australia (Hansen 1985, quoted in McLachlan 1985) their estimations were 1,200 - 2,179 kg/m²/yr and 1,900 kg/m²/yr, respectively. Griffiths et al. (1983) calculated that for a high wave energy beach with an estimated 1,200 – 2,179 kg/m²/yr of kelp wrack that there was an energy flux of > 2 million KJ/m/yr. It was not possible to extrapolate from this as the species composition of the macroalgal deposits was very different. It does, however, show the potential importance of the quantities deposited at Elmer. The amount of decaying macroalgae at Climping and Felpham beaches was comparable to the beaches studied in Southern California (Dugan et al. 2003) and New Zealand (Marsden 1991a), with estimated inputs of 473 kg/m²/yr and < 400 kg/m²/yr, respectively; they considered these biomasses to be small deposits. It is important to bear in mind that the amount of macroalgae deposited in the intertidal depends on the standing stock of macroalgae on nearby subtidal rocky reefs and the local environmental drivers, such as geomorphology, hydrodynamics and beach type.

There were certain limitations when comparing my data to other studies. Environmental parameters that may influence the deposition of decaying macroalgae, for example, the wind, wave, temperature and tidal environments will differ, and their extent are often not stated in the literature. Most importantly, species composition can vary and different species may have different implications for the sediment environment they are deposited on. For example, kelp species are nutritionally important large, heavy macrophytes (Duggins et al. 1989, Kirkman & Kendrick 1997), and have been shown to harbour diverse invertebrate communities after deposition. Whereas, filamentous red algae and ephemerals are light in biomass, and as a result of their complex morphology retain large amounts of water when the tide recedes (Orr et al. 2005), in addition, species-specific toxic phenolic compounds are known to be released (Malm et al. 2004, Eklund et al. 2005). C. crispus, the dominating species in this study, is a very slowdecaying species of poor nutritional value when first stranded, requiring mechanical break down before being nutritional valuable (Ochieng & Erftemeijer 1999). So, although there were large quantities of stranded decaying macroalgae, it was not possible at this stage to infer the nutritional importance to the surrounding ecosystem without investigating the immediate decay rate and nutritional properties (see Chapter 6 for more details) of the dominant species in the deposits on Elmer Beach.

The amount and timing of deposits is extremely variable and may differ geographically depending on climate, hydrodynamics, the vicinity to rocky reefs (Ochieng & Erftemeijer 1999, Colombini et al. 2000), and the dominating macroalgal composition on the reefs. This study has shown that rapid sea temperature rise over a short period of time (e.g. one or two days) was potentially an important driver of detrital algae deposition, causing strong seasonal and daily patterns to occur in both the quantity and species composition of macroalgae stranded on the beaches in this study. From these results, it was estimated depositions of $800 - 2,700 \text{ kg/m}^2/\text{yr}$ at Elmer in the summer, when there were no storms and the seas were calm for long periods;

this was twice the amount deposited in the winter months (400 - 1,500 kg/m²/yr), when storm frequency and severity were the greatest. These findings differed from the majority of studies in this field of research, where, for example, in South Africa (Griffiths et al. 1983), Kenya (Ochieng & Erftemeijer 1999), Australia (Lenanton et al. 1985, Crawley et al. 2006) and Argentina (Piriz et al. 2003) decaying macroalgae deposits were greatest during seasons with frequent storms and heavy swells (i.e. winter or monsoon seasons). The macrophyte composition in these particular studies mainly consisted of kelp, other brown algae and seagrass, but little red or green algae. Nevertheless, studies in South Africa by McLachlan and McGwynne (1986) and Van der Merwe and McLachlan (1987), and on the Baltic coast by Malm et al. (2004) reported similar findings to this study with the greatest biomasses occurring in the spring and summer when the seas were calm. Furthermore, following a study on a Polish beach, Jedrzejczak (2002) stated that only during a storm was the beach completely devoid of debris.

A possible reason for the difference in the peak macroalgae deposits in this investigation in the summer to those studies with large algal deposits in the winter season may have been because of the difference in the macroalgae species composition of the nearby sourcing subtidal reefs. From the published literature, beaches in the vicinity of large shallow kelp beds appear to experience deposits in the winter months, as the storms tear up the senescent stages of the kelp, other large brown algae and seagrasses (Hanisak 1993, Olabarria et al. 2007); these deposits are considered important to beaches of low productivity (Dugan et al. 2003, Olabarria et al. 2007). In contrast, those beaches in the vicinity of deeper reefs dominated by filamentous algal species, are more likely to be influenced by sea temperature and nutrient influxes (Malm et al. 2004), thus resulting in large beach deposits in the summer months. There may be graver consequences for beaches close to reefs with filamentous algal species, as during the summer months beaches are of higher economic importance than in the winter months because of tourism. Summer deposits may, therefore, be more of a nuisance, particularly because of the reduced aesthetic qualities of the beaches for human use (Lavery et al. 1999). Furthermore, high temperatures mean algal deposits decay more rapidly (Olabarria et al. 2007), often inducing unpleasant smelling, toxic hydrogen sulphide compounds (Eklund et al. 2005) both in the sediment and between the sediment-algae interface (Norkko & Bonsdorff 1996b), this can result in oxygen deficient sediments, which is detrimental to benthic organisms (Kolbe et al. 1995, Raffaelli et al. 1998).

The use of quantitative wave data in this study has shown that storm events were not the main drivers of algal deposition, which is what many studies have stated (e.g. Lavery et al. 1999), often without quantitative measurements of the wave height or severity of storms. Instead deposition is driven by tides and sea temperature, with greater quantities of decaying macroalgae being deposited during spring tides; this concurs with the findings of Ochieng and Erftemeijer (1999). Although, when large swells and strong winds coincide with strong spring currents (Ochieng & Erftemeijer 1999), the deposition can be greater than without. There is little doubt that monthly sampling would have observed the seasonal findings mentioned earlier, correlating stormy weather with low depositions. However, the importance of tidal currents and temperature would not have been observed without daily surveillance over a range of temporal scales.

Orr et al. (2005) stated that it is not possible to predict deposition patterns daily deposition having only studied one tidal cycle. These findings showed that temporal replication at a range of scales are absolutely necessary to be able to predict the environmental influences and main drivers. Another example of how decaying macroalgae deposits can be misinterpreted if studies lack a range of temporal scales is annually. For example, this study showed that when investigating the summer seasons 2005 and 2006 at Elmer, the biomass quantities were very similar (3.6 and 3.5 t/m²). However, when observing on daily, weekly and monthly scales for the same period, it became clear that there were significant differences. Greater fluxes in algal deposits were experienced in 2006, coinciding with an unusually warm sea in comparison to 2005 (2° C difference). In support of this, Malm et al. (2004) suggested that the annual differences seen in annual deposits on Baltic beaches were also due to changing sea temperatures. If only seasonal sampling had been carried out, this complex pattern would not been observed, resulting in a distorted perception of the extent of decaying macroalgae deposits.

3.4.2 Spatial Deposition of Decaying Macroalgae

Turning now to the spatial distribution of decaying macroalgae deposits around the CDSs; this was heterogeneous, with the structure type affecting the amount of deposition. Not only was there overall greater amounts of macroalgae deposited within the breakwater scheme Elmer than the groynes, but the pattern of horizontal and vertical shore distribution was more affected by the presence of the breakwaters than by the groynes. The breakwater scheme resulted in

complex tidal current characteristics, with the gap width between the breakwaters strongly influencing spring and neap tidal current fluxes (Plomaritis 2006; see Section 2.5). The gap width would appear to have impacted the amount and spatial deposition of stranded macroalgae. Bays 3-4 and 4-5 received large deposits of macroalgae, this was where there was greatest flow constraint as the gap widths were the smallest (44 m and 60 m, respectively), which results in the fastest alongshore currents (> 0.4 m/s) over the adjacent tombolos into the bays, and slow restricted currents flowing out through the gaps from these bays (see Section 2.5). With a width of 140 m, two or three times the width of the other bays, bay 6-7 experienced reduced water flow (< 0.2 m/s) because the gap was designed to allow free-flow (Plomaritis 2006). This bay received less algal deposits, which was similar to the beaches with groynes (particularly Climping). Beaches with groynes do not experience vertical on- and offshore flow restriction as experienced by the presence of the breakwaters; this therefore leads to the assumption that gap width plays an important role in determining the degree of decaying macroalgae deposits in areas with high amounts of source material, for example at Elmer.

The current flow regime at Elmer beach appears to correspond to the amount of algal deposits within the breakwater scheme; the most likely reason for this, is because macroalgae accumulates in the bottom layer of water (Bock & Miller 1995), thus reducing the water to algae ratio causing greater quantities of macroalgae to be pushed through the system on the incoming tide. On the receding tide the algal species with the least buoyancy will get deposited first (Orr et al. 2005), accounting for the greater biomass to the amount of cover on the landward compared to the seaward sides of the structures. Less macroalgae was deposited on tombolos than bays; current flow is greatest over the tombolos during high tide (Plomaritis 2006) with fast currents flowing into the bays carrying the macroalgae with it on a receding tide. Where tombolos were closest to the MHWS mark (e.g. tombolo 2 and 8) there was restricted flow with slower currents, resulting in higher algal cover than tombolos further from the upper shoreline, with less constricted flow. Less decaying macroalgae was deposited on the seaward sides of the breakwaters, as there were no flow restrictions as found on the landward sides. The cover was thin and light, as the majority of decaying macroalgae had been deposited landward of the structures on the receding tide.

These findings show that alongshore current strength within the scheme and on- and offshore wave fluxes, determined by the presence of the structures potentially determine the spatial

deposition of decaying macroalgae deposits on the beach, particularly when there is flow restriction; the weaker and more constricted the flow, the more detrital algae appears to have been deposited. The restriction of the vertical flow (i.e. in- and offshore waves) combined with the alongshore currents within the low crested breakwater scheme has more far-reaching consequences than defence structures that just interfere with longshore drift (e.g. groynes). This agrees with the findings of Lavery et al. (1999), who stated that 'poorly flushed' beaches had higher macrophyte biomass than well-flushed beaches. Furthermore, Ochieng and Erftemeijer (1999) indicated that the coastal morphology (e.g. rock protrusions) changes the hydrodynamics and thus will impact the accumulation process, as greater detrital algal deposits were found near rocky outcrops. Groynes, although these restrict the horizontal longshore drift and, therefore, perhaps affect the current circulation, do not by any means restrict the vertical flow (i.e. oncoming waves) that appears to be the most important.

The understanding of the depositional patterns of decaying macroalgae can help understand the influence on the sediment macrofaunal communities on these sandy beaches; this was investigated and reported in Chapter 4. This is an important issue because there may be threshold effects, with detrimental consequences from excess deposits (e.g. high toxicity and reduced oxygen availability (Malm et al. 2004)), particularly, when consisting of ephemeral and filamentous algae that may release toxic phenolic compounds (Eklund et al. 2005). Macrofauna inhabiting sandy beaches have been reported in past studies to respond to the spatio-temporal variability in the supply of drift macrophytes (e.g. Koop & Griffiths 1982, Stenton-Dozey & Griffiths 1983, McGwynne et al. 1988a, McGwynne et al. 1988b, Dugan et al. 2003). So, when there are smaller more regular deposits, there may be the beneficial addition of nutrients (Rossi & Underwood 2002).

3.5 Conclusions and Recommendations for Further Work

The decaying macroalgae deposits at Elmer were taxa and species diverse and predominantly subtidal species. The diversity changed with time, though red algae were the most dominant. In the summer months the algae were dominated by filamentous red and opportunistic ephemeral green algae, whereas in the winter months *Chondrus crispus*, a tough red algae, was dominant. This study also described the temporal decaying macroalgae depositional patterns along with the environmental variables of waves, spring and neap tidal currents and sea surface temperature at

Elmer beach. In the year that this study was carried out (2005 - 2006), it was found that greatest algae deposits occurred in the summer months $(800 - 2,700 \text{ kg/m}^2/\text{yr})$, when the sea was calm and warm. The amount of algae was greatly reduced in the winter months $(400 - 1,500 \text{ kg/m}^2/\text{yr})$ when there was a higher frequency of storms and increased wave action. In the summer months, tidal cyclicity (i.e. neaps and spring tides) had a strong correlation with the quantity of macroalgae deposits; with the greatest amount of algae being deposited around spring tides and the least around neap tides. In the summer months,

Furthermore, the spatio-temporal patterns in algal deposits were primarily studied at Elmer beach within the breakwater scheme, as well as at Felpham and Climping beaches with groyne structures. The spatial deposition patterns of algae on Elmer beach were complex. The results illustrated that overall there was three times the amount of algae deposition within the bays compared to the tombolos; this difference was more accentuated in the summer months when the deposits were overall at their greatest, and less so during the winter months. The results indicated that greater amounts of decaying macroalgae were deposited or trapped within the breakwater scheme $(600 - 2,300 \text{ kg/m}^2/\text{yr})$ than around groynes on the nearby beaches of Felpham $(200 - 800 \text{ kg/m}^2/\text{yr})$ and Climping $(200 - 600 \text{ kg/m}^2/\text{yr})$.

Future research should clarify the indications that there were more algae within the breakwater scheme in comparison with that at Felpham and Elmer. Investigations should compare the decaying macroalgae deposits within other low crested breakwater schemes, as well as a thorough comparison with adjacent beaches using a balanced design. The source of the macroalgae is very important and to investigate where this had come from would be extremely beneficial and would give a greater understanding into which types of beaches are likely to experience such problems. In addition, studies should assess the threshold influence of decaying macroalgae deposits on the sandy beach communities surrounding CDSs, as their response will depend on algal deposit patch size (Olabarria et al. 2007). In addition, the decomposition, colonisation and consumption of the decaying macroalgae deposits around CDSs needs to be investigated, so as to gain an understanding of the consequences and importance of this allochthonous resource.

Chapter 4: Sediment Faunal Assemblages and Decaying Macroalgal Deposits

4.1 Introduction

Sandy beaches are dynamic systems and the most widely distributed intertidal ecosystem, dominating both temperate and tropical shores (Rodil et al. 2007). Extensive research has shown that the species composition, density, biomass and zonation patterns of the macrobenthos of sandy beaches are extremely variable in both space and time (McLachlan 1977, 1980, Morrisey et al. 1992a, Morrisey et al. 1992b, Jaramillo et al. 1993). Sandy beaches are often characterized by high wave action, mobile sediments and the absence of attached macrophytes (McLachlan, 1980). In exposed intertidal environments, intertidal fauna are mainly controlled by physical conditions and are dominated by crustaceans (Short & Wright 1984, McLachlan et al. 1993), whilst sheltered environments are controlled by biological factors and dominated by molluscs and polychaetes (Brown & McLachlan 1990). It has been suggested that the hydrodynamic stress (e.g. dislodgement risk from wave exposure) is the major limiting factor of biological richness at exposed localities (McLachlan et al. 1996), and that several ecological factors interact to influence community composition and structure rather than a single key factor (Rodil & Lastra 2004). On more stable muddy sheltered shores biological factors are more important, such as the activities of ecosystem engineers providing biogenic habitats (seagrasses, reef forming mussels and oysters) and bioturbation. Biological interactions such as competition (Dexter 1992, Defeo et al. 1997) and predation (Thrush 1999, Barros 2005) can also be important.

The sediment regime can determine the trophic status of benthic assemblages (Martin et al. 2005). Fine organically rich muds have a tendency to contain more burrowing deposit feeders (Martin et al. 2005), whereas coarser sediments usually harbour suspension feeders and more mobile animals (Martin et al. 2005). Beaches that receive decaying macroalgae deposits at regular intervals may experience communities dominated by deposit feeders and detritivores as more organic matter would be expected to enter the ecosystem.

Major contributors to the detrital pools in coastal systems are decaying plant material, especially marine seagrasses and seaweeds, and animal faecal pellets. Organic detritus has long been recognized as an important food resource in shallow water aquatic environments (Tenore et al. 1982). However, if seaweed detritus occurs in excess quantities the underlying sediment can become more reducing, often leading to anoxia and the accumulation of toxic hydrogen sulphide, with potentially negative effects on the sediment faunal communities (Bolam et al. 2000). Although these effects have been well studied (Hull 1987, Bonsdorff 1992, Everett 1994, Bolam et al. 2000, Kelaher & Levinton 2003), the effects of detrital algae cover on sediment fauna (Bonsdorff 1992) and the mechanisms by which these effects are brought about (Raffaelli et al. 1991) are poorly understood, and will be dependent on the type, quantity and length of residence time of the detritus. For example, Hull (1987) found the effect of seaweed detritus on Pygospio elegans Claparède was algal biomass-dependent, with lower biomasses causing increases in P. elegans, whilst at higher biomasses P. elegans declined. More recently, a study by Bolam et al. (2000) found that after six weeks, intertidal seaweed mats significantly increased the macrofaunal diversity, but after 20 weeks the diversity was markedly reduced, being dominated by opportunistic species e.g. Capitella capitata (Fabricius). They concluded that the effect of weed cover on species abundance were both dramatic and complex and can play an important role in structuring benthic assemblages. In concurrence, Kelaher and Levinton (2003) stated that detritus enrichment can generate the complicated spatio-temporal patterns observed in natural annelid assemblages seen in soft-sediment assemblages. The long term ecological consequences of seaweed detritus depend upon the spatial distribution of the dominant macrofaunal species and the spatial heterogeneity of detritus deposition.

The deployment of artificial rocky defence structures along sandy shores prevents coastal erosion by interrupting wave action. They modify the coastlines exposure to waves (Martin et al. 2005, Moschella et al. 2005) and cause changes to the near-shore circulation (Zyserman et al. 2005) and cross-shore/offshore transport of sediment (Thomalla & Vincent 2003, Cuadrado et al. 2005), which changes the bottom topography, sediment grain size and organic content (e.g. Bull et al. 1998). Hydrodynamics have long been considered as the ultimate factor not only affecting the spatial distribution of different sediment types but also the associated benthic organisms (e.g. Nowell & Jumars 1984, Miller & Sternberg 1988). The modified wave regimes and depositional processes caused by the CDSs may, therefore, impact the composition, abundance and trophic structure of benthic assemblages inhabiting the surrounding sediments

(Bacchiocchi & Airoldi 2003, Degraer et al. 2003, Martin et al. 2005, Bertasi et al. 2007) and further influence the depositional patterns of decaying macroalgae deposits.

Despite the global proliferation of CDSs (see Chapter 1 for further details), there have been only a small number of studies investigating the impact of hard coastal defence structures on the adjacent soft bottom fauna (Davis et al. 1982, Ambrose & Anderson 1990, Correggiari et al. 1990, Coosen et al. 1994, Barros et al. 2001, Fabi et al. 2002, Jaramillo et al. 2002, Barros et al. 2004, Martin et al. 2005, Bertasi et al. 2007). There have been no studies to date that have investigated the impact of CDSs in conjunction with the effect of detrital macroalgae deposits on the surrounding benthic communities. There have, however, been many studies on the effects of macroalgal mats on soft-bottomed subtidal areas and intertidal mud and sand flats (e.g. Soulsby et al. 1982, Hull 1987, Raffaelli et al. 1991, Bonsdorff 1992, Everett 1994, Bolam et al. 2000).

Until the last decade, most benthic faunal studies have focused on one site and/or at single times and mostly around subtidal man-made structures (e.g. artificial reefs). Observed changes in benthic assemblages adjacent to such artificial structures may be caused by alterations in the intensity of movement of water, direction of currents, rates of erosion or sedimentation and organic content of sediments (Fabi et al. 2002). These subtidal studies are comparable on some levels with the intertidal zone, in terms of the alteration to the local hydrodynamics, but in a high energy intertidal environment there is the added complexity of wave and tidal current hydrodynamics. Macrobenthic distribution patterns of intertidal beaches have long been shown to be related to beach elevation and wave exposure, with species occurring at specific tidal levels (e.g. McLachlan & Jaramillo 1995, Degraer et al. 2003). Consequently, it is important to understand that local factors (e.g. shore morphodynamics, tidal range, wave exposure) together with design criteria of LCSs (e.g. number of modules, size, orientation, porosity, distance from the coastline) can result in a variety of changes to the hydrodynamic and the sediment environment (Burcharth 1993). The impact of LCSs on the surrounding benthic environment is clearly context dependent (Bertasi et al. 2007), making generalization difficult.

Recently, Jaramillo et al. (2002) conducted a study on an intertidal beach in Chile before and after a seawall was constructed, to investigate the effects of the changing morphodynamics on the beach fauna. Their findings showed no changes in the infaunal community between before

and after or control and impact sites, showing that the presence of the seawall had no influence on the physical and macro-infaunal characteristics of the beach. These findings contrasted with those reported by Castellanos et al. (2003), who examined the long-term changes in macrofaunal assemblages before and after the construction of an offshore breakwater in North West Spain. They found the breakwater introduced modifications to the hydrodynamic and sedimentary regime, which resulted in changes in the distribution of the three benthic assemblages recorded.

Furthermore, a number of comprehensive studies were carried out on intertidal beach environments along European coastlines as part of an integrated European project DELOS (Martin et al. 2005, Bertasi et al. 2007, Burcharth et al. 2007). The main findings from this project were summarised by Martin et al. (2005); their objectives were to identify, describe and quantify both the negative and positive effects of low crested coastal defence structures on five defended beaches in Spain (Mediterranean Sea), Italy (Adriatic Sea) and the UK (English Channel and Irish Sea). Martin et al. (2005) stated that changes to the sediment environment and benthic fauna on beaches where LCSs were constructed would be inevitable, with a tendency towards negative changes for the sediment faunal communities, particularly on the landward side of the structures. The study by Bertasi et al. (2007) looked further at the effect of the LCS scheme at Lido di Dante (Italy), specifically investigating the structure of macrofaunal communities and their interactions with the environment at three different exposure levels with respect to wave action, as well as the combined effect of beach elevation. Their findings showed greater species numbers in the sheltered locations behind the LCSs compared to exposed zones; these results were not reported in previous studies dealing with CDSs (Davis et al. 1982, Ambrose & Anderson, 1990, Barros et al. 2001, Fabi et al. 2002, Jaramillo et al. 2002, Burcharth et al. 2007). The reasoning given for this increase in species numbers not seen previously by other studies was because at Lido di Dante the breakwaters were enclosed at either end by groynes, resulting in a marked reduction of flow in the sheltered zone. This design feature was rare on the other European beaches studied or in any of the earlier studies prior to the DELOS project.

The LCSs at Elmer was the main study site for this research; this defence system was also examined as part of the DELOS project, where a preliminary study investigated the effect of the LCSs on the surrounding benthic communities (Martin et al. 2005). Martin et al. (2005) found

that the presence of the breakwaters at Elmer did not significantly change the sediment environment (e.g. grain size, carbon content and chlorophyll content) across the beach, either in close proximity to the structures or at increasing distances from them. There were also no differences between the sediment environment at Elmer and the control beaches (without breakwaters). Although there were no significant differences in the number of species or trophic structure between the landward and seaward sides of the breakwaters at Elmer, the community structure showed patterns indicating an overall increase in diversity on the landward sides. Martin et al. (2005) found that the influence of the Elmer LCSs on the surrounding sediment communities was localized, with small impacts. They concluded that the more the wave and water regimes are altered, the greater the changes will be in the sediment faunal communities; in particular LCSs will increase diversity by changing uniformly exposed, coarse sand assemblages to a localized mosaic of different types of assemblages.

There still remains little information on the influence of arrangement and layout of structures on the degree of impact on the fauna (Martin et al. 2005). The scheme at Elmer is multifaceted in design (e.g. varying breakwater lengths, gaps and distances from the shore) resulting in complex hydrodynamics and sediment transport pathways (Plomaritis 2006). Previous work at Elmer (e.g. Martin et al. 2005) was carried out by investigating the impacts of the LCSs on the communities on the landward and seaward sides of the structures (i.e. on the tombolos), but not in the bays created between the breakwaters. The bays within the scheme experience reduced tidal currents (see Chapter 2), in comparison the tombolos experience fast currents, similar to the seaward sides of the structures (Plomaritis 2006); furthermore, the beach elevation differs between the bays and tombolos (author's pers. obs., see Chapter 2). These factors may influence the benthic communities, resulting in differences that have not been studied to date. Furthermore, the tidal currents at Elmer have been shown to vary in both speed and direction during neap and spring tides across different areas of the scheme (Plomaritis 2006), further complicating any prediction of the responses of the surrounding benthic fauna. The study by Martin et al. (2005) at Elmer, investigated the annual differences of two summers, which is the period of the year when the wave impact is lowest and decaying macroalgae deposits were greatest (author's pers. obs., see Chapter 3). Infaunal communities may exhibit large differences in vertical shore zonation patterns between landward and seaward communities and horizontally between bays and tombolos at other times of the year when decaying macroalgae deposits are less and wave exposure is greater.

The general aim of this study was to describe the spatial variation in the benthic infaunal communities surrounding the low crested structures within the breakwater scheme at Elmer on the West Sussex coastline near Bognor Regis. Two neighbouring beaches with granite groynes and wooden groynes were also studied in order to compare the differences or similarities in the benthic communities. The field survey was conducted during six different months over one year. Furthermore, to determine whether the decaying macroalgal deposits (determined in Chapter 3) on these beaches had any positive or negative impact on the species diversity or abundances of individuals of the benthic communities. The macrobenthic communities on the beach at Elmer had been recently studied by Martin et al. (2005); this work extends on their spatial and temporal coverage.

There were three specific objectives:

- 1. To describe temporal and spatial variations in the sediment environment at Elmer beach (with the LCSs), as well as at Felpham (granite groynes) and Climping (wooden groynes) beaches. Thus, the null hypothesis, that there were no differences in the sediment characteristics (e.g. grain size, carbon content, sediment water retention and depth of hydrogen sulphide layer) for each of the three beaches with different types of structures was formally tested.
- 2. To describe the spatial-temporal variation in the benthic communities at these three beaches. Four null hypotheses were formally tested; that there were no:
 - a. Differences in the benthic communities between different vertical shore levels: landward (upper and lower) and seaward sides of the CDSs.
 - b. Differences in the benthic communities between ten horizontal shore locations from three beaches with different CDSs (breakwaters and two types of groynes), and that there were differences in the type of horizontal shore (i.e. between and within bays and tombolos of the breakwater scheme at Elmer beach).
 - c. Interactions between the vertical shore level and horizontal shore locations.
 - d. Temporal changes in the benthic communities.
- 3. To determine which environmental variables (e.g. sediment environment, wave variables, current flow and amount of decaying macroalgae) most influenced the spatial and temporal differences in communities adjacent to the CDSs.

4.2 Materials and Methods

4.2.1 Study Location

The West Sussex coastline between Bognor Regis and Littlehampton, on the south coast of England, is protected by different types of CDSs (Fig. 2.1) (Chapters 1 and 2 give a detailed area description). This coastline is subjected to high wave action in the autumn and winter months due to the predominantly southwesterly winds. Continuous survey data from the Channel Coastal Observatory (CCO) for March 2005 to February 2006 revealed an average height and period of the waves along this coastline of 0.8 m and 6.6 s, respectively, while 6.6 m and 15.2 s were the maximum measured maximum wave height and period. The area has a semi-diurnal, macrotidal regime; with a spring tidal range of 5.3 m and a neap tidal range of 2.9 m. Protection by an assortment of CDSs has changed the hydrodynamics and degree of exposure to wave action of the beaches on this stretch of coast (Plomaritis 2006, Burcharth et al. 2007). The main study site of Elmer beach and the two neighbouring beaches (Felpham and Climping) as those studied in Chapter 3 (see section 3.2.1) were used to investigate the influence of different CDSs on the surrounding benthic communities and the impact of decaying macroalgae deposits on the benthos.

4.2.2 Macrobenthic Survey

The benthic faunal communities around the three different CDSs: granite breakwaters (Elmer), and granite and wooden groynes (Felpham and Climping), were surveyed for five times over a year (March, May, August, November, January) between March 2005 and January 2006. These five sampling months were to represent winter (March 2005, January 2006), spring (May), summer (August) and autumn (November). The survey design used for describing spatiotemporal variation was the same as that described for the assessment of decaying macroalgae deposits in Chapter 3 (more details of the survey can be found in section 3.2.2.4). The beaches were vertically divided (relative to the granite breakwaters at Elmer) into three shore parallel levels (upper and lower landward, and seaward) and horizontally divided into two types of shore location: bays (areas adjacent to / between CDSs) and tombolos (areas immediately behind and in front of the Elmer breakwaters) (Fig. 4.1). In total there were ten horizontal shore locations: one bay at both Felpham and Climping, four bays and four tombolos at Elmer (Fig. 4.1).

In each shore location, for each month and for each shore level (referred to as a 'station') cores were collected for the assessment of the benthic communities and sediment analysis (see sections 4.2.3 and 4.2.5 for further details). Extra cores were taken in June for the three sites, although at Elmer only Tombolo 4 and Bay 4-5 were sampled. This was to determine the effect of very large algal deposits that occurred in May ($> 7 \text{ kg} / \text{m}^2$).

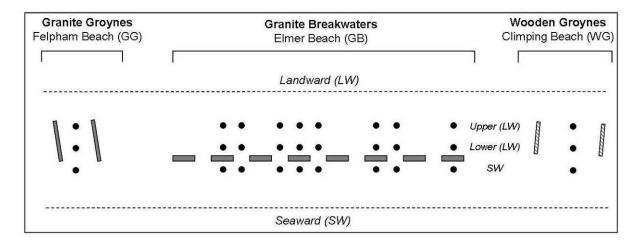


Figure 4.1 Schematic diagram of sampling strategy used to assess the influence of different types of coastal defence structures on the surrounding benthic communities. Black dots (station) show the ten horizontal shore locations across the three beaches (Felpham, Elmer and Climping) with three vertical shore levels (upper and lower landward, and seaward). Four replicate faunal samples were taken at each station.

4.2.3 Measurement of Physicochemical Beach Variables

At each station, one core (diameter, 2 cm) was collected for sediment analysis. Recordings were taken of the subsurface sediment temperature (measured at 10 cm depth), the depth of oxic layer (the depth from the sediment surface to the black hydrogen sulphide layer), and the sediment water retaining ability (rank scale 1 to 5, where 1 is dry and 5 is waterlogged). The sediment water retention was measured by observing the speed with which the hole (where the cores were taken) filled with water. Furthermore, salinity measurements were taken but these were inaccurate as they depended on the amount of water in the sediment. There was however a significant positive relationship between the sediment water retention rank scale and the salinity measurements ($r^2 = 0.786$, p < 0.05), thus allowing the salinity measurements to be used a numerical form of sediment water retention.

Sediment samples were immediately dried on return to the laboratory at 60° C for 48 hours; the grain size distribution was then determined by dry sieving through the Wentworth size scheme (mesh sizes 8, 4, 2, 1, 0.5, 0.25, 0.125, 0.063 and < 0.063 mm) using a mechanical shaker for 10 min. Three replicate dried sediment sub-samples were ashed at $500 \pm 50^{\circ}$ C for 4 hours to determine the percentage of Total Organic Matter (TOM), by loss of mass on ignition.

The beach elevation (metres above Ordnance Datum Newlyn (ODN)) for each of the stations sampled at Elmer Beach were obtained from lidar-derived data from the CCO and cross-referenced with Global Positioning System (WGS 84 ± 0.2 m) points for each station (Fig. 4.2; see Section 2.3 for the lidar originated digital elevation model and further details)

4.2.4 Measurement of Decaying Macroalgae Deposits

The amount of macroalgae deposited at each of the three beaches was assessed in detail in Chapter 3 (Sections 3.2.2.3 and 3.2.2.4). The same spatial survey used for the algal deposits was used to assess the benthic faunal communities; this was so that the effect of detrital deposits on the communities could be directly compared with statistical validity. The amount of decaying macroalgae deposited was measured by cover (%) and biomass (kg/m² wet weight).

4.2.5 Measurement of Benthic Macrofaunal Communities

The composition and density of sediment macrofaunal communities was determined for six months (Mar, May, Jun, Aug, Nov, Jan) between March 2005 and January 2006, each time sampling on one randomly chosen spring tide (one beach per day). Sampling always started at high tide and followed the receding water down the beach, ending at low tide. Sampling was carried out by taking four replicate cores (surface area: 57 cm²) to a depth of 10 cm at each sampling point. The sediment within the core was immediately transferred to 1 litre plastic containers and transported to the laboratory, where the samples were fixed, stained and preserved in a 4 % formaldehyde-seawater solution with 0.01 % Rose Bengal, and later stored in 70 % propanol. Macrofaunal samples were wet-sieved through a 0.5 mm mesh in the laboratory and organisms were sorted and identified to species (where possible) with a microscope. Faunal densities were extrapolated to the number of individuals per m² (ind/m²).

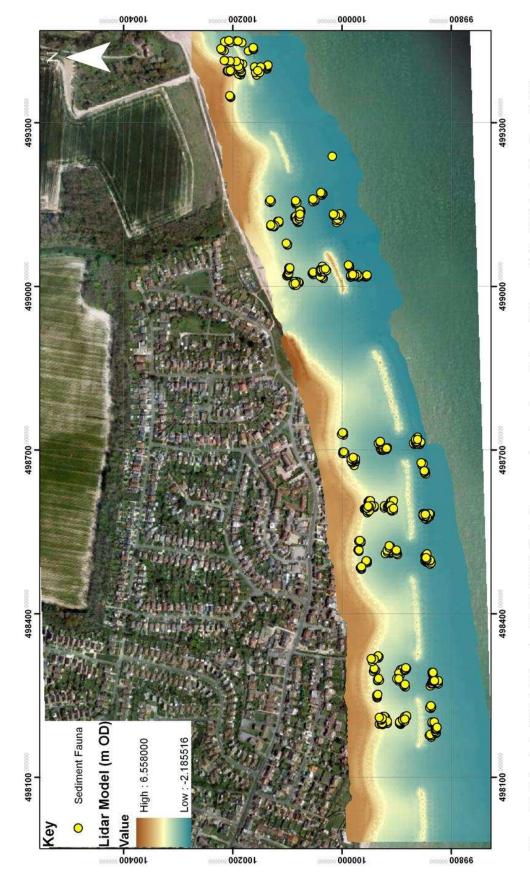


Figure 4.2 Lidar-derived Digital Elevation Model (DEM) illustrating cross-shore beach morphology at Elmer, with the GPS-derived location of all the sediment cores takem to survey the spatio-temporal benthic macrofaunal communities.

4.2.6 Statistical Analysis

4.2.6.1 Calculating beach variables

Grain size parameters were determined using a grain size distribution and statistics package for analysis of unconsolidated sediments (GRADISTAT, Blott, 2000). The mean, sorting, skewness, kurtosis and median grain size (D⁵⁰ (µm)) sample statistics were calculated using the Method of Moments in Microsoft Visual Basic programming language. The percentage of grains falling into size fractions modified from Udden (1914) and Wentworth (1922) were used: very fine gravel (2000 - 4000 μ m), very coarse sand (1000 - 2000 μ m), coarse sand (1000 - 500 μ m), medium sand (500 - 250 μ m), fine sand (250 - 125 μ m), very fine sand (125 - 63 μ m), and silt (< 63 µm). Linear interpolation was also used to calculate statistical parameters by the Folk and Ward (1957) graphical method, deriving physical descriptions (e.g. very coarse sand and moderately sorted). The other sediment environmental parameters were sediment temperature, depth of oxic layer, draining efficiency of the sediments, TOM and beach elevation. The variables used to assess the decaying macroalgae deposits were decaying macroalgae cover (%) and biomass (kg/m² wet weight), using data generated from Chapter 3. The current speeds at each vertical shore level for the eight horizontal beach locations at Elmer for both neap and spring tides were extrapolated from data modelled by Plomaritis (2006) and averaged between the tides.

Dean's dimensionless parameter was calculated for all ten shore locations at each horizontal shore level for each month sampled (Fig. 4.1). Beach states were numerically indexed according to wave and sediment characteristics via the Dean's dimensionless fall velocity (Ω) (Short and Wright, 1984), as expressed in Equation (1),

$$\Omega = H^b/W^sT,$$

where H^b is wave breaker height (cm), W^s is the sediment fall velocity (cm s⁻¹) from Stokes Law (Gibbs et al., 1971), and T is the wave period (s). Beaches with $\Omega < 1$ are considered reflective, $\Omega > 6$ dissipative, Ω and = 1-6 intermediate systems. Wave height (H^b) and wave period (T) were calculated from data provided by the CCO ($H^b = H^s$ (significant wave height) and $T = T^p$ (wave period)), also used in Chapter 2 and 3 (see Chapter 2 for further details). Mean grain size

was obtained from statistical sediment analysis by calculating the moment's computational method (Blott, 2000) and used to estimate sand fall velocity (Gibbs et al., 1971).

The beach state index (BSI) was also calculated, combining the effects of tidal range and Ω (McLachlan et al., 1993), so that the beach morphodynamic states (i.e. reflective (< 0.5), low- to medium- energy intermediate (0.5-1.0), high-energy intermediate to dissipative (1.0-1.5), fully dissipative (1.5-2.0), and ultradissipative macrotidal beaches/tidal sand flats (> 2.0)) could be classified. The BSI index is expressed in Equation (2),

(2) BSI =
$$\log ([H^b M/W^s TE] + 1),$$

where M is the maximum tidal range of the beach in question and E is the theoretical equilibrium tide for the earth covered in water (E = 0.8).

4.2.6.2 Spatial and temporal patterns of community structure

Hypotheses about the spatio-temporal patterns of the overall community descriptors of the benthic fauna adjacent to different coastal defence structures were tested using analysis of variance (ANOVA). Separate three-factor ANOVAs were carried out on the community descriptor variables of mean total densities (ind/m²), number of species and species diversity (Shannon's Index).

The first null hypothesis tested was that there were no significant differences in community descriptors over five sampled months between the three vertical shore levels, nor between the ten horizontal shore locations adjacent to different CDSs. Factor one (shore location) had ten levels (Felpham; Climping; Elmer bays: 2-3, 3-4, 4-5 and 6-7; and tombolos: 2, 4, 6 and 8), factor two (shore level) had three levels (upper landward (LW (U)), lower landward (LW (L)), and seaward (SW)), and factor three (time) had five levels (months: Mar 2005, May 2005, Aug 2005, Nov 2005, Jan 2006). All factors were random and orthogonal.

The second null hypothesis tested that there were no significant differences within the two different types of horizontal (bays and tombolos) at Elmer over time. This was tested with two separate three-way ANOVAs, one for bays and one for tombolos. Factor one (bays/tombolos) had four levels each (Bays: 2-3, 3-4, 4-5 and 6-7, or Tombolos: 2, 4, 6, and 8), factor 2 (shore

level) had three levels (upper landward, lower landward, and seaward), and factor 3 (time) with 5 levels (months: Mar 2005, May 2005, Aug 2005, Nov 2005, Jan 2006). Again, all factors were random and orthogonal.

All analyses were done on log (x+1) transformed data. Prior to analysis, data were tested for homogeneity of variances using Kolmogorov-Smirnov normality tests. The total densities of individuals and species diversity (Shannon's index) remained non-normal even after double log (x+1) transformations, therefore the more stringent criterion of $\alpha = 0.01$ was used to reject null hypotheses (Underwood 1997). ANOVA is robust for the departure from this assumption when there are many independent replicates and sizes of samples are unequal (Underwood 1997). Significant results were, however, interpreted with caution. When ANOVA indicated significant differences among means, Tukey's HSD and Games-Howell *post hoc* tests were used to distinguish between them (at $\alpha = 0.01$). Reasoning for use of these tests was given in Chapter 3 (see section 3.3.3.2). All parametric ANOVAs were carried out using SPSS (SPSS 2005).

4.2.6.2 Spatio-temporal patterns of beach environment, decaying macroalgae deposits and benthic faunal communities

Multivariate analysis (PRIMER software package, version 6; Plymouth Marine Laboratory, U.K.) was used to investigate whether there were similarities in the beach environment and benthic faunal community structures between sampled stations and whether these were consistent over different months. Specifically, to test for similarities in these variables between: (1) the different vertical shore levels (upper landward, lower landward and seaward); (2) the different horizontal shore locations adjacent to different CDSs (Felpham, Elmer Bays (2-3, 3-4, 4-5 and 6-7), Elmer Tombolos (2, 4, 6 and 8) and Climping), as well as between and within the different horizontal shore locations (i.e. Elmer bays and tombolos, replicates pooled); and (3) the interactions of horizontal shore levels and vertical beach sections with time.

Of the beach sediment variables, only the percentage very fine gravel, very coarse, coarse, medium and very fine sand, very coarse silt and TOM needed to be log (x) transformed and then normalized. All identified species, meio- and macrofauna were included and data were square root transformed so that species would contribute more evenly to the analyses and minimise the stress of the nMDS plots. First, a ranked triangular matrix of similarities was calculated between

each replicate using Euclidean distance similarity matrices for environmental variables, and Bray-Curtis similarity matrices for faunal data. These were then used to carry out significance tests for differences between samples for each of the hypotheses using analysis of similarity (ANOSIM) permutation tests (Clarke & Green 1988). Non parametric multidimensional scaling analysis (nMDS) and cluster analysis were used to generate two-dimensional ordination plots and dendrograms (Clarke 1993). The cluster analysis results were overlaid to visualise the similarity groupings between samples. Finally, the dominant species contributing to the spatial and temporal differences in community structure were investigated using the similarities percentage procedure, (SIMPER, Clarke 1993).

4.2.6.3 Local environment influences on spatial and temporal communities

The BIOENV procedure (PRIMER v6.0, Clarke & Warwick 2001) was used to assess and distinguish the optimum combination of sediment environmental variables, decaying macroalgae deposits, and beach exposure indices that explain the structure and composition of the benthic communities adjacent to granite (Felpham) and wooden (Climping) groynes, and granite breakwaters (Elmer). In addition, the influence of the varying currents created by the breakwater scheme at Elmer (see Chapter 2 for further details) was used. The optimum combination of environmental variables was then used to create Euclidean distance similarity matrices (Bray & Curtis 1957). All the variables, with the exception of percentage of fine sand, depth of oxic layer, and beach elevation were $\log (x + 1)$ transformed and further normalized. These matrices, along with the Bray-Curtis matrices for faunal community data were used to produce dendrogram and nMDS plots for visual assessment of dissimilarities in the assemblage structure. LINKTREE analysis with SIMPROF significance tests (p > 0.05) was carried out to further aid understanding the quantitative link between community patterns and the optimum combination of environmental variables (for further details see Clark & Warwick 2001).

One-tailed bivariate correlation analysis was performed between the benthic community variables (total densities of benthic faunal individuals and the dominant species (*Bathyporia sarsi*, *Bathyporeia pilosa*, *Pontocrates arenarius*, *Spio filicornis*, *Eteone picta*, *Glycera tridactyla*, *Phyllodoce maculata*)) and environmental influences (decaying macroalgae cover and biomass and sediment variables (sediment temperature, carbon content and depth of oxic

layer) at Elmer (n = 496), Felpham (n = 64) and Climping (n = 64) beaches using Pearson's correlation coefficientSPSS (SPSS 2005).

4.2.7 *Caveats of the study*

The same caveats apply to this chapter as those stated in Chapter 3 (see Section 3.2.4). The limitations were that there was a lack of available undefended control sites and two neighbouring beaches (Felpham and Climping) with two different types of CDSs had to be used with made the study complex. Furthermore, the number of sampling stations at Felpham and Climping were limited due to time and resources being finite.

4.3 Results

4.3.1 Beach Environment

4.3.1.1 Current flow in the Elmer breakwater scheme

The currents and sediment transport pathways at Elmer have been studied extensively (see Chapter 2 for further detail). There are differences in current intensity during neap and spring tides along the course of the breakwater scheme, with distinct deceleration of flow from the east to the west of the scheme. Recently, Plomaritis (2006) found tidal currents accelerate as they flow over the tombolos, thus enhancing the sediment mobility, and are reduced when flowing through the bays (< 0.2 m/s). The hydrodynamic environment between breakwaters 6 and 7 is different because reduced water flow enters the scheme between these breakwaters, and the current intensity reaches a peak in the central part of the scheme (Table 4.1). The central breakwaters (3-4 and 4-5) are further from the coastline (MHWS) and the gaps between the breakwaters are smaller (see Chapter 2 for more detail), resulting in flow constriction. On incoming and outgoing tides there are differences in the water flow through the gaps between the breakwaters; bays 3-4 and 4-5 particularly experienced strong fluxes in comparison with bay 2-3 and 6-7 (see Chapter 2: Fig. 2.2). During spring tides, water flow over tombolo 4 is fastest and then is forced to exit out of bay 3-4.

Table 4.1 Average current speeds (m/s) for each vertical shore level in each horizontal shore location sampled at Elmer beach. Values in **bold**, are the strongest currents at each vertical shore level. Data taken from neap and spring modelled currents from Plomaritis (2006).

		Horizontal Shore Level							
		LW(U)	LW(L)	SW					
IS	T2	0.16	0.15	0.15					
tioı	B2-3	0.12	0.16	0.14					
Sec	B3-4	0.12	0.20	0.14					
ch	T4	0.22	0.27	0.15					
Bea	B4-5	0.14	0.19	0.23					
Vertical Beach Sections	T6	0.20	0.22	0.27					
erti	B6-7	0.11	0.16	0.24					
>	T8	0.13	0.14	0.26					

4.3.1.2 Sediment environment

The average median grain size for each vertical shore level for the three beaches varied between 176 and 1068 μ m (Table 4.2). Elmer and Climping beaches were similar, with average median grain size being medium moderately sorted sand, whereas Felpham beach had generally coarser and poorly sorted sand.

Table 4.2 Sedimentological and morphodynamic characteristics of sampling sites: Felpham Beach with granite groynes (GG (F)), Elmer Beach with granite breakwaters (GB (E)), and Climping Beach with wooden groynes (WG (C)).

	Median G	rain			Depth of O	xic	Beach			
	Size ^b		TOM^{c}		$\mathbf{Layer}^{\mathrm{d}}$		Elevation ^e			
			Min-					·		
	Min-Max	Mean	Max	Mean	Min-Max	Mean	Min-Max	Mean	$\Omega^{ m f}$	BSI ^g
GG (F)	180-3459	745	0.2-0.9	0.5	5.0-20.0	13.4		0.07	1.5	2.0
GB (E)	104-3536	336	0.1-1.5	0.6	0.0-20.0	9.5	-2.03-3.54	-0.5	3.7	2.4
∠ T2 ^a	120-243	177	0.2-0.9	0.6	1.0-20.0	10.4	-1.23 - 3.20	0.80	6.6	2.7
B2-3	124-194	176	0.1-1.0	0.6	0.5-20.0	10.0	-1.41-2.97	0.14	7.0	2.7
B3-4	135-197	178	0.1-1.1	0.7	1.0-20.0	9.9	-1.56-2.41	-0.20	7.0	2.7
J T4	119-3407	395	0.2-1.0	0.7	1.0-20.0	9.0	-1.69 - 2.96	0.66	5.0	2.5
B4-5	103-600	226	0.3-1.5	0.7	1.0-15.0	7.4	-1.82 - 2.45	-0.59	6.3	2.7
T6	143-192	177	0.3-1.0	0.6	0.5-20.0	10.2	-1.95 - 1.84	-0.24	6.6	2.7
B6-7	165-1544	305	0.3-0.9	0.6	1.0-20.0	10.2	-2.03-2.75	-0.68	4.3	2.5
\sim T8	177-3535	1068	0.3-1.3	0.7	0.0-20.0	9.3	-1.76 - 3.54	0.78	1.9	2.1
WG (C)	130-2829	356	0.4-1.3	0.8	2.0-20.0	8.5			3.5	2.4

^aHorizontal shore locations (bays (B) and tombolos (T)) separated out for Elmer Beach. ^bMedian grain size (d50), μm; ^cTotal Organic Matter (TOM), % mass; ^dDepth of oxic layer, cm; ^eBeach elevation above Ordnance Datum Newlyn, m; ^fDean's parameter or dimensionless fall velocity, Ω (dimensionless); ^gBeach State Index, BSI (dimensionless).

The average median grain size was more variable within the scheme at Elmer. Tombolo 6 was the most sorted with moderately well sorted fine sand. At Elmer, there was a tendency for sediments to get coarser moving west to east: the western end of the scheme (Tombolo 2 to Bay 3-4) mainly consisted of fine moderately sorted sand (Table 4.2), the central section of the scheme (Tombolo 4 and Bay 4-5) consisted of medium sand, and towards the eastern end of the scheme (Table 4.2), Tombolo 8 was dominated by coarse sand (Fig. 4.3). In addition, the sediments get coarser higher up the shore, with increasing amounts of gravel and decreasing amounts of fine sand. The shore at all three beaches is backed by a steep shingle embankment.

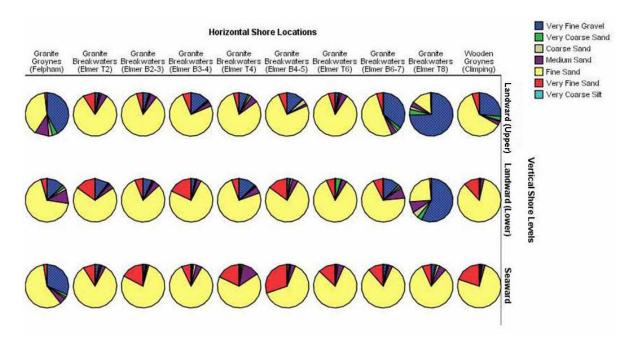


Figure 4.3 Average grain sizes categories (% weight) of the ten horizontal shore locations (Felpham, Elmer and Climping Beaches) at different vertical shore levels (landward and seaward).

During the sampling period, the sediment temperature ranged from 2.9° C in January (2006) to 24.7° C in August (2005). The average total organic matter for each of the three beaches was relatively average for a sandy beach (Kelaher & Levinton 2003, Table 4.2); Climping had the largest average (0.8 % TOM), whilst, Elmer had the largest maximum value (1.5 % TOM). The oxic layer was deeper at Felpham than Elmer and Climping, with the lower landward level of Bay 4-5 showing the shallowest average oxic layer (5.9 cm \pm 1.4).

The temporal variability of each of the sediment variables (total organic matter, depth of the oxic layer and the mean grain size) was very different for each of the beaches (Fig. 4.4). The amount of TOM was more variable over time at Elmer and Climping than Felpham, with the

latter sediments lower in TOM than the other two beaches. At Elmer, the TOM of the sediments was highest in May, reaching 1.5 % carbon content in the upper landward levels, these values then fell in June 2005 (ca. 0.6 %), before rising again in August (ca. 1 %) and November (ca. 1.2 %). Sediments in the three vertical shore levels at Elmer showed generally similar temporal shifts. At Climping Beach there were different temporal patterns, with elevated levels in the March and a reduction in May, whilst at Felpham the TOM in the sediments was highest in November (Fig. 4.4a). The depth of the oxic layer was most variable in the sediments at Felpham and Climping beaches (Fig. 4.4a); the latter showed no patterns of consistency between the vertical shore levels. At Elmer, the sediments in each of the shore levels showed relative homogeneity; the oxic layer was shallowest in August (< 5 cm) and deepest in March and January (15 cm) (Fig. 4.4b). The temporal variability in sediment grain size at the three beaches shows high variation occurred within both Climping and Felpham (Fig. 4.4c) sediments, varying between gravel and sand domination. Elmer showed little variation in comparison.

When considering all the measured sediment variables together, overall the ten horizontal shore locations sampled across all three beaches had almost the same sediment environments (ANOSIM, R=0.09, p=0.001), as did the vertical shore levels at each of the beaches (ANOSIM, R=0.141, p=0.001), though marginally more differences. The largest difference occurred between Tombolo 6 at Elmer and the beach at Felpham (ANOSIM, R=0.356, p=0.001), but with considerable overlap. The sediment environments of Climping beach and the bays at Elmer were the same (ANOSIM R=0.071, p=0.17), whereas small differences were observed between Climping and Felpham (ANOSIM R=0.341, p=0.001) (Fig. 4.5a). The horizontal shore locations that showed the most differences were at Felpham and Tombolo 8 (Fig. 4.3 and 4.4a).

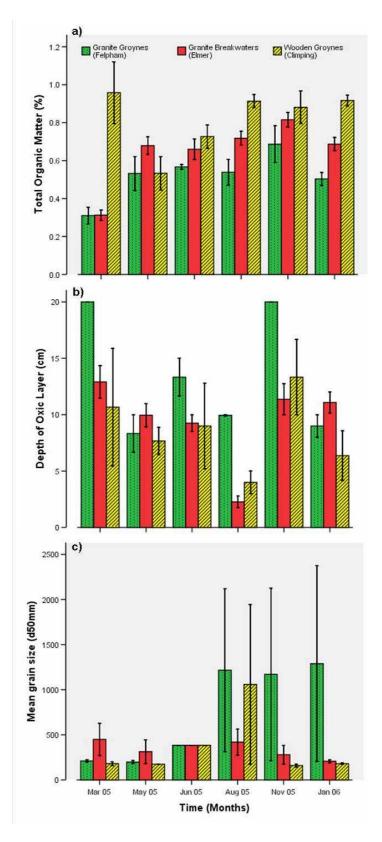


Figure 4.4 Temporal variability in: a) total organic matter, b) mean depth of oxic layer, and c) the average median grain size of sediments for the three beaches (Felpham, Elmer, and Climping) sampled over a period of one year.

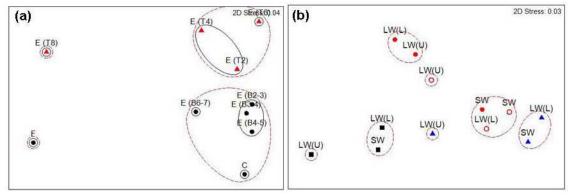


Figure 4.5 MDS plots showing dissimilarities in the sediment environment (variables: grain size parameters, temperature, depth of oxic layer, thixotrophy, TOM, beach elevation) between **a**) the ten horizontal shore locations sampled from three beaches with different CDSs (F: Granite Groynes (Felpham); C: Wooden Groynes (Climping); E: Granite Breakwaters (Elmer)). Differences within and between bays (**B**ays (**•**): 2-3, 3-4, 4-5 and 6-7 at Elmer) and tombolos (**T**ombolos (**o**): 2, 4, 6, and 8 at Elmer) in sediment environment can also be seen. Contour line from cluster analysis (Euclidean distance: 1.3 (solid) and 1.9 (dotted)) and **b**) the vertical shore levels (upper landward (LW (U)), lower landward (LW (L)), and seaward (SW) of breakwaters) for each of the three beaches (Felpham (**■**), Elmer Bays (**o**) Elmer Tombolos (**•**), and Climping (**△**). Contour line from cluster analysis (Euclidean distance: 1.7 (dotted)).

When comparing vertical shore levels for Felpham, Elmer bays, Elmer tombolos, and Climping the sediment environments were very similar (ANOSIM; R = 0.161, p = 0.001). The MDS plot (Fig. 4.5b) shows that for Felpham, Climping and Elmer bays the beach environments between the lower landward and seaward were similar within each beach.

The similarities shown between the beach sections are because they were exposed to similar wave conditions (Table 4.2), due to their geographical proximity. Climping and Elmer beaches were classified as ultra-dissipative macrotidal beaches (> 2.0 BSI) and Felpham a fully dissipative beach (1.5 - 20 BSI). Dean's parameter (Ω), which does not take into account the tidal range of the area, illustrated that dissipative high wave energy (> 6 Ω) was experienced in the bays on the western and central parts of the breakwater scheme at Elmer, whilst intermediate wave conditions (1-6) were experienced in Bay 6-7 (eastern end) at Elmer beach, Felpham and Climping (Table 4.2).

4.3.3 Benthic Macrofaunal Communities

4.3.3.1 Composition and abundance of the benthic infaunal communities

In total 51 species from six phyla were collected. The overall average benthic faunal density was 6,521 ind/m² (Table 4.3). The total number of species per horizontal shore location ranged from 16 to 27 species; Climping beach had the least (16 species), Elmer ranged from 20 to 27,

with no obvious differences between bays and tombolos, whilst Felpham had comparable numbers to Elmer (Table 4.4). All three beaches were dominated by crustaceans (81 % of total ind.), mostly made up of harpacticoid copepods (38 %), amphipods (27 %), and cumaceans (16 %, Table 4.3). Polychaetes only made up 16 % of the individuals found at the three beaches, however, this class was the most diverse group with 20 species present.

Spio filicornis (O. F. Müller) was the dominant polychaete (14 % of total ind), occurring in 51% of the samples (Table 4.4). Amphipoda were less diverse with only 7 species present, dominated by two species, *Bathyporeia pilosa* Lindström (15 % of total ind.) and *Bathyporeia sarsi* Watkin (10 % of total ind). Oligochaetes were present in low numbers (2 %), but they occurred in 20 % of the samples and were dominated by tubificids. There were also occurrences of terrestrial species typically found in the strandline, such as Coleoptera (3 %), as well as decapods such as juvenile *Carcinus maenas* (Linnaeus) (1 %).

Combining the six numerically dominant species from each vertical shore level yielded a total of only 10 species (Table 4.4). *B. sarsi* (56 - 1,437 ind/m²), *Cumopsis goodsiri* (Van Beneden) (404 - 2,424 ind/m²), harpacticoid copepods (842 - 4,795 ind/m²), and *S. filicornis* (289 - 1,773 ind/m²) were dominant at all the ten beach sections. *B. pilosa* was numerically dominant in all vertical levels at Elmer beach at the same time, other than Tombolo 8, with average densities ranging from 274 - 3,781 ind/m². *Urothoe brevicornis* Bate (86 - 142 ind/m²) and *Eteone picta* (Fabricius) (49 ind/m²) were only numerically dominant at one or more levels of Elmer beach (Table 4.4), whilst, *Pontocrates arenarius* (Bate) was found to only dominate at Felpham beach (318 ind/m²).

Bathyporeia pelgagica (Bate) was dominant in four of the ten shore locations (Felpham, Climping, Elmer bay 2-3, and tombolo 8), with average densities ranging from 42 - 274 ind/m², and finally, tubificids were present in half of the beach locations (Climping and four locations at Elmer; Table 4.4) with average densities of 64 - 311 ind/m².

Table 4.3 The average (per m^2) number of individuals and frequency of occurrence for each species/taxa; **Columns 1-3**: samples taken from the three beaches adjacent to different CDSs: granite groynes (GG Felpham), granite breakwaters (GB Elmer), wooden groynes (WG Climping). **Columns 4-9**: total numbers of individuals (per m^2) in the three different vertical shore levels (upper and lower landward (LW) and seaward (SW)) for both bays and tombolos at Elmer. **Columns 10-11**: the percentage contribution and frequency of occurrence of each species to the total number of individuals sampled. Data collected on one day per five seasons between March 2005 and January 2006. n = 1148.

					Elmer - Bay			Elm	er - Tomb	olo		
Phylum	Order/Species	GG Felpham	GB Elmer	WG Climping	Upper LW	Lower LW	SW	Upper LW	Lower LW	SW	Total (%)	Occurrence (%)
Crustacea	Amphipoda	1,019	2,090	350	460	3,652	907	1,660	5,308	414	27.35	
	Atylus swammedali	0	1	0	0	0	0	0	0	7	0.01	0.31
	Bathyporeia pilosa	83	1,282	2	215	1,204	492	820	4,591	44	14.88	29.06
	Bathyporeia sarsi	343	701	88	160	2,251	272	820	680	190	9.55	33.91
	Bathyporeia pelagica	274	67	260	76	124	108	18	16	64	1.81	15.63
	Pontocrates arenarius	318	7	0	2	0	14	0	0	27	0.68	6.56
	Unidentifiable	0	3	0	0	5	2	0	11	0	0.04	0.78
	Urothoe brevicornis	0	30	0	7	69	18	2	9	82	0.38	4.06
	Caprella linearis	0	0	0	0	2	0	0	0	0	0.00	0.16
	Cumacea	2,429	905	1,234	92	795	1,376	121	403	1,882	16.18	
	Bodotria arenosa	2	0	0	0	0	0	0	0	0	0.00	0.16
	Cumopsis goodsiri	2,424	905	1,234	92	795	1,376	121	403	1,882	16.17	50.00
	Iphinoe trispinosa	2	0	0	0	0	0	0	0	0	0.00	0.16
	Decapoda	0	3	0	0	5	5	0	0	7	0.03	
	Carcinus maenas	0	3	0	0	5	5	0	0	5	0.03	0.94
	Corystes cassivelaunus	0	0	0	0	0	0	0	0	2	0.00	0.16
	Crangon crangon	2	1	0	0	0	2	0	0	5	0.02	0.63
	Harpacticoida	1,376	2,612	1,771	133	7,043	4,067	291	742	3,613	37.64	
	Harpacticoid Copepod	1,376	2,612	1,771	133	7,043	4,067	291	742	3,613	37.64	43.75
	Isopoda	0	2	0	0	0	0	0	0	11	0.02	
	Idotea pelagica	0	1	0	0	0	0	0	0	5	0.01	0.31
	Janiropsis brevinenius	0	1	0	0	0	0	0	0	7	0.01	0.16
	Ostracoda	0	1	0	0	0	7	0	0	0	0.01	0.16
Annelida	Polychaeta	429	1,193	1,207	222	1,367	2,585	103	387	2,118	16.61	
	Arenicola marina	69	39	47	69	25	21	23	80	9	0.67	11.72
	Capitella capitata	0	1	0	0	0	0	2	5	0	0.01	0.47
	Eteone picta	10	62	44	11	101	80	23	50	92	0.81	17.81
	Glycera tridactyla	20	28	24	25	25	78	2	18	16	0.41	11.09
	Magelona mirabilis	2	0	0	0	0	0	0	0	0	0.00	0.16
	Malaceceros fuliginosus	7	2	0	7	2	0	2	0	2	0.04	1.41

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Table 4.3 continued

					Elmer - Bay			Elm	er - Tomb			
Phylum	Species/taxa	GG Felpham	GB Elmer	WG Climping	Upper LW	Lower LW	SW	Upper LW	Lower LW	SW	Total (%)	Occurrence (%)
	Nephyts spp.	0	1	0	0	2	0	0	0	2	0.36	11.25
	Ophryotrocha puerilis	2	0	0	0	0	0	2	0	0	0.01	0.31
	Perinereis cultrifera	0	0	0	0	0	0	0	0	2	0.00	0.16
	Phyllodoce maculata	12	27	47	7	30	60	0	14	64	0.46	8.13
	Scololepis foliosa	0	1	0	0	2	0	0	0	2	0.01	0.31
	Scololepis squamata	2	13	0	0	5	11	5	53	0	0.15	4.22
	Spio filicornis	289	990	1,014	94	1,143	2,299	37	167	1,859	13.63	51.41
	Spionid sp.	0	2	0	5	0	0	0	0	7	0.02	0.63
	Spiophanes bombyx	0	1	0	0	2	0	0	0	0	0.00	0.16
	Unidentifiable	0	1	0	2	7	0	0	0	0	0.02	0.31
	Oligochaeta	34	122	86	53	71	60	32	437	27	1.58	
	Enchytraeid worm	0	0	0	0	0	0	0	2	0	0.00	0.16
	Oligochaete sp. 2	0	6	0	2	0	0	0	34	0	0.07	0.63
	Tubificid	34	116	51	50	71	60	32	401	27	1.51	19.53
Nemertea	Nematode	5	31	0	27	23	16	16	60	23	0.34	6.88
Hexapoda	Isotomidae	2	4	5	2	5	5	2	9	2	0.06	
	Axelsonia littoralis	2	1	2	0	2	0	0	0	0	0.01	0.47
	Kelp Fly: Mycetophilidae	0	4	2	2	2	5	2	9	2	0.05	1.56
	Diptera (Flies)	2	0	0	0	0	0	0	0	0	0.00	0.16
	Nematocera	2	0	0	0	0	0	0	0	0	0.00	0.16
	Coleoptera	10	9	2	16	11	0	14	2	7	0.13	
	Aleocharnae (Family)	0	0	0	0	0	0	2	0	0	0.00	0.16
	Carabidae (beetle)	0	0	0	2	0	0	0	0	0	0.00	0.16
	Coleoptera puporium	2	2	0	5	2	0	5	0	0	0.03	0.16
	Eurynebria complanata	0	0	0	0	0	0	2	0	0	0.00	0.16
	Kelp Fly	7	6	0	9	9	0	5	2	7	0.08	2.66
	Micralymma marium	0	0	2	0	0	0	0	0	0	0.00	0.16
Chelicerata	Arachnida	0	1	2	0	2	0	0	0	5	0.02	0.63
	Haplodrassus minor	0	1	2	0	2	0	0	0	5	0.02	0.63
Pycnogonida	Pycnogonida	0	0	0	0	0	0	0	0	2	0.00	0.16
	Mean per m ²	5,302	6,943	4,658	978	12,951	9,010	2,223	7,289	8,090		

Table 4.4 Distribution of the six most dominant species found at each of the ten horizontal shore locations at the three beaches (GG: granite groynes (Felpham), GB: granite breakwaters (Elmer), WG: wooden groynes (Climping)). Tombolos (T) and bays (B) are shown for Elmer.

. 1 5,,	Vertical Shore Sections									
Order/Species	GG Felph	GB Elmer	WG Climpin							
	am	(T2)	(B2-3)	(B3-4)	(T4)	(B4-5)	(T6)	(B6-7)	(T8)	g
Bathyporeia pilosa		•	•	•	•	•	•	•		
Bathyporeia sarsi	•	•	•	•	•	•	•	•	•	•
Bathyporeia pelagica	•		•						•	•
Eteone picta							•			
Pontocrates arenarius	•									
Cumopsis goodsiri	•	•	•	•	•	•	•	•	•	•
Harpacticoid Copepod	•	•	•	•	•	•	•	•	•	•
Spio filicornis	•	•	•	•	•	•	•	•	•	•
Tubificid					•	•		•	•	•
Urothoe brevicornis		•		•						
Total ind/m ²	5,307	4,019	4,104	8,228	5,375	9,252	7,227	3,308	2,824	4,672
Total species	25	22	24	20	25	27	24	23	24	16

4.3.3.2 Spatial patterns of overall community measures

Horizontal shore location and vertical shore levels

The total average number of individuals and species per station ranged from 0 to 52,101 ind/m2 and 0 to 8 species, respectively, with averages of 6,521 ind/m2 and 3 species. At Elmer there were significant differences (ANOVA: p < 0.001) both between the horizontal and vertical shore positions in the total average number of individuals, species and species diversity (overall community measures, Table 4.5).

Table 4.5 Results from three-factor analysis of variance testing for the spatio-temporal effects of LCSs on the total number of individuals, total number of species, and species diversity (Shannon's Index) of the benthic communities adjacent to three types of CDS. Variables were factor 1, 'horizontal shore location' with 10 fixed levels (Felpham, Climping, Elmer (E) bay (B) 2-3. EB3-4, EB 4-5, EB 6-7, E tombolo (T) 2, ET 4, ET 6, ET 8; n = 60), factor 2, 'vertical shore level' with 3 fixed levels (Landward upper & lower, and Seaward; n = 200), and factor 3, 'time' with 5 random levels (months; n = 120). p set to 0.01; *p < 0.05, **p < 0.01, ***p < 0.001.

		Total nun individ			number of ecies	Species Diversity (Shannon's Index)		
Variable	df	MS	F	MS	F	MS	F	
HS	1	11669.60	7.81***	20.75	12.82***	1.51	12.50***	
VS	2	85385.66	57.15***	220.42	136.15***	5.65	46.72***	
T	4	105947.85	70.92***	121.07	74.79 ***	2.49	20.62***	
HS x VS	2	7918.80	5.30***	11.96	7.39***	0.70	5.78 ***	
HS x T	4	4743.80	3.18 NS	8.83	5.45 NS	0.61	5.00 NS	
VS x T	8	20362.61	13.63***	10.45	6.46 ** *	0.61	5.05***	
HS x VS x T	8	3844.33	2.57***	6.13	3.79***	0.31	2.60***	

HS = horizontal shore, VS = vertical shore, T = Time

There were significant differences (p > 0.05) in the community species diversity between each vertical shore level (Fig. 4.6); the communities became more diverse towards the low shore (seaward side of the LCS).

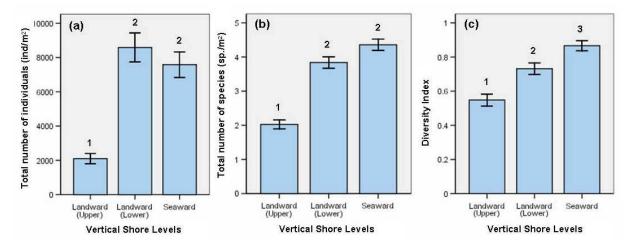


Figure 4.6 Mean a) total number of individuals (ind/m²), b) total number of species, and c) Shannon's diversity index for each vertical shore level (LW: landward (U: upper, L: lower), SW: seaward) across all beaches sampled. Error bars are \pm SE and numbers 1 to 3 above error bars correspond to Tukey's HSD *post hoc* test subset groupings from one-way ANOVAs.

The total densities were most variable between the horizontal shore locations (Fig. 4.7). Bays 3-4 (9,874 ind/m²) and 4-5 (9,659 ind/m²) supported the greatest number of species and bay 6-7 (3,970 ind/m²) and tombolo 8 (3,382 ind/m²) had the least; there was much overlap between the rest of the horizontal shore locations (Fig. 4.7). The greatest total average number of species (> 3.5) was at Elmer, but there were fewer at either end of the scheme; the least average number of species were at tombolo 8 (2 species).

The number of individuals in the sediment at Felpham and Climping beaches was just below the average for all the beaches (6,102 ind/m²), with sediments at Felpham also having below average number of species (3 species), and Climping had just above this value (Fig. 4.7). The community species diversity was lowest at Felpham Beach (0.54) and tombolo 8 (0.3); the other beach sections showed no differences and had a greater average species diversity of 0.8.

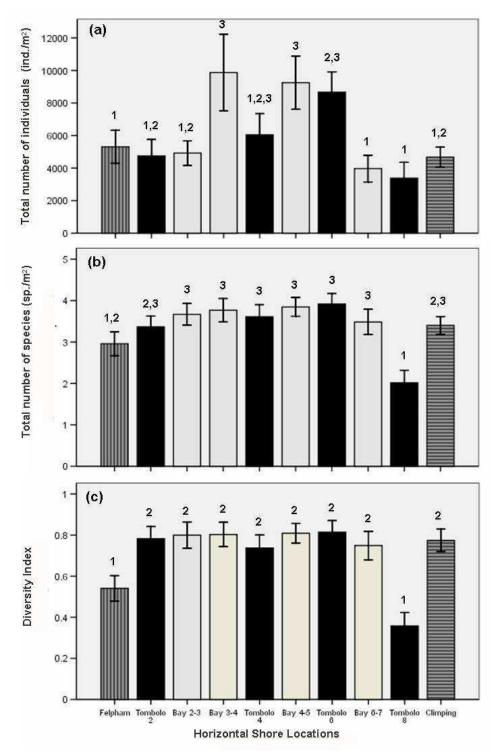


Figure 4.7 Mean a) total number of individuals, b) total number of species, and c) Shannon's diversity index for each horizontal shore locations (n = 72) adjacent to different types of CDSs (Felpham: granite groynes (vertical stripped bars); Elmer: granite breakwaters (solid bars); Climping: wooden groynes (horizontal stripped bar)). Tombolos (solid black) and bay (solid white) shore locations at Elmer shown (Tombolos 2, 4, 6, and 8; Bays 2-3, 3-4, 4-5, and 6-7). Shore locations displayed in order of geographical situation from west to east (Felpham to Climping). Error bars are \pm SE and numbers 1, 2 and 3 above error bars correspond to Tukey's HSD *post hoc* test subset groupings from 3-way ANOVA (Table 4.5).

Horizontal shore type (bays and tombolos)

When analysing the community measures between the four bays, there were only significant differences (p > 0.05) in the total number of individuals and not in the numbers of species or species diversity (Table 4.6).

Table 4.6 Results from two 3-way ANOVA's testing for the spatio-temporal effects of different bays and tombolos on the total number of individuals, total number of species, and species richness of the benthic macrofaunal communities within the Elmer Beach offshore breakwater system. Variables were factor 1, 'bays' or 'tombolos' with 4 fixed levels each (bays: 2-3, 3-4, 4-5 and 6-7; n = 60; tombolos: 2, 4, 6, and 8; n = 60), factor 2, 'vertical shore levels' with 3 fixed levels (Upper and Lower Landward and Seaward; n = 80), and factor 3, 'time' with 5 random levels (months; n = 48). p set to 0.01; *p < 0.05, **p < 0.01, ***p < 0.001. **NS** = not significant (p > 0.5).

			number of ividuals		number of pecies	Species Richness (Shannon's Index)		
Variable	df	MS	F	MS	F	MS	F	
Bays								
В	3	0.97	14.99***	0.03	1.44 NS	0.02	1.08 NS	
VS	2	18.97	293.52***	1.53	71.56***	0.06	4.59*	
T	4	4.58	70.84 ***	0.68	31.63***	0.17	12.30***	
B x VS	6	0.30	4.65***	0.02	0.77 NS	0.05	3.32**	
BxT	12	0.65	10.08***	0.19	9.04***	0.08	5.49***	
VS x T	8	0.67	10.30***	0.05	2.21*	0.01	0.64 NS	
B x VS x T	24	0.40	6.23***	0.04	2.06**	0.01	1.04 NS	
Tombolos								
То	3	4.71	72.49 ***	0.92	44.58***	0.27	22.67***	
VS	2	11.66	179.39***	2.00	97.31***	0.38	32.00***	
T	4	5.04	77.46***	0.42	20.22***	0.08	6.55***	
To x VS	6	1.97	30.26***	0.39	18.95***	0.11	9.74***	
To x T	12	0.84	12.97***	0.06	2.88**	0.01	0.73 NS	
VS x T	8	0.46	7.12***	0.10	4.81***	0.06	5.50***	
To x VS x T	24	0.70	10.72***	0.10	4.90***	0.03	2.68***	

B = bays, VS = Vertical Shore, T = Time, To = Tombolo.

The central bays 3-4 and 4-5 had approximately 50 % more individuals than bays 6-7 (3,970 ind/m²) and 2-3 (4,925 ind/m²). The differences seen between the different tombolos (Table 4.6) were because tombolo 6 had greater densities of individuals (> 8,500 ind/m²) than any other tombolo, whilst tombolo 8 had the least total densities (> 2,500 ind/m²). Differences in the numbers of species and species richness were seen between benthic communities of different tombolos (Table 4.6); tombolo 8 was different from the other tombolos, with reduced species diversity, whilst there were no differences between the other tombolos (Fig. 4.8).

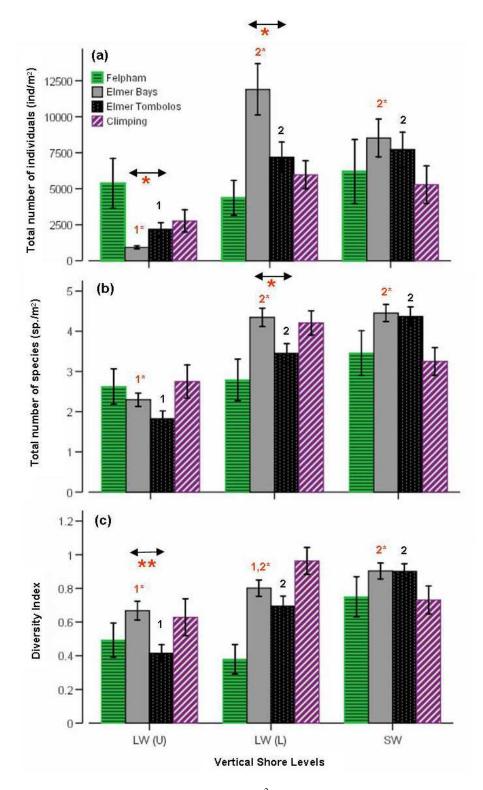


Figure 4.8 Mean a) total number of individuals (ind/m²), b) total number of species, and c) Shannon's diversity index for each vertical shore level (LW: landward (U: upper, L: lower), SW: seaward) for Felpham, Elmer (Tombolos and Bays), and Climping beaches. Error bars are \pm SE and numbers 1 to 2 above error bars correspond to Tukey's HSD *post hoc* test subset groupings (p < 0.01) from a series of ANOVAs. Black arrows with asterisk between bays and tombolos at Elmer indicate significant differences (*p < 0.05, **p < 0.01, *** p < 0.001).

Spatial interactions between vertical and horizontal shore positions

Overall, there were very significant vertical shore level and horizontal shore location interactions for all the beaches (Table 4.5). Tukey's HSD *post hoc* tests of the community measures showed that there were no significant differences (p > 0.05) in communities at different shore levels at either Felpham or Climping; however, there were shore level differences within the bays and tombolos at Elmer (Fig. 4.8). In both bays and tombolos, there were no significant differences in the numbers of individuals and species between the lower landward and seaward communities, although the lower landward of bays did show tendency to have more species than the seaward sides; both community measures were significantly greater than in the upper landward. This was similar for the species diversity for both communities; with a gradually increasing trend in diversity towards the seaward sides of the structures (Fig. 4.8). In each shore level, there were no significant (p > 0.05) differences between bays and tombolos for any of the community measures.

Nevertheless, there were indications that the communities were more densely populated in the upper landward of the tombolos than the bays and no difference in number of species, but the bays were more diverse than the tombolos (Fig. 4.8). Furthermore, in the lower landward level of the beach there were indications that there were more individuals, species and species diversity in the bays compared to the tombolos, for example, there were 1.6 times higher densities of individuals in bays (> 11,500 ind/m²) compared to tombolos (Fig. 4.8). On the seaward sides of the breakwaters there were no differences in community measures between bay and tombolo shore locations.

4.3.3.3 Temporal patterns of overall community measures

There were significant differences in all the community measures over time (Table 4.5, Fig. 4.9). The total number of individuals showed the most temporal change, with a significant peak in average total abundances was in May (> 15,000 ind/m²), whilst the least abundances were observed in November and January (< 3,000 ind/m²). The total abundances of individuals were low in the August, similar to those in November, March, and January. The changes over time in number of species and species diversity were more gradual in comparison to the abundances.

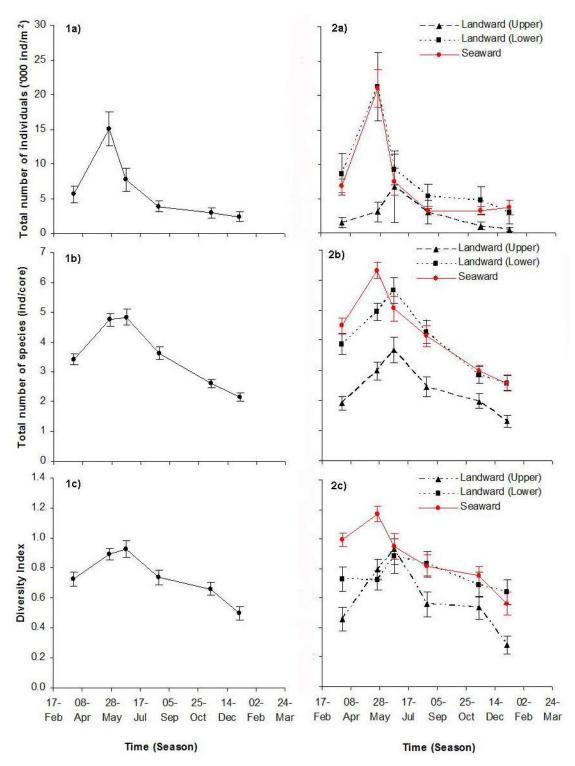


Figure 4.9 Mean a) total number of individuals, b) total number of species, and c) Shannon's diversity index for each time period sampled for 1) all beaches sampled and 2) vertical shore levels across all beaches sampled. Error bars are \pm SE and numbers 1 to 4 above error bars correspond to Tukey's HSD *post hoc* test subset groupings from ANOVAs. X Axis scales are dd/mm/yy so in temporal proportion.

The number of species was greatest in May and June, with no significant difference between the two time periods (Fig. 4.9 (1b)); this was followed by a gradual decrease to an average of 2.2 species in January. The species diversity showed much overlap between time periods sampled, with only the communities in January being totally significantly separate with an average diversity of 0.5. There were no significant interactions of shore location with time (p > 0.05). The same temporal patterns were seen at each horizontal shore location. This was not the case for the vertical shore levels; there were significant (p < 0.001) community differences in shore level over time.

The lower landward and seaward benthic communities (all beaches pooled for each vertical shore level) had the same large peak in density of individuals in May (Fig. 4.9 (2a)), reaching an approximate average of $21,000 \text{ ind/m}^2$. This abundance peak was followed by a large decrease in individuals in June, approximately $13,000 \text{ ind/m}^2$. In contrast, in the upper landward, the abundance of individuals did not see a peak in May, but in June instead, but this was only small in comparison and was not significantly different from the other shore levels (p > 0.05). The number of species in both the upper and lower landward benthic communities peaked in June (3.7 and 5.7 species, respectively; Fig. 4.9(2b)), whereas, the numbers of species in the seaward communities peaked earlier in May with slightly greater average number of species (6.3 species). Although the densities of individuals were high in May for the lower landward, the diversity indices showed that it was not very diverse, unlike the seaward sides of the structures (Fig. 4.9 (2c)). The diversity of the lower landward communities did not change very much with time, whereas it did for the upper landward and seaward communities. The species diversity in the upper landward and seaward communities showed the same temporal pattern as the densities of individuals.

4.3.3.4 Spatial patterns of the benthic infaunal communities

Overall, the infaunal community structures of the ten horizontal shore locations were comprised of a core of similar species (see section 4.3.3.1), with virtually no differences (Global R = 0.094, p < 0.01). Whereas, vertical shore level had a slightly stronger effect on community structure than horizontal shore location, but overall the benthic communities at different shore levels at Felpham and Climping beaches, and the Elmer bays and tombolos were similar (ANOSIM, Global R = 0.287, p = 0.001).

4.3.3.4.1 Horizontal shore locations

Small trends were observed in the abundances of the dominant species at certain horizontal shore locations. The MDS ordination plot (Fig. 4.10) shows that communities within Elmer beach formed an aggregated group separated from those communities at Felpham and Climping beaches; with the exception of tombolo 8 communities, which showed the most differences from all the other shore locations. There were also three distinct aggregations of similarity within the beach at Elmer. Bays 3-4 and 4-5 were grouped very tightly with 89 % similarity in community structure, bays 2-3 and 6-7 and tombolos 2 and 4 were grouped with 80 % similarity, whilst, the communities within tombolo 6 showed the least similarity with only 65 % similarity to these two aggregations.

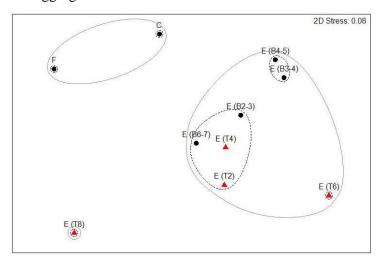


Figure 4.10 MDS ordination plot of all species found at each horizontal shore location with different CDS types (F = Felpham (Granite Groynes), C = Climping beach (Wooden Groynes), E = Elmer (Granite Breakwaters)). Differences within and between bays (**B**ays (\bullet): 2-3, 3-4, 4-5 and 6-7 at Elmer) and tombolos (**T**ombolos (\blacktriangle): 2, 4, 6, and 8 at Elmer). Contour line from cluster analysis: 65% (grey solid line) and 80% (black dotted line) similarity.

Similarity-percentage analysis (SIMPER) showed that the very small faunal differences between the different shore locations were due to a small variety of dominant species, either specific species were only present in certain areas, or there were significant differences in abundances (Fig. 4.11). The faunal differences seen for Felpham were due to the high abundance contributions of *C. goodsiri* (52 %).

Although *C. goodsiri* was present at all the other sites, they were not present in such high abundances ($> 2,000 \text{ ind/m}^2$) as at Felpham, this was twice that found at Climping, and 2 - 6 times that found at Elmer beach (Fig 4.11).

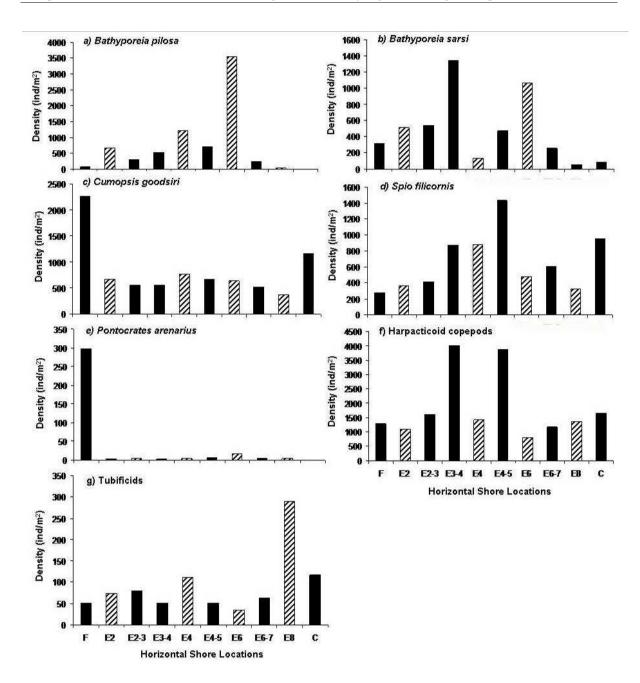


Figure 4.11 Mean densities of a) *Bathyporeia pilosa*, b) *Bathyporeia sarsi*, c) *Cumposis goodsiri*, d) *Spio filicornis*, e) *Pontocrates arenarius*, f) Harpacticoid copepods and g) tubificids in each horizontal shore location of beach (n = 72) adjacent to different types of CDSs (F, Felpham (granite groynes); E, Elmer (granite breakwaters); C, Climping (wooden groynes)) that influence the differences in community structure. Tombolos (horizontal lines) and bay (solid black) locations at Elmer are shown (Tombolos 2, 4, 6, and 8; Bays 2-3, 3-4, 4-5, and 6-7). Vertical shores displayed in order of geographical situation from west to east (Felpham to Climping). **NB** of different y-axis scales.

In addition, *P. arenarius* (10 % contribution) was only present at Felpham. Climping was least similar to those shore locations at Elmer because of a combination of reasonably high abundances of *C. goodsiri* (> 1,100 ind/m²), *S. filicornis* (948 ind/m²), and harpacticoid

copepods (> 1,600 ind/m²). The high abundances of *C. goodsiri* at both Felpham and Climping beaches accounts for the similarity between these two beaches (Fig. 4.11). The faunal differences seen for Tombolo 8 at Elmer were due to the high abundance contribution from tubificids (14.8 %) and a lack of significant contribution from either *Bathyporeia* sp. or harpacticoid copepods, which were found singularly or in combination in all other beach sections.

Tombolo 6 showed dissimilarities to the other bays and tombolos at Elmer because of the especially high abundance contribution from $B.\ pilosa$ (32.8 %) with an average abundance of > 3,500 ind/m². This abundance was on average five times greater than at any other beach section at Elmer, Felpham or Climping. In addition, the lowest abundances of harpacticoid copepods (> 700 ind/m²) were found in Tombolo 6 (Fig. 4.11). The grouping of Bays 6-7 and 2-3, and Tombolos 2 and 4, were due to the high abundance contributions of Bathyporeia spp., $C.\ goodsiri$, harpacticoid copepods, and $S.\ filicornis$ as they were in relatively similar abundances, whilst the similarities between bays 3-4 and 4-5 were because of high contributions from $S.\ filicornis$ abundances (47 % and 43 %, respectively) with the highest abundances (868 ind/m² and 1,434 ind/m², respectively) sampled. Furthermore, harpacticoid copepods were high abundance contributors (17 % and 21%, respectively) to the communities in Bays 6-7 and 2-3, and Tombolos 2 and 4, with the highest average abundances sampled (> 4,000 ind/m² and > 3,800 ind/m², respectively), three times that of other horizontal shore locations.

4.3.3.4.2 *Vertical shore levels*

There were no differences (ANOSIM, p > 0.05) in the communities between different vertical shore levels at Felpham or Climping, whereas, there were some differences in the communities in the bays and tombolos at Elmer (Table 4.7). The greatest differences occurred between upper landward and the seaward communities for the tombolos, where the communities were as different as they were similar (Table 4.7). In the tombolo locations, both landward (upper and lower) shore levels showed similarity, whilst these communities showed some overlap in similarities with those on the seaward sides of the breakwaters (Table 4.7). The MDS ordination plot (Fig. 4.12) shows the similarity between the bay and tombolo seaward communities at Elmer (88 % similarity), and show separation from the landward tombolo communities. In contrast, the bay communities showed stronger differences between the upper and lower

landward levels, than between the lower landward and seaward sections, which were extremely similar (Fig. 4.12).

Table 4.7 Results of ANOSIM and pair-wise tests for differences in faunal community structure between vertical shore levels at Felpham, Elmer bays, Elmer tombolos, and Climping. Analyses performed on square-root transformed data *p < 0.05, **p < 0.01, ***p < 0.001, **NS** = not significant (p > 0.05).

	Felpham	Elmer: Tombolos	Elmer: Bays	Climping
Levels compared	R	R	R	R
LW (U) - LW (L)	-0.142 NS	0.155**	0.314***	0.0.28 NS
LW (U) - SW	−0.074 NS	0.578***	0.516***	0.035 NS
LW (L) - SW	−0.183 NS	0.503***	0.089**	−0.044 NS

Similarity-percentage analysis (SIMPER) showed that *B. pilosa* was the numerically dominant species in the upper and lower landward communities (46 % and 35 %, respectively) of the tombolos. The small differences seen between these two shore levels were primarily due to a high abundance contribution from tubificids (18 %) in the lower landward zone (Fig. 4.13). There were also differences in the abundances of *B. pilosa*, with 82% greater densities in the lower than in the upper landward zone (Table 4.3, Fig. 4.13). The polychaete, *S. filicornis* was the highest abundance contributor to communities seaward of the tombolos, with harpacticoid copepods and *C. goodsiri* also typically dominant (Fig. 4.13).

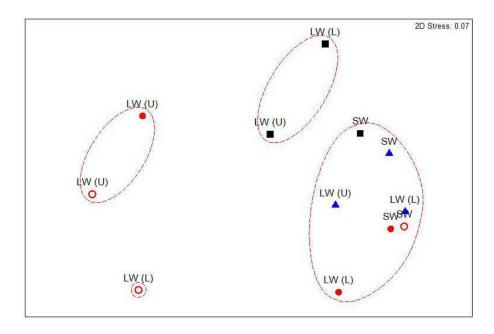


Figure 4.12 MDS ordination plot of benthic infauna at different vertical shore levels for Felpham (■), Elmer bays (●), Elmer tombolos (○), and Climping (▲). Dotted line shows Bray-Curtis similarity (60%) results.

The contrasting differences between shore levels seen for Elmer bays (Table 4.7) were due to the dominance of *B. sarsi* and *B. pilosa* in the upper landward shore communities (25 % and 20 %, respectively), whereas, *S. filicornis* was typically the most dominant species in both the lower landward and seaward communities (28 % and 34 %, respectively), with total contributions from *Bathyporeia* spp. only accounting for 18 % and 2 % (respectively) of the abundances. Furthermore, harpacticoid copepods and *C. goodsiri* were also typically dominant in the lower shore levels and not in the upper landward shore communities.

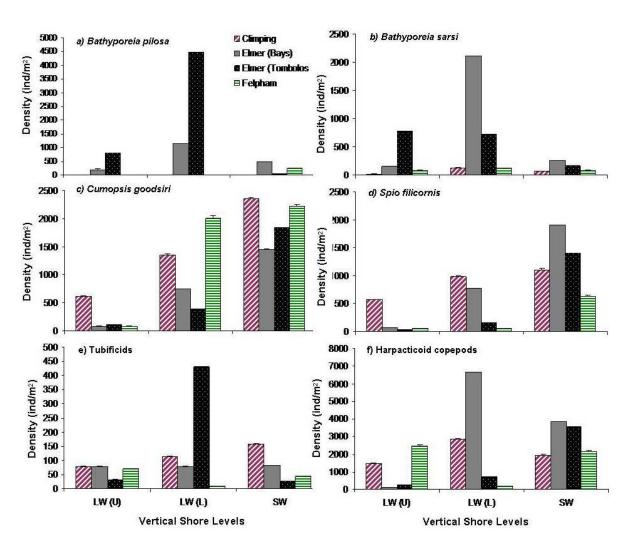


Figure 4.13 Mean densities a) *Bathyporeia pilosa*, b) *Bathyporeia sarsi*, c) *Cumposis goodsiri*, d) *Spio filicornis*, e) tubificids and f) Harpacticoid copepods in each vertical shore level (upper landward (LW (U)), lower landward (LW (L)), and seaward (SW)) of the three beaches adjacent to different CDS (Felpham & Climping, n = 20; Elmer bays & tombolos, n = 80). **NB**: different y-axis scales.

4.3.3.4.3 Interactions of shore locations and levels

ANOSIM and MDS ordination analysis of the benthic communities were carried out to assess the relationships between all ten horizontal shore locations at each vertical shore level (Fig. 4.14). The ANOSIM tests showed that the communities were significantly similar (p > 0.05) at each shore level (Global R = 0.264, p = 0.001). The greatest similarity was between communities on the seaward sides of structures, whilst the lower landward zones had the most differences (Fig. 4.14). The MDS plots show that the relationships between the shore locations were different at each shore level (Fig. 4.14). For example, the upper landward and seaward communities at Climping were similar to communities at Felpham, and less so to Elmer; whereas, lower landward communities were extremely similar to communities in Elmer bays and not Felpham.

The lower landward communities were similar, with some small differences between bays and tombolos at this level (ANOSIM R = 0.252, p = 0.001). There were, however, no differences (p > 0.05) between bays and tombolos in the upper landward and seaward levels (Figs. 4.12 & 4.14). The lower landward communities for Elmer and Climping beaches were tightly aggregated in similarity. The communities sampled on the seaward sides of the breakwaters, in front of both bays and tombolos, were more than 80 % similar in species composition (Fig. 4.14). The communities on the landward side of structure 8 (tombolo 8) were shown to have the least similarity (> 20 %). The other tombolos and bays had little similarity between the upper and lower sections (> 30 %) of the landward side. Furthermore, the lower landward communities in the western and central bays (Bays 2-3, 3-4, and 4-5) showed more similarity to the seaward communities (65 %) than to tombolos or bay 6-7 (50 %).

The small differences in communities between the lower landward communities of bays and tombolos were partially due to the total densities of amphipods, with less abundance in bay communities compared to tombolos; this contributed to 22 % of the dissimilarity. The lower landward tombolo communities were dominated by *Bathyporeia* spp. (68 % contribution); *B. pilosa* (53 %) was more than 6 times more numerically dominant that *B. sarsi* (15 %), with average densities of 4483 ind/m² and 723 ind/m², respectively (Fig. 4.13).

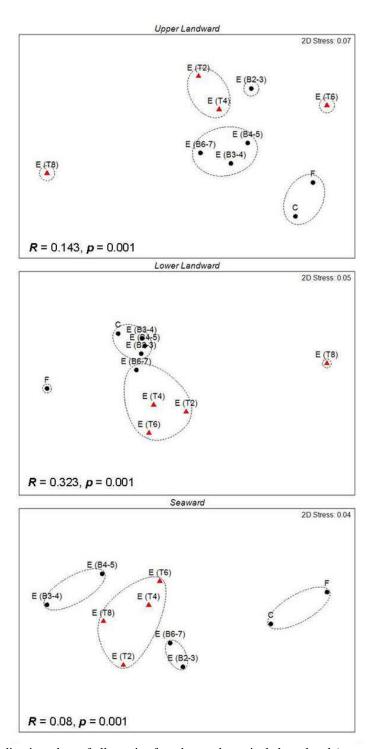


Figure 4.14 MDS ordination plots of all species found at each vertical shore level (upper and lower landward, and seaward) for each horizontal shore location with different CDS types (F = Felpham (Granite Groynes), C = Climping beach (Wooden Groynes), E = Elmer (Granite Breakwaters)). Differences within and between bays (**B**ays (•): 2-3, 3-4, 4-5 and 6-7 at Elmer) and tombolos (**T**ombolos (▲): 2, 4, 6, and 8 at Elmer) are shown. Contour line from cluster analysis: 82 % (black dotted line) similarity.

Conversely, at this level in the bays, *B. pilosa* (6 %) was less dominant (1.8 times) than *B. sarsi* (16 %), with average densities of 1,155 ind/m² and 2,125 ind/m², respectively. The highest

densities of tubificids (11 %) occurred in the lower landward zones of the tombolos, with an average of 432 ind/m² (Fig. 4.14), whereas, on average 79 ind/m² were in the bays. *S. filicornis* (32 %) and harpacticoid copepods (27 %) were the most dominant fauna in the lower landward section of the bays (782 and 6,680 ind/m², respectively) - more than 4 and 9 times the abundance found in the tombolos. The polychaete, *S. filicornis* was also the highest abundance contributing species (40 %) on the seaward sides of the breakwaters, thus explaining the aggregation of the lower landward and seaward bay communities (Fig 4.14), although the abundances were over twice as large in the seaward shore level (1,911 ind/m²).

The differences in communities in the upper landward shore levels between Elmer and Climping were due to the densities of harpacticoid copepods (27 %), *C. goodsiri* (20 %) and *S. filicornis* (17 %). The densities of these species were much greater at Climping than found at Elmer (Fig. 4.15). Furthermore, the abundance contribution from amphipods was negligible (< 5 %), with densities less than 100 ind/m², approximately ten times less than at Elmer Beach. In contrast, the lower landward communities at Climping Beach were very similar to those in the bays at Elmer (Fig. 4.13b); this was because of the similar high abundance contributions from copepods (35 %), *C. goodsiri* (31 %) and the polychaete, *S. filicornis* (32%). Felpham showed dissimilarities at this shore level to the other two beaches because of the high abundance contributions of the amphipod *P. arenarius* (20 %) and *C. goodsiri* (57 %); the latter, with densities of 2,010 ind/m², which was more than twice as great as at Elmer. Large similarities were seen between seaward communities of all horizontal shore locations. All the communities were dominated by the species, *S. filicornis*, *C. goodsiri*, and harpacticoid copepods.

4.3.3.5 Temporal patterns of the benthic infaunal communities

The structure of communities significantly changed over time at each of the beaches when vertical shore levels were combined (Table 4.8). The greatest changes were experienced in the communities adjacent to the granite groynes at Felpham and wooden groynes at Climping; greater than across the Elmer bay and tombolo communities. The largest temporal changes did not occur between the same months at each of the beach types. The largest change in community composition at Climping Beach occurred from August to November (Fig. 4.15c), where the communities were almost completely different from each other (Table 4.8).

Table 4.8 ANOSIM Global R and pair-wise tests for temporal differences on infaunal community structure for the horizontal shore locations at three beaches adjacent to different types of CDS (differences for bays and tombolos at Elmer were separated). Analyses performed on square-root transformed data. p set to 0.01; *p < 0.05, **p < 0.01, ***p < 0.001, **NS** = not significant (p > 0.05). Largest significant temporal change in **bold**.

	Felpham	Elmer: Tombolos	Elmer: Bays	Climping
	R	R	R	R
Global test	0.436***	0.108***	0.204***	0.438***
Levels compared				
Mar 05 - May 05	0.469***	0.043*	0.094***	0.428***
May 05 - Jun 05	0.146*	−0.022 NS	0.243**	0.434***
Jun 05 - Aug 05	0.657***	−0.044 NS	−0.024 NS	0.508***
Aug 05 - Nov 05	0.26**	0.133***	0.127***	0.951***
Nov 05 - Jan 06	0.303**	0.006 NS	0.073**	0.156**

The temporal community changes at Felpham were not as large (as judged by R values) as at Climping, and occurred at a different time, between June to August (Fig. 4.16a). The communities at Elmer were the most similar over time (Table 4.8). The bay communities changed more than tombolo communities, but only marginally, with the largest community temporal changes between May and June in the bay communities (ANOSIM R = 0.243), and between August and November in the tombolo assemblages (ANOSIM R = 0.133) (Fig. 4.15b, Table 4.8).

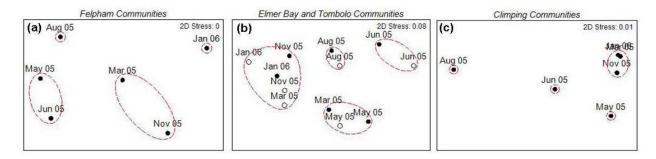


Figure 4.15 MDS ordination plots of changes in community structure over time (Mar, May, June, Aug, Nov 2005, and Jan 2006) at a) Felpham, b) Elmer bays (●) and tombolos (○), and c) Climping beaches. Contour line (dotted line) from cluster analysis: a) 40 % similarity, b) and c) 60% similarity contour line.

MDS ordination analysis showed that in June and August the communities at Climping Beach, and Elmer bays and tombolos were separated at 60 % similarity (Fig. 4.14a), whilst, at Felpham, communities in June and May were grouped, but with only 40 % similarity, with communities in August showing dissimilarity. The benthic communities adjacent to the wooden groynes at Climping Beach had the greatest changes in community structure over time because of changes in both species composition and densities of individuals.

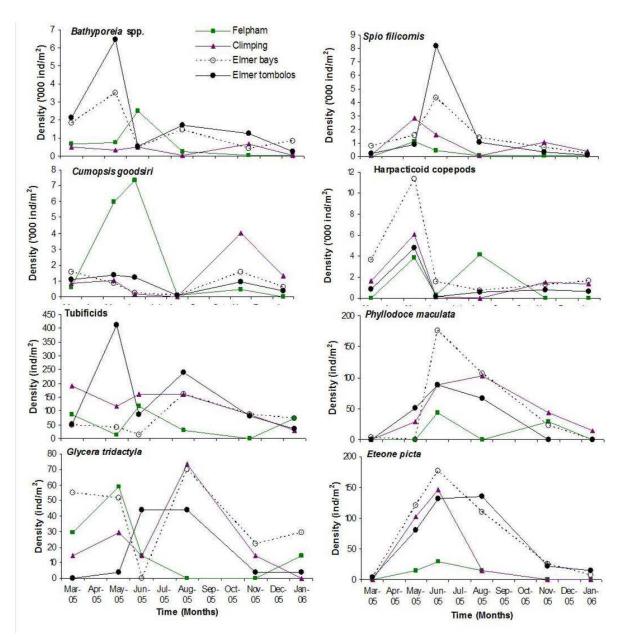


Figure 4.16 Mean densities of dominant species influencing the temporal changes in benthic community structure in Felpham, Climping, Elmer bay and Elmer tombolo sediments. **Attention**: y-axis scales are different.

Harpacticoid copepods were the main abundance contributor in March (59 %) and May (46 %), this then changed to *S. filicornis* in June (40 %), with little contribution (< 10 %) from the copepods. In August the high abundance contributing species, changed completely to tubificids (59 %), *Phyllodoce maculata* (Linnaeus) (19 %) and *Glycera tridactyla* Schmarda (15 %). Whilst in November and January, *C. goodsiri* were the highest abundance contributors (60 % and 42 %, respectively), with *S. filicornis* (21 % and 25 %, respectively) and harpacticoid copepods (15 % and 27 %, respectively) also contributing significantly to the community

structure at that time. *C. goodsiri* was the only species to be consistently dominant through time, with the exception of August, when they were not recorded to have been present in the sediments; this was followed by a large increase in densities in November, from 0 to 4,026 ind/m² (Fig. 4.16), this dramatic change accounts for 41 % of the dissimilarity in community structures between August to November when the communities were the most different.

There were also considerable changes in the benthic communities on the beach with granite groynes at Felpham, because in each season the dominant species was not often present in other seasons, similar to Climping. For example, in March, *Pontocrates arenarius* was the main abundance contributor (45 %), and otherwise was only in significant abundance to contribute to the community structure in June (17 %). *C. goodsiri* was then the main abundance contributor in the May (40 %) and June (57 %), as the abundances were over 6 times as high as in any of the other months (Fig. 4.16). In August, *B. sarsi* (50 %) dominated, with harpacticoid copepods (30 %) also in high abundance contribution. In November, *C. goodsiri* contributed to 90 % of the community structure, whereas it was tubificids (66 %) in January, which were also only present in the March (13 %).

When differences in the shore level communities at each beach were investigated separately for each month sampled (except June), the community structures were not significantly dissimilar (p > 0.05) at either Climping or Felpham for any of the months sampled (Table 4.9). There were, on the other hand, significant differences in the community structure between the shore levels for both bays and tombolos at Elmer in March, May, August, and November, but not in January (Table 4.10). This showed that the temporal changes seen at Felpham and Climping occurred across all shore levels, whilst at Elmer the interactions with shore level and time were more complicated.

There were small temporal changes in the bay and tombolo communities at each vertical shore level (Fig. 4.17). The overall trend seen for the bay communities were that the upper landward communities were very different from those in the lower landward and seaward areas. The latter two communities were shown to be aggregated together in similarity (Fig. 4.17), with no significant differences in August, November and January, but in March and May the communities had overlapping similarities and dissimilarities (Table 4.9).

Table 4.9 ANOSIM pair-wise R tests for each month (excluding June) for spatial differences on infaunal community structure between vertical shore levels across Elmer bays and tombolos. Analyses performed on square-root transformed data. p set to 0.01; *p <0.05, **p<0.01, ***p<0.001. Felpham and Climping results not shown as none were significant. Levels of difference or similarity is given (**D: different**; O: overlapping; S: similar).

		Elmer: Bays		Elmer: Tombolos	
Month (Global <i>R</i>)	Levels compared	R		R	
Mar-05	LW (U) - LW (L)	0.51*	О	NS	-
(0.56***)	LW (U) - SW	0.99*	D	0.84*	D
	LW (L) - SW	0.52*	O	0.82*	D
May-05	LW (U) - LW (L)	1*	D	NS	-
(0.472***)	LW (U) - SW	1*	D	0.68*	O
	LW (L) - SW	0.29*	S	0.62*	O
Aug-05	LW(U) - LW(L)	0.37*	S	NS	-
(0.367***)	LW (U) - SW	0.59*	O	0.57*	O
	LW (L) - SW	NS	-	0.51*	O
Nov-05	LW(U) - LW(L)	0.32*	S	NS	-
(0.345*)	LW (U) - SW	0.93*	D	0.56*	O
	LW (L) - SW	NS	-	NS	-
Jan-06	LW (U) - LW (L)	NS	-	NS	-
(NS)	LW (U) - SW	NS	-	NS	-
-	LW (L) - SW	NS	-	NS	-

The largest significant difference in shore level occurred in May; the lower landward communities were completely different (ANOSIM R = 1, p = 0.02) from the upper landward and seaward communities. The landward tombolo communities were very similar to each other across all the time periods (Table 4.9); but both the upper and lower landward communities showed overlap in similarities and differences with the seaward communities (Table 4.9) for March, May, and August (Fig. 4.17). There were no vertical shore differences in January for either the bays or the tombolos.

Table 4.10 shows the similarities and dissimilarities between the bays and tombolos at each shore level for each time period (Figure 4.17). The bay and tombolo communities were consistently similar over time in the upper landward and seaward sides of the breakwaters. In contrast, in the lower landward levels, the bay communities showed significant (p < 0.05) overlapping with as many differences as similarities to tombolos communities.

Table 4.10 ANOSIM pair-wise R tests for each month (excluding June) for spatial differences on infaunal community structure between bays and tombolos at each vertical shore level (upper landward: LW (U), lower landward: LW (L), and seaward: SW). Analyses performed on square-root transformed data. p set to 0.01; *p < 0.05, **p < 0.01, ***p < 0.001; The largest significant spatial difference is in **bold**. Ashows difference when p < 0.1

	LW (U)	LW (L)	SW
	R	R	R
Mar	NS	0.47*	NS
May	NS	0.54*	NS
Aug	NS	NS	NS
Nov	NS	0.44 ^A	NS
Jan	NS	0.30 ^A	NS

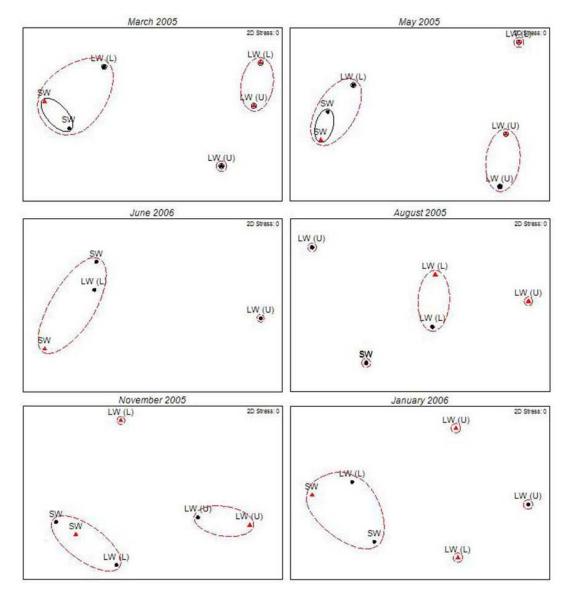


Figure 4.17 MDS ordination plots of differences in community structures between horizontal shore levels (upper landward (LW (L)), lower landward (LW (U)), and seaward (SW)) for bays (\bullet) and tombolos (\triangle) at Elmer for each time period (Mar, May, June, Aug, Nov 2005, and Jan 2006). Cluster analysis contour lines: 60% similarity (dotted line), 80% similarity (solid line). See Figures 4.9 and 4.10 for ANOSIM Global *R* and pairwise test results that correlate to these MDS plots.

These differences were seen in March and May, but not August (Table 4.10). The strongest difference was seen in May when the communities were as similar as they were dissimilar. The upper landward communities were different from those in the lower landward and seaward levels in the bays for the majority of the months. This was because the densities of individuals (F $_{2, 252} = 107$, p < 0.001) and number of species (F $_{2, 252} = 33.7$, p < 0.001) were significantly lower (< 5000 ind/m², < 3 species) in the upper sections of the beach (Fig. 4.18), particularly in March, May and June, than either the lower landward or seaward communities (> 5,000 ind/m², > 3 species). SIMPER analyses showed that *Bathyporeia* spp. were dominantly abundant (37 - 63 %) in the upper landward communities in all months, except August. Their dominance was less in the lower landward (25 - 33 %) and seaward (< 12 %) because *S. filicornis*, harpacticoid copepods, and *C. goodsiri* became more typically abundant.

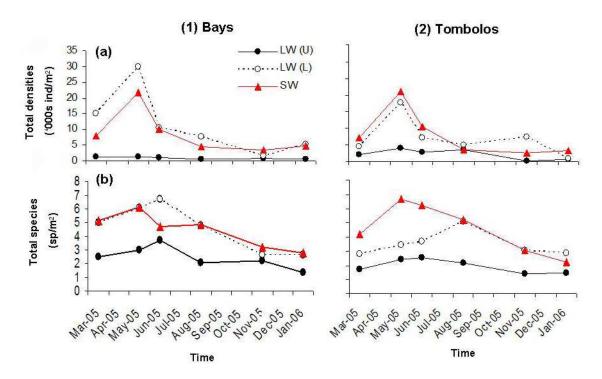


Figure 4.18 Temporal changes in total mean (a) densities and (b) number of species in different vertical shore levels (upper landward: LW (U), lower landward: LW (L), and seaward: SW) for (1) bays and (2) tombolos at Elmer beach.

In contrast, the landward communities on the tombolos were significantly similar (Table 4.9), because although there were differences in the densities of individuals and number of species (Fig. 4.18), the differences were not as large as those in the bays, and importantly the species compositions were very similar. *B. pilosa* was consistently dominantly abundant in most of the

months in both the upper (except January) and lower landward (except August) communities, and only present in May and January in the seaward communities, but then only contributing to less than 10 % of the densities of individuals. The seaward communities, as with in front of bays, were typically dominated by *S. filicornis* in all months, also with *C. goodsiri* and harpacticoid copepods being dominant (Fig. 4.19).

The most obvious difference in the composition of lower landward communities between bays and tombolos was in the amphipods, with *B. pilosa* abundantly dominant in the tombolo communities, and *B. sarsi* in the bay communities (Fig. 4.19). There were also differences in the numbers of *S. filicornis*, which was only dominant in the bays and not the tombolos, and furthermore there were greater abundances of copepods in the bays than tombolos. The other main difference was in the densities of *A. marina*, which was more abundant in the upper and lower landward tombolo communities, and upper landward bay communities, but in far lower densities in the lower landward bay communities, also similar to that in the seaward communities.

The changes in communities over time were relatively similar at all vertical shore levels for both the bays and tombolos, for example the increase in total densities in May was seen at all levels (Fig. 4.18). There were similar changes between the two horizontal shore locations (bays and tombolos). For example, in August there was no particular dominating species in any of the communities, but rather an increase in the number of contributing species, particularly from carnivorous polychaetes, such as *E. picta*, *G. tridactyla*, and *Phyllodoce maculata*. In May, when the densities of individuals were the greatest in bays and tombolos (Fig. 4.18), the upper and lower landward tombolo communities were dominated by *B. pilosa* (74 % and 53 %, respectively), with the lower landward densities exceeding averages of 14,000 ind/m². In the bays, although *B. sarsi* were extremely dominantly abundant (lower landward average of > 7,000 ind/m²), harpacticoid copepods were the most dominantly abundant in both the upper and lower landward communities (36 % and 38 %, respectively), with average densities of > 19,000 ind/m² in the latter communities.

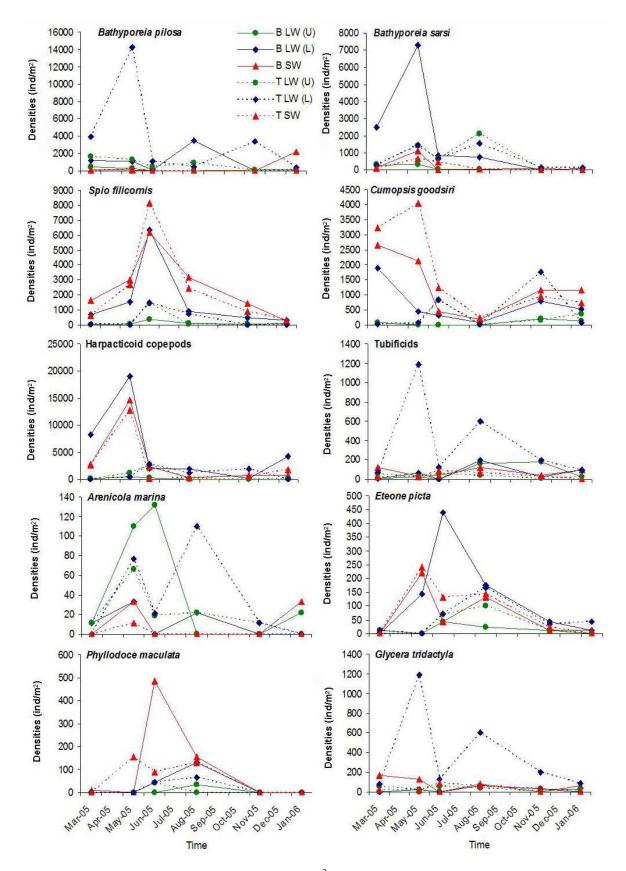


Figure 4.19 Temporal changes in mean densities (ind/m²) of dominant species at different shore levels in bay (solid lines) and tombolo (dotted lines) benthic communities at Elmer. **NB**: y-axis scales are different.

The upper landward communities of the bays were completely different (ANOSIM R = 1) from the lower landward and seaward levels in May (Table 4.9). This was because of the increase in A. marina densities, from less than 20 ind/m² to more than 100 ind/m² in May and June, whilst, they remained below 35 ind/m² in the latter communities.

Following the extreme increase in densities in May, there were acute decreases of some species by June, for example, *Bathyporeia* spp. (ca. –80 %), harpacticoid copepods (ca. –85 %), tubificids (ca. –89 %), and *C. goodsiri* (ca. –70 %). Coinciding with these decreases, there were increases in densities of other species from May to June, for example, polychaetes, such as the surface deposit feeder *S. filicornis* (ca. +65 %) and the carnivores, *P. maculata* (ca. +75 %) in seaward communities and *E. picta* (ca. +75 %) in lower landward communities (Fig. 4.19).

These species dominance changes were particularly seen in the lower landward and seaward communities. In the colder months of November, January and March, a vertical shift up the shore was seen in some species, which is why there were no differences between communities in January and little in November. *C. goodsiri* was abundantly dominant in these months, they were typically dominant in the seaward and lower landward bay communities, but in January they were also found to be dominantly abundant in the upper landward of tombolos and bays, along with *S. filicornis*.

4.3.4 Influence of environmental parameters and decaying macroalgae deposits on macrofaunal communities

4.3.4.1 Environmental influences on spatial faunal community patterns

There were several measurable environmental variables that could have influenced the community structures of the three beaches sampled, including sediment grain size, carbon content of sediment, sediment temperature, amount of water in the sediment, depth of oxic layer, beach elevation, decaying macroalgae deposits (% cover and biomass), and beach exposure to waves and tides (Beach State Index). These environmental variables showed spatial variation both vertically and horizontally across the three beaches in this study. These variables were used in BIO-ENV and LINKTREE analysis (PRIMER, for further information see Clarke

& Warwick 2001) to determine to what degree these variables could explain the faunal community spatial differences that have been observed.

The optimum combination of environmental variables resulting from the BIO-ENV analysis to match the faunal community spatial variation in sediments on the seaward and landward (lower and upper) levels of shore at Felpham and Climping beaches, and the bays and tombolos at Elmer were the depth of the oxic layer, sediment draining efficiency, beach elevation (above ODN) and amount of decaying macroalgae cover ($\rho^{\rm w}=0.822$). These four variables together explained 82 % of the variation, with beach elevation being the best single environmental predictor, explaining 78 % of the spatial changes (Fig. 4.20). The decaying macroalgae cover only explained 6% of the spatial changes.

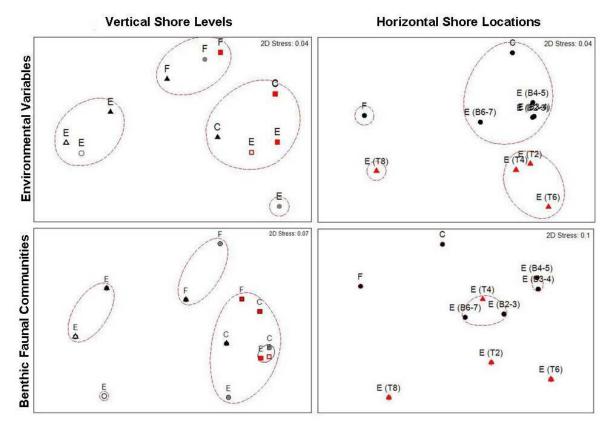


Figure 4.20 MDS ordination plots of spatial changes of **a**) the optimum combination of environmental variables (depth of oxic layer, sediment draining efficiency, beach elevation and decaying macroalgae cover; $\rho_{\rm w}=0.810$) to predict the benthic faunal community structures for the upper landward (\blacktriangle), lower landward (\bullet) and seaward (\blacksquare) sections of bay (solid shape) areas of Felpham, Elmer, and Climping, and tombolo (hollow shape) areas of Elmer. Cluster analysis similarity lines for environmental variable plot (Euclidean distance: 1.1) and benthic faunal communities (Bray-Curtis similarity: 40% (dotted), 60% (solid). **b**) the optimum combination of environmental variables (median grain size, v fine gravel, v fine sand, v coarse silt, depth of oxic layer, sediment draining efficiency, sediment carbon content, and decaying macroalgae biomass; $\rho_{\rm w}=0.859$) to predict communities in different horizontal shore locations (bays (\bullet) and tombolos (\blacktriangle)). Euclidean distance: 1.3 and 80 % Bray-Curtis similarity.

LINKTREE analysis showed that when linking the faunal communities and optimum environmental variables together, there were six groups, although three of these were relatively closely linked. The most separated communities (ANOSIM R = 0.92, LINKTREE B % = 97) were the upper landward sections of the bays and tombolos at Elmer, as well as lower landward tombolo communities (Fig. 4.20). They were the most elevated (> 1.8 m above ODN) areas of the beach (Chapter 2), with high sediment draining efficiency. The upper and lower landward levels of Felpham Beach were aggregated together and were separate from the other groups (ANOSIM R = 0.84; LINKTREE B % = 61) because the sediments were very oxic in comparison (> 13.3 cm deep). The beach areas can be further divided into the upper landward of Climping beach and the lower landward level of bays at Elmer (ANOSIM R = 0.55; LINKTREE B % = 33), and the seaward sides of the structures of all the beaches (ANOSIM R = 0.83; LINKTREE B % = 23). The division between these last two groups is because the former retained less water than the latter sediments. The separation of the seaward community at Felpham from the other seaward communities seen (Fig. 4.20) was because the sediments at Felpham were more oxic (> 13.3 cm deep) than the others (< 9.19 cm deep).

The differences observed between the vertical shore levels of different bays at Elmer (Fig. 4.14 & 4.20), where the communities in the lower landward and seaward areas of the beach were tightly aggregated could not be explained by the gap length between breakwaters, their exposure to waves and tides (Dean's Parameter (Ω) or BSI) or current speeds. Instead, a combination of nine variables explained 71 % of this variation (median grain size, amount of v fine gravel, v fine sand, and v coarse silt, depth of oxic layer, sediment draining efficiency, sediment carbon content, beach elevation, and macroalgae deposits (cover and biomass)). These variables may, however, have been correlated with or influenced by gap length and exposure to waves and tides. There was not one single variable that explained these community structure differences. The amount of very coarse silt (47 %), beach elevation (45 %) and carbon content (44 %) together were the main explanatory variables, with decaying macroalgae cover and biomass explaining a reasonable amount (26 and 12 %, respectively). The main cause for the aggregation of communities seen in Fig. 4.20 was because the upper landward sections were significantly (SIMPROF p < 0.01) more elevated (> 1.36 m above ODN) than the lower landward and seaward. The communities in the upper landward level of Bay 2-3 was slightly separated from the other bays of the same vertical shore levels, this was because the elevation was marginally

less (< 1.36 m in comparison to > 2 m above ODN), as well as there being half the amount of decaying macroalgae deposited (< 0.32 kg/m^2) compared to the other bays (> 0.65 kg/m^2).

The small differences between the tombolo communities (Fig. 4.10) could not be explained by either the length of the breakwaters or their distance from the shore. The different vertical shore levels of the tombolos were aggregated differently from the bays, with differences between the landward and seaward communities. These differences can be 72 % accounted for by differences in the median grain size, amount of very fine gravel, very coarse sand, and fine sand in the sediments, depth of oxic layer, sediment water retention, and decaying macroalgae biomass, but not elevation as with bays. There were three significant groupings (SIMPROF, p < 0.01) for the horizontal shore positions of different tombolos. The upper and lower landward communities of Tombolo 8 were the most different (ANOSIM R = 0.88, LINKTREE B % = 95). This was because the sediment grain size was larger (> 907 μ m), with more very fine gravel (> 23 %) and less fine sand (< 59 %) than the sediments of all the other communities (< 824 μ m, < 13 %, and > 67 %, respectively). The seaward communities were significantly different from the landward communities (ANOSIM R = 0.80, LINKTREE B % = 59) because more water was retained in the sediments.

The very small differences in community structure between the horizontal shore locations (Felpham, Climping, Elmer bays (2-3, 3-4, 4-5 and 6-7), and Elmer tombolos (2, 4, 6 and 8)) seen in Fig. 4.10 (ANOSIM, Global R = 0.094, p < 0.01) can be explained very well (86 %) by the differences in the median grain size, amount of very fine gravel, very fine sand, and very coarse silt, depth of oxic layer, sediment draining efficiency, carbon content of sediment and the biomass of decaying macroalgae deposited on the beaches ($\rho^{\rm w} = 0.859$). The single best environmental variable to determine the small scale differences in community structure between each section was the median grain size (67 %), followed by the amount of very fine sand (66 %) and very fine gravel (63 %). The carbon content was also an important variable explaining 31% of the variation, whereas macroalgae biomass explained a small amount of variation (8 %). The communities and environmental variables at Felpham Beach and Tombolo 8 at Elmer Beach were different from the other shore locations (ANOSIM R = 0.84; LINKTREE B % = 94), due to the median grain size being larger than 745 μ m, whereas the median grain size of the other locations was less than 395 mm (Fig. 4.20). A large portion (25 %) of the sediment was made up of very fine gravel (2-4 mm) and very little of very fine sand (< 5.7 %) and silt (< 0.07 %).

Although, the other groupings seen in Fig. 4.20 were only marginally different, it is worth mentioning the environmental differences observed between them. Tombolo 6 and Climping Beach were separated from the other remaining locations because they received less macroalgae deposits ($< 0.597 \text{ kg/m}^2$) than the other tombolos and bays at Elmer (excluding Felpham and tombolo 8), where more than an average 1.15 kg/m² of decaying macroalgae was deposited. The grouping of Bays 3-4 and 4-5, which have been previously discussed (Fig. 4.10) had more average carbon content (> 0.67 %) than Bays 2-3 and 6-7 (< 0.62 %).

4.3.4.2 Environmental influences on temporal faunal community patterns

A seasonal pattern was shown in the sediment environment (Fig. 4.4) and the in amount of decaying macroalgae deposits (Chapter 3: Fig. 3.20). These variables could potentially give some explanation of the temporal biotic patterns seen in the benthic communities at the different sites (Fig. 4.17).

Felpham

The optimum combination of variables to explain the temporal community changes adjacent to the granite groynes at Felpham Beach were changes in the percentage contribution of very fine gravel, very coarse, coarse, medium and fine sand, depth of oxic layer, sediment temperature, sediment draining efficiency, and macroalgae cover ($\rho^{\rm w}=0.507$). These nine variables together accounted for 51 % of a ranked match to the biotic patterns (Fig. 4.21). LINKTREE analysis showed that when linking the faunal communities and optimum environmental variables together there were two very distinct groupings (B % = 95). The first was November and January, these two months showed differences from the other months (ANOSIM R=0.82) because the sediment temperature was below 6.2° C and the sediment grain size was larger and less well sorted, with more very coarse sand (> 3.4 %) and very fine gravel (> 33.7 %). The other months, March, June, May and August showed a further split (B % = 49) with March being different from the latter three months but the differences were not as great (ANOSIM R=0.56). The reasons for this were because the sediments were more oxic in March (> 20cm deep) than the other three months.

Climping

At Climping, only three environmental variables were needed to account for 73 % of the temporal variation in the faunal assemblages (Fig. 4.21); these were the median grain size, amount of fine sand and biomass of decaying macroalgae deposits ($\rho^{w} = 0.725$).

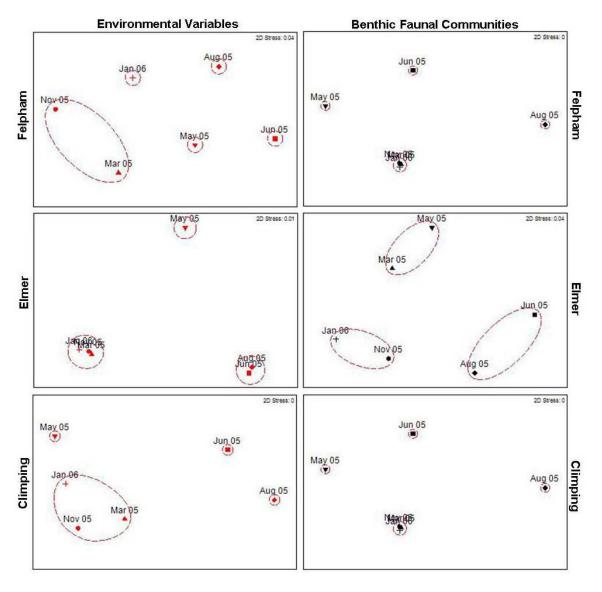


Figure 4.21 MDS ordination plots of the temporal changes of the optimum combination of environmental variables (left column – red symbols) to predict the benthic faunal community structures for Felpham (very fine gravel, very coarse, coarse, medium and fine sand, depth of oxic layer, sediment temperature, sediment draining efficiency, and decaying macroalgae cover; $\rho_{\rm w}=0.507$), Elmer (median grain size, very fine gravel, medium sand, depth of oxic layer, sediment temperature, beach elevation, and decaying macroalgae cover; $\rho_{\rm w}=0.761$), and Climping (median grain size, fine sand, and decaying macroalgae biomass; $\rho_{\rm w}=0.725$). MDS plots for the benthic faunal community structure (right column – black symbols) with cluster analysis percentage similarity lines (Felpham: 40% (solid), 60% (dotted); Elmer: 60% (dotted); Climping: 60% (dotted)). Cluster analysis Euclidean distance lines for environmental variable plots (Felpham: 2; Elmer: 1.8; Climping: 0.63).

Linking the environmental variables and community patterns observed in the MDS plots (Fig. 4.21), there were three different aggregations of months. The first was August, which was shown to be completely different from the other months (B % = 100 %; ANOSIM R = 1), this was because the average median grain size was very large (> 1000 μ m) in comparison to the other months (< 384 μ m), with less portions of fine sand (August: < 58 %, others: > 68 %).

The other split in months was between May and June in one group, and March, November and January in the other (B % = 54; ANOSIM R = 0.75), this was because of differences in the average amount of decaying macroalgae biomass deposited on the beach, with May and June (> 0.494 kg/m^2) experiencing greater quantities than the latter group, with less than 0.177 kg/m^2 .

A combination of seven environmental variables ($\rho^{\rm w}=0.761$) best explained the temporal changes seen by faunal communities surrounding the shore parallel breakwaters at Elmer Beach (Fig. 4.21). These were median grain size, the amount of very fine gravel and medium sand, depth of oxic layer, sediment temperature, the beach elevation (above ODN) of the sampled community, and finally the decaying macroalgae cover. There were two distinct groups (B % = 90), although the differences between them was not as strong as seen with Felpham (ANOSIM R=0.63). March, November and January (winter months) were grouped together, as were May, June and August (summer months); this was because of a combination of differences, where the winter months had colder sediments (< 12.5° C), less algal cover (< 10.6 %) and more oxic sediments (> 11.1 cm), whilst in the summer months, the sediment was warmer (> 16° C), with more algal cover (> 12.3 %) and the oxic layer was shallower (< 9.95 cm).

There were complex vertical shore level community changes over time for the bays and tombolos at Elmer (Fig. 4.22). The environmental variables that explain the vertical community differences in March for bays and tombolos were differences in the current speed, sorting, skewness, and kurtosis of sediments, depth of oxic layer, sediment water retention and beach elevation. These seven variables together accounted for 99.3% of the differences in the biotic patterns (Fig. 4.22). LINKTREE analysis showed that when linking the faunal communities and these environmental variables together, there were two distinct significant groups (SIMPROF, p < 0.05; ANOSIM R = 1). The upper landward communities of both bays and tombolos and lower landward tombolo communities were grouped together (Group A), whilst the seaward and lower landward bay communities were grouped together (Group B). These groupings occurred because in the former the beach elevation was greater than 1.8 m above ODN, the depth of the

sediment oxic layer was deeper (> 10 cm), were able to retain less water, and the sediments were better sorted (> 342 mm). These groupings were consistent for most months except in August and November (Fig. 4.22). In May, the optimum variables to explain the differences changed slightly, with the differences accounted for by Beach State Index (BSI), current speed, the median grain size and sediment water retention, again these accounted for a high percentage of the biotic pattern (98.6 %). The median grain size was greater (> 186 μ m) in Group A than Group B (< 178 μ m), with a BSI lower (< 2.68) than the more exposed sections of the beach (> 2.7).

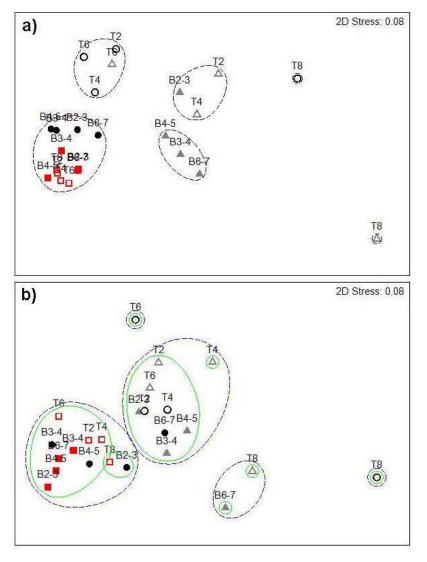


Figure 4.22 MDS ordination plots for differences in vertical shore levels (upper landward (\blacktriangle), lower landward (\bullet) and seaward (\blacksquare)) for bays (solid symbols) and tombolos (empty symbols) at Elmer for a) benthic faunal community structure and b) the optimum combination of environmental variables to predict the benthic faunal community structures for Elmer (current speed, sorting, skewness, and kurtosis of sediments, depth of oxic layer, sediment water retention and beach elevation; $\rho_{\rm w}=0.993$). Cluster analysis percentage similarity lines for benthic fauna (Elmer: 60 % (dotted). Cluster analysis Euclidean distance lines for environmental variable plots (1.8).

In August, the optimum variables to match the biotic patterns were the sediment sorting, amount of very coarse sand, depth of oxic layer, sediment temperature and decaying macroalgae biomass, accounting for 82 % of the variation. These variables grouped the communities into three significantly different (p > 0.05) groups, Group B remained the same but Group A was split, with the upper landward of the bays different from the upper and lower landward of the tombolos (ANOSIM R = 0.68, B % = 88). This was because the upper landward of the bays had more very coarse, less well sorted sand (> 2.1 %, > 514 mm) than the other communities (< 1.2 %, < 344 μ m). The differences between the landward tombolo communities from the both seaward and lower landward bay communities was because the temperature was greater in the former (> 19° C), with slightly deeper oxic layers (> 3.8 cm) than the latter (< 17° C and < 1.8 cm, respectively).

In November, seven combined variables accounted for 91.8 % of the spatial differences in biotic pattern, dividing the stations in three significantly different groups: Group A (upper landward bay and tombolo communities), Group B (lower landward tombolo communities), and Group C (lower landward bay and seaward communities), these can be seen in Fig. 4.22. Group A had less TOM (< 0.75 %) in the sediments than Group B or C (> 0.82 %), as well as having greater amounts of fine well sorted sand (> 77 % and > 335 μ m). The lower landward tombolo communities (Group B) were different from Group C because there was the most TOM in the sediments (> 0.91 %), but sediments were less well sorted, with a large median grain size (> 802 μ m), because there was more than 1.6 % very coarse sand compared to less than 0.8 % and a median grain size of 167 μ m (Group C). In January, the beach was divided into two significantly different groups, the same as March and May, with only one environmental variable needed to account for the community differences. This was the BSI, which accounted for 86 % of the match. The BSI was greater (> 2.72) for the seaward and lower landward bay communities than the communities in the upper landward and behind the tombolos (lower landward) (< 2.65).

4.3.4.3 Environmental influences on community measures and dominant species

Relationships between the optimum variables discovered in the community analysis, the overall community measures (total densities of individuals, total species and species diversity), and dominant species were also investigated. Positive relationships existed between the sediment temperature and the total numbers of individuals at Felpham (r = 0.54), Elmer (r = 0.49) and Climping (r = 0.64) beaches, where, as the temperature increased, the total densities increased. However, only some of the temporal variation in densities of individuals at Felpham and Elmer was explained, whereas, 64% of the variation in the temporal changes in densities at Climping was explained. Pearson's correlation analysis showed that there were extremely strong significant (p < 0.01) correlations between the total densities of individuals and both the decaying macroalgae cover and biomass at Elmer Beach (r = 0.95 and r = 0.93, respectively) The algal cover could explain 89% of the variability in the faunal densities at Elmer, and the biomass 81% of the variability (Fig. 4.23). There was no significant relationship for Climping (r = 0.07), but a reasonably strong relationship between the faunal densities and decaying macroalgal cover at Felpham (r = 0.60).

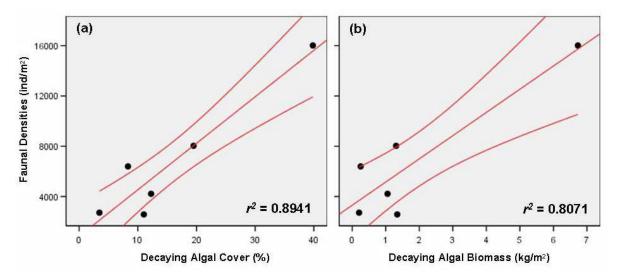


Figure 4.23 The influence of decaying macroalgae deposits on benthic communities. Average total faunal densities (ind/m^2) for each month sampled against the average monthly a) macroalgae cover (%) and b) macroalgae biomass (kg/m^2 wet) of deposits at Elmer beach. Scatterplot with best fit line and 95 % confidence intervals. Strength of correlation is given with R-squared value.

There were no significant correlations between the amount of decaying macroalgae (cover and biomass) and the sediment environment (e.g. sediment temperature, carbon content or depth of oxic layer) at Elmer over time. It is, therefore, an independent environmental variable and any correlations between dominant fauna and the decaying macroalgae deposits can be interpreted to be influenced directly by the deposits. At Elmer, average Bathyporeia pilosa densities over time were significantly (p < 0.05) and strongly correlated with the amount of algal cover (r = 0.94) and biomass (r = 0.93), as well as the densities of B. sarsi (r = 0.93, p < 0.01). There were not, however, any significant relationships between the amphipod species and the sediment temperature, depth of oxic layer, carbon content or percentage content of sand in the sediment. There were relationships between the Bathyporeia spp. densities at Felpham and the amount of algal deposits (low quantities e.g. < 10 % cover), as well as the sediment temperature and carbon content. However, the overall densities were low (Fig. 4.19), and because there was collinearity between the decaying macroalgae deposits, sediment temperature and other variables, it is impossible to ascertain what caused the temporal changes in abundances. At Climping Beach, B. pilosa was correlated with algal deposits but B. sarsi was not. Neither species were correlated with any of the sediment variables. The densities of copepods had significantly correlated relationships with both algal cover and biomass; like the amphipods, there were no correlations with the sediment variables. The copepod densities were intercorrelated with the Bathyporeia spp. and Pontocrates arenarius, all of which had density peaks when the decaying macroalgae deposits were greatest in May 2005 (Fig. 4.20).

Spio filicornis appears to have had a threshold relationship with the *Bathyporeia* spp., when the latter was high in abundance the former was not and vice versa (Fig. 4.20); this was particularly noticeable at Elmer Beach (Fig. 4.22). There were no relationships between this polychaete and the amount of algal deposits or sediment environment variables. There were two carnivorous polychaetes that were positively correlated (p < 0.01) with *S*, *filicornis* densities, these were *P*. *maculata* (r = 0.92), and *E*. *picta* (r = 0.85). At Climping, *G*. *tridactyla* densities were correlated with *S*. *filicornis* (r = 0.81), with peaks in their densities in August (Fig. 4.19).

4.5 Discussion

The presence of the breakwaters at Elmer has caused the accumulation of sediment (referred to as 'tombolos') on the landward sides of these structures, thus raising the beach and/or tidal elevation. On the landward side of the scheme between the breakwaters, there is no sediment accretion, but some erosion (Plomaritis 2006); these areas are like 'bays', and have much lower tidal elevations. The beach profiles at Felpham and Climping beaches are similar to the bays at Elmer, not the tombolos. The main findings of this study were that this difference in vertical shore elevation (bays and tombolos) has led to major differences in benthic faunal densities between groynes and breakwaters because shore elevation level (or tidal height) is the most important determinant of species distribution (Gray 1981). Changes in tidal height over the intertidal zone creates less predictable environments where there are more extreme changes in temperature, salinity, dissolved oxygen and water content in the upper intertidal than the lower intertidal (Hayward 2004).

When considering the different horizontal shore locations (with the vertical shore levels pooled) the sediment environments of Felpham, Elmer and Climping beaches were similar, probably because these locations were proximate and consequently exposed to the same wave and longshore current regime. The minor sedimentary differences between the three beaches were paralleled by only minor differences in the faunal community species composition. There were also similar average total densities per shore location. The average faunal densities ranged from 5,302 to 6,943 ind/m² for Elmer, Climping and Felpham, with the total number of species ranging from 16 to 27 species. Degraer et al. (2003) carried out a study on eight beaches along the Belgian coast with similar morphodynamic (3.5 m maximum wave height, 7 s maximum wave period) and tidal environments (5 - 3.7 m) to this study. The total number of species was similar among the beaches they sampled; with between 19 and 23 species per beach Degraer et al. (2003), which was also similar to many other studies (Jaramillo et al. 1993, James & Fairweather 1996). However, the infaunal densities in the present study were on average 7 times greater than those found by Degraer et al. (2003). Similarities in the total number of species were observed between Felpham and Elmer beaches, whereas, Climping had marginally less. Species richness and densities generally increased from MHWS to MLWS. The three beaches were similarly dominated by crustaceans and polychaetes in terms of species composition, which is typical of dissipative beaches (Rodil et al. 2007). The most dominant species were harpacticoid copepods, the amphipods *Bathyporeia pilosa* and *Bathyporeia sarsia*, the polychaete *Spio filicornis*, and the cumacea *Cumopsis goodsiri*.

The division of the beach at Elmer into elevated tombolos and concave bays has influenced the vertical distribution of the benthic fauna. There were differences in the community composition per vertical shore level (landward (upper & lower) and seaward) both within and between the bays and tombolos at Elmer, but not adjacent to the granite and wooden groynes at Felpham and Climping. Two infaunal zones could be defined at Elmer: (1) the upper beach zone, which consisted of the upper landward of both bays and tombolos, as well as the lower landward area of the tombolos; this zone was dominated by B. pilosa; and (2) the lower beach zone, which consisted of the lower landward of the bays and the seaward sides of both the bays and the tombolos: the dominant species in this zone were B. sarsi, S. filicornis, harpacticoid copepods and C. goodsiri. These community differences were primarily accounted for by the difference in beach elevation; the upper beach zones have well drained sediments with deeper oxic layers than the lower beach zones. The two Bathyporeia species showed clearly differentiated zonation patterns between the upper and lower beach zones, with B. pilosa living higher on the shore than B. sarsi. This zonation is because the two species have different preferences and tolerances to tidal elevation (e.g. Nicolaisen & Kanneworff 1969, Preece 1971, Coosen et al. 1994, Degraer et al. 1999).

Species that inhabit more exposed sites, such as *Bathyporeia* spp., can give an indication of the extent to which the hydrodynamics properties of the coastal defence scheme influence the habitat for benthic organisms (Coosen et al. 1994). The arrangement and layout of the breakwaters at Elmer has created areas of fast and slow currents on the landward side of the structures (Plomaritis 2006); this study has found that this has led to localised differences in the sediment environment, particularly in the sediment grain size, and variation in the densities of some of the numerically dominant species was probably largely caused by this localised variation in environmental conditions. For example, on the landward side of structure 6 where there were relatively strong currents and high sediment deposition rates (Plomaritis 2006) highest tidal elevation point in the scheme, with very fine, well sorted, and extremely well drained sediments. The greatest average densities of *B. pilosa* (ca. 3,500 ind/m²) were found here, twice as great as other upper beach zones (< 1,250 ind/m²). *B. pilosa* are found high on the shore in dry fine sediments because the sandy sediments are unstable, providing enough water

movement and oxygen supply that enables then to dig and feed in their typical way (Preece 1974). In comparison, the sediments in bay 3-4 and 4-5 were the least drained, and the most organically rich, probably because the largest amount of decaying macroalgae was deposited in these bays. Large densities of harpacticoid copepods (ca. 4000 ind/m²) and the tube-building spionid polychaete *S. filicornis* (ca. 1500 ind/m²) were found here. These two infaunal taxa are predominantly found in areas of organically rich wet sediments where they may feed directly on suspended and settled detritus (Ferner & Jumars 1999, Degraer et al. 2003, Pagano et al. 2006).

The sediment environment at Climping Beach was almost entirely like the lower beach zone of the Elmer bays, and dominated by C. goodsiri, harpacticoid copepods and polychaetes all in similar proportions (ca. 1,500 ind/m²). The sediments there drained poorly at low tide as the beach profile was flat and long and with a shallower incline in comparison with the landward sides of the breakwaters at Elmer (author's pers. obs.). On beaches with flat slopes, the surf zone is wide (> 10 m) and the wave energy is more dissipated, creating hydrodynamically benign conditions for the benthos, and thus favouring the more fragile macrobenthic organisms (Degraer et al. 2003), such as spionid polychaetes like Scolepsis squamata (O. F. Müller) and Spio filicornis. This would explain the vertical shift in the zonation of species within communities at Climping. Lower shore species (e.g. S. filicornis, C. goodsiri and harpacticoid copepods) existed further up the beach, extending into the upper beach zone. The sediments at Climping were not suitable for amphipods such as *Bathyporeia* spp. (av. 350 ind/m²), as they were too wet. Bathyporeia amphipods prefer fine and dry sediments (Khayrallah & Jones 1980) like those found in the upper beach zones at Elmer (ca. 2,000 ind/m²). The sediment conditions were also unfavourable for *Bathyporeia* spp. at Felpham beach (ca. 650 ind/m²) where the sediments were coarse, poorly sorted, highly oxic and retained reasonable amounts of water. The benthic infaunal communities at Felpham were instead dominated by high average densities (ca. 2,000 ind/m²) of C. goodsiri and the amphipod Pontocrates arenarius (av. 318 ind/m²), which reached much lower abundances at the other two beaches (ca. 1,000 and < 27 ind/m², respectively).

The three beaches in this study, with the different types of CDSs, will affect sediment deposition and the resulting morphology will be different: sediment deposition adjacent to groynes generate a concave sloping shore profile, but LCSs cause even more complex localised hydrodynamic conditions, which generate 'lower shore' bays in areas between structures and

higher shore tombolos behind structures. This has led to important implications on a local scale for the benthic infaunal communities, because shore elevation here was found to be the most important determinant of species densities and vertical zonation patterns. Martin et al. (2005) suggested that the potential impacts of breakwaters were mainly determined by changes in the hydrodynamic conditions and sediment transport rather than changes in tidal elevation. More profound impacts on the benthic infaunal communities were observed in this study in comparison with the study by Martin et al. (2005). This was because Martin et al. (2005) only sampled the tombolo areas and not the bays. Contrary to some of the conclusions of Martin et al. (2005), the results from this study would suggest that the observed differences in faunal densities and species zonation patterns were mainly due to differences in tidal elevation, as seen in the zonation of communities in the bays and tombolos. Bertasi et al. (2007) carried out a very detailed study on the impact of the breakwater scheme at Lido di Dante in Italy, following the study by Martin et al. (2005). The findings of this study support the results of Bertasi et al. (2007) in that they found a marked change in current flow, which changes the sediment dynamics on the landward side of the breakwaters, thus affecting the composition and densities of species within the benthic infaunal communities.

The combination of sediment characteristics and amount of decaying macroalgae deposits appeared to strongly influence the densities of species. When there were large amounts of detritus available in the spring months infaunal populations increased probably taking advantage of the extra food resource. Bolam et al. (2000) found that after six weeks, presence of seaweed mats significantly increased macrofaunal diversity. All the species in this study that experienced population fluctuations in accordance with the decaying macroalgae deposits in the spring were deposit or detrital feeders (e.g. Bathyporeia spp. and S. filicornis). Levinton & Stewart (1988) and Cheng et al. (1993) described similar spring blooms in the abundances of deposit feeders, initiated by the high deposition of algal detritus. In the months following the spring bloom, I found rapid declines in Bathyporeia spp. and harpacticoid copepods. This might be because heavy macroalgae deposition makes sediments more reducing, leading to anoxia and the accumulation of toxic hydrogen sulphide (Bolam et al. 2000, Eklund et al. 2005), which are not ideal conditions for Bathyporeia spp. and harpacticoid copepods. The decrease in the latter species enabled more hardy opportunistic species, such as the spionid polychaetes (S. filicornis) to colonize in a spasmodic manner. This algal biomass-dependent trend has been seen by other studies (Hull 1987, Everett 1994, Kelaher & Levinton 2003). For example, Hull (1987) found

the effect on *Pygospio elegans* was algal biomass-dependent; at lower biomasses *P. elegans* increased, presumably as a result of increased detrital food supply, whilst at higher biomasses *P. elegans* declined, probably due to interference with the feeding behaviour of the polychaete (Hull 1987, Everett 1994). Here, the excess algal deposits declined by the late summer (August), and combined with high sediment temperatures and an increase in carnivorous polychaetes, which led to crashes in populations of the opportunistic deposit feeders (e.g. *S. filicornis*). This temporal response by deposit feeders to decaying macroalgae deposits was also similarly observed by Marsh and Tenore (1990) and Cheng et al. (1993).

The domination by deposit feeders because of increased trapping of organic matter within the breakwater scheme was also hypothesised by Martin et al. (2005), suggesting that it would further enhance secondary productivity of juvenile fish and crustaceans. The benthic infaunal communities were never numerically dominated by populations of *Capitella capitata* (< 0.01 % of the community population), which are indicators of extremely enriched anoxic sediments (Bolam 2000, Kelaher & Levinton 2003). This suggests that the amount of decaying macroalgae at the three beaches, in particular Elmer, did not have a particularly negative impact on the benthic communities, but rather provided an important food resource. Many other studies have shown that inputs of algal detritus clearly influence patterns of spatial and temporal variation of micro- and macro -faunal assemblages in soft-sediment habitats (Tenore 1977, Cheng et al. 1993, Raffaelli et al. 1998, Rossi & Underwood 2002). Overall, my findings have shown that detrital enrichment by trapped macroalgae deposits at Elmer were probably the driving force in altering the abundances of deposit feeders, such as *Bathyporeia* spp. Furthermore, the degree of population increases of deposit feeders over time was not seen at Felpham and Climping beaches, probably because far less macroalgae was deposited on these two beaches.

4.6 Conclusions and Further Research

Exposed sandy beaches are mainly physically controlled (Rodil et al. 2007). The addition of CDSs changes the local hydrodynamics and sediment transport pathways (Plomaritis 2006). The breakwater scheme appeared to have changed the environmental conditions more than the groynes have, creating a more complex spatial environment to inhabit. The presence of the breakwaters has changed the beach morphology (i.e. shore elevation height), and this study has shown that this shore elevation is the greatest influence on the zonation patterns of the benthic

communities across the beach. The detrital enrichment from the trapped decaying macroalgae deposits appeared to influence the population abundances of dominating deposit feeders seasonally, such as *Bathyporeia* spp., and subsequently the carnivores. Dugan et al. (2003) stated that organic matter plays a major role in positively affecting benthic communities and benthic metabolism. The deposition of decaying macroalgae within breakwater scheme at Elmer has been shown to be beneficial to the benthic communities.

Further research is clearly required to clarify the importance of this organic input before conclusions can be completely drawn. Algal deposition at Elmer is unusually high and of long duration for an exposed/dissipative beach. The seasonal peak and troughs in some species densities, in response to temporal patterns in algal deposition, implies there are population thresholds to algal biomass. Such thresholds have been observed in other studies (e.g. Hull 1987), and have implications for the management of decaying macroalgae deposits. Firstly, repeat studies over several years should be carried out to further investigate the direct effects of the varying biomasses of decaying macroalgae deposits on the underlying benthic infauna; to eliminate whether temporal fluctuations in the abundances of deposit feeders were due to temperature, or were in fact the detritus availability, or a combination of both. Secondly, factors that influence the nutritional value of deposits should be examined: the influence of the algal decay environment, the species of algae deposited and their value to different faunal groups: some of these aspects are dealt with in Chapters 6 and 7. Experiments and surveys are needed to determine what mobile fauna utilise the macroalgae on the beach; whether this is for food, shelter from predators, or if it is un-utilized because it is indigestible. The last experimental chapter (Chapter 7) attempts to find out what species utilise this organic resource and whether a foodweb can be mapped.

Chapter 5: Communities Colonising CDSs

5.1 Introduction

Coastlines are increasingly being protected from erosion and flooding through the deployment of hard coastal defence structures (CDSs). There needs not only to be an understanding of the hydrodynamics and sedimentology of the coastal location, but it is also imperative to have sound scientific knowledge of the communities that will colonise the structures. Knowledge of the biology and ecology of these man-made structures aids the enhancement of biodiversity, by working with the engineers in the design process. Although breakwaters and artificial structures have long been the subject of study (e.g. Southward & Orton 1954, Houghton 1978, Hawkins & Hartnoll 1983, Carter et al. 1985, Reggio 1987, Fabi & Fiorentini 1994, Jensen et al. 1994, Seaman 1997) there has been renewed interest in recent years, particularly in urban areas such as ports, marinas and docks (e.g. Connell & Glasby 1999, Glasby 1999a, Glasby & Connell 2001, Chapman 2003, Bulleri & Chapman 2004, Blockley 2007). In comparison, there has however, been less research on CDSs (e.g. Davis et al. 2002, Bacchiocchi & Airoldi 2003, Moschella et al. 2005, Pinn et al. 2005). What research there has been in the last 20 years, has mostly concentrated on the engineering design and the resulting hydrodynamics and sediment transport around CDSs (Barber & Davies 1985, Bull et al. 1998, Black & Andrews 2001, Thomalla & Vincent 2003, Ranasinghe & Turner 2006, Birben et al. 2007). Recognition of the need to understand the ecology and impacts of CDSs has become more important (e.g. Davis et al. 2002, Bacchiocchi & Airoldi 2003, Martin et al. 2005, Moschella et al. 2005, Pinn et al. 2005), particularly, with the ever increasing requirements to comply with European environmental legislation during the construction of CDS; with procedures such as Environmental Impact Assessments (85/337/EEC).

Low crested breakwater structures (LCSs) are designed to reduce the wave energy in their lee, thereby reducing the sediment erosive capacity of the waves reaching the shore. The construction of these breakwaters and other coastal defence structures result in considerable changes to the coastal landscape and natural environment, and consequently to the ecology. These consequences occur at local scale, but may also scale up to the whole coastline

(Airoldi et al. 2005). Effects may be site specific, reflecting the variability of natural systems (Burcharth et al. 2007). Quantifying the scale of variation of populations and communities is important to understand better ecological patterns and processes (Levin 1992, Underwood et al. 2000, Jackson et al. 2006). The scale of observations may influence perceptions of the community patterns and processes (Levin 1992), thus hierarchical spatial and temporal scale investigations are needed to understand how scales influence community structure in complex systems. The structure of rocky shore communities is highly variable both in time and space (Balata et al. 2006), whereby different spatial scales may hold different levels of importance in determining community structure (Levin 1992, Blanchard & Bourget 1999). Environmental variables at the coastal level, such as wave climate and sea surface temperature may effect temporal variations in the communities colonising CDSs (Jenkins & Hartnoll 2001, Bourget et al. 2003), whilst the engineering design of the coastal defence schemes (e.g. structure length, distance from the shore, crest height) may have an influence on these communities, as well as changing the local hydrodynamics of the site (Plomaritis 2006).

Exposure to wave energy plays a role in the structure of communities in rocky, open-coast systems (e.g. Stephenson & Stephenson 1949, Lewis 1964, Bustamante & Branch 1996, see Raffaelli & Hawkins 1996 for a review, Jonsson et al. 2006). Species richness has been found to be higher in exposed rather than sheltered sites (Davis et al. 2002, Bacchiocchi & Airoldi 2003). In the same way, this factor may serve to structure communities on artificial hard substrata in bays and estuaries. Higher wave energy is associated with increased water flow and circulation; these patterns of water flow and turbulence are likely to vary among rocky shores, breakwaters and groynes. Organisms and populations may be affected by these flow patterns negatively and positively (Davis et al. 2002). Higher flow can provide a greater rate of nutrient, food, and recruit delivery (Leonard et al. 1998), enhancing growth and survivorship of individuals and populations (Debrot 1990). However, higher energy can lead to decreased handling efficiency of food particles (Davis et al. 2002), lower settlement success (Mullineaux & Garland 1993), higher energy cost necessary to maintain position on the substratum (Boulding et al. 1999), and damage to biota by debris (Debrot 1990). Although CDSs are associated with regions of high wave and water flow energy: the reason for their placement (Jonsson et al. 2006), these environmental variables have not been specifically investigated and correlated with the spatio-temporal distribution patterns of the colonizing communities.

A variety of factors have been observed to determine the composition and structure of intertidal communities inhabiting man-made structures. The vertical and horizontal distribution patterns have been investigated with relation to man-made structures, in order to determine the more important spatial scale (Glasby & Connell 1999, Connell 2001, Knott et al. 2004, Pinn et al. 2005). Communities on rocky shores vary with tidal height resulting in zonation patterns (Stephenson & Stephenson 1949, Lewis 1964, Raffaelli & Hawkins 1996, Balata et al. 2006), which is also seen on groynes (Pinn et al. 2005) and other artificial structures (Southward & Orton 1954, Knott et al. 2004). Little has been done on comparing horizontal and vertical CDS with respect to spatio-temporal patterns (e.g. Bacchiocchi & Airoldi 2003).

The communities on the different sides of CDSs (landward, seaward and the ends) may experience differences in wave exposure, sunlight, temperature and sediment scouring, which can influence community structure (Dobson & Frid 1998). Communities may be different between the different types of CDSs (e.g. breakwaters and groynes), as the LCSs (situated in the mid-intertidal) are not exposed to the vertical shore range of tidal heights that shore-connected groynes are. Vertical shore level is an important factor in determining the species composition of a community in temperate intertidal regions in relation to air exposure and related factors such as temperature and desiccation (e.g. Raffaelli & Hawkins 1996). The low crested breakwater scheme at Elmer (south coast of England) experiences a complex hydrodynamic regime as a result of its design (Plomaritis 2006); whereby the distance from the shoreline (MHWS), length and crest height of each structure, together with the varying length of gaps between each structure has changed the current speed and direction (Plomaritis 2006).

The overall aim was to the identify the temporal change (monthly) in the assemblages colonising four LCSs within the breakwater scheme at Elmer Beach, taking into account the physical design of structure placement (e.g. different structures, sides of structures, distance from shore, crest height, structure length and gap width between structures) in relation to the physical environmental variables (e.g. wave climate, local hydrodynamics and sea

temperature). Furthermore, to compare the communities that colonised the breakwaters with those on two groynes at Felpham Beach on the nearby coastline.

There were four specific objectives:

- 1. To identify the differences in epifaunal assemblage composition on the LCSs at Elmer and the granite groynes at Felpham, in order to test the following hypotheses:
 - a. Assemblages will be different on each structure within the breakwater scheme at Elmer and groyne field at Felpham;
 - b. Assemblages will be different between different sides of the structures on the CDSs;
- 2. To examine the epifaunal assemblages on different sampling occasions and how the spatial variation in these assemblages changes with time;
- 3. To identify the spatial differences in epifaunal assemblages at different vertical shore levels on the granite groynes at Felpham; and
- 4. To determine which engineering design features and/or environmental parameters influenced the community structures on the CDSs.

5.2 Methods

5.2.1 Study Sites

The study sites are on the south coast of England in West Sussex, between Bognor Regis and Littlehampton (Chapter 2: Fig. 2.1). There were two study sites for this investigation; the primary site was on the LCSs within the scheme at Elmer Beach, and the second site was on the groynes at Felpham Beach (Fig. 5.1). No direct comparisons were made with local natural rocky habitat because of the absence of any natural rocky shores along this stretch of coastline. Therefore, it was of more use to compare the LCSs at Elmer with other man-made CDSs within the same geographical cell; subsequently the rock groynes at Felpham were studied. These groynes were created from the same material, granite rock, and of similar age (approximately 10 years old); therefore because the substratum was the same, comparisons could be made.

This coastline has been heavily protected for the last two hundred years because of its exposure to strong southwesterly winds and elevated wave action (see Chapter 2 for in detail

description). There is an array of structure types protecting this coastline, with granite groynes protecting the frontage of Bognor Regis and Felpham, LCSs at Elmer and wooden groynes to the east protecting the beach from Climping Beach through to Littlehampton. The CDSs at both sites consist of 4 - 8 tonne Norwegian granite blocks, of approximately 1.5 m across. There are eight LCSs within the scheme at Elmer of varying length, width apart, distance from the backshore and crest elevation (see Table 5.1), and are located in the lower intertidal foreshore. The presence of the breakwater scheme has caused the local hydrodynamics of the beach to change from what they were, and are now more complex than they were (Plomaritis 2006). The groynes at Felpham are perpendicular to the shore and are attached to the concrete wall that backs the shore. They extend down to the mean low water neap mark and are totally exposed on a spring tide. The local hydrodynamics around the groynes has not been studied to date and so therefore no data could be used when assessing this environmental parameter.

5.2.2 Sampling Design

The sampling design involved sampling from two sites with different CDSs: low crested breakwater structures at Elmer (Fig. 5.1a), and additionally, groynes at Felpham (Fig. 5.1b). Four structures at Elmer (2, 4, 6 and 8) and two structures at Felpham (A and B) were investigated for the study (Fig.s 5.1a & b). At Elmer, each structure had 4 sides (seaward (SW) and landward (LW) sides, and westward (WW) and eastward (EW) ends) and at Felpham there were three sides (seaward (SW), westward (WW) and eastward (EW) sides). In addition, four vertical shore levels (1, 2, 3, and 4) were sampled at Felpham; where 1 was at mean low water (MLW), and 4 was at mean high water (MHW) (Fig. 5.1b). The lowest shore levels 1 and 2 were comparable with the shore location of the breakwaters at Elmer. The same shore level (mid-upper intertidal) was sampled on both types of structures, as determined by the zonation of the different species.

The assemblages colonising the different sides of the structures were sampled using digital photography with eight random replicate quadrats (0.24 x 0.24 cm²) on each side. Sampling was carried out one five occasions from 2005 to 2006 during different seasons; in 2005 these were: 24th March (Winter), 11th May (Spring), 20th July (Summer), 1st Nov (Autumn), and in

2006: 2nd February (Winter). This resulted in 960 photographs, 640 from Elmer and 320 from Felpham over the course of the study.

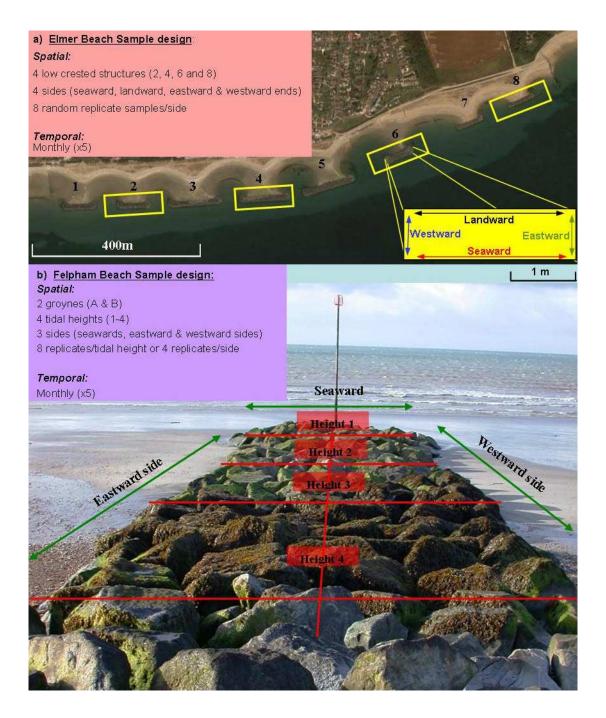


Fig. 5.1 The spatio-temporal sampling design of the assemblages sampled on the CDSs at (a) Elmer and the groynes at Felpham (b).

5.2.3 The Engineering Features of the Elmer Breakwater Scheme

There were several specific design features (breakwater length, distance of the structures from the high water mark (MHWS), breakwater crest height and angle of the breakwater sides to the oncoming waves) which define the scheme at Elmer Beach (Table 5.1 and Fig. 2.4 in Chapter 2).

Table 5.1 Environmental measures for structures in the Elmer offshore breakwater scheme

Structure	Breakwater Length (m)	Distance from MHWS (m)	Crest Current Direction ^a Elevation (m)		Current Strength ^a
2	90	79	4.5	Circular (anti-clockwise)	Weak
4	140	77	4.5	Linear (west-east)	Strong
6	80	54	4.5	Linear (west-east)	Strong
8	80	38	3	Circular (clockwise)	Weak

^a Data taken from hydrodynamic studies previously carried out at Elmer (Plomaritis 2006)

These measurable features were used to assess the effect of the design of the scheme on whether and how they influenced the assemblages on the CDSs (Table 5.1). These design features changed the hydrodynamics of the system and was studied in detail by Plomaritis (2006; see Chapter 2 for further details). The hydrodynamic variables used in this study were current direction and strength. The angle that each side of the structures (groynes and breakwaters) faced relative to magnetic north were recorded, as this angle is a measurable variable, specific for each side and helps determine how exposed these sides are to the typical oncoming waves (Table 5.2).

Table 5.2 The angles relative to N (degrees) that each of the sides faces for each of the coastal defence structures at both Elmer and Felpham.

	Felp	ham	Elmer					
	A B		Structure	Structure	Structure	Structure		
Aspect			2	4	6	8		
Landward	-	-	358	359	337	338		
Eastward	90	88	88	92	79	74		
Seaward	190	159	178	181	157	158		
Westward	270	252	268	272	240	254		

5.2.4 Environmental Variables

Elmer Beach and Felpham Beach are in the same geographical cell (Chapter 2: Fig. 2.1). The influence of the wave climate variables: significant (H_s) and maximum (H_{max}) wave height, wave length (T_p), zero crossing period (T_z) and wave direction (dir), as well as sea surface temperature (SST), sea level and surge (for further detail of wave climate variables see Chapter 2) were selected *a priori* for analysis with community data. The seasonal means and maximums of these variables were calculated (Table 5.3) and used to see if they correlated with seasonal variability in the assemblages on the CDSs.

Table 5.3 Seasonal averages of wave climate (maximum wave height (Hmax), significant wave height (Hs), wave length (Tp), zero up crossing period (Tz) and wave direction (Dir)) and sea environmental variables (sea surface temperature (SST), sea level and tidal surge (residual surge)) recorded from Rushington WaveRider buoy. Maximum (H_{max}) (m) and significant (H_s) (m) wave heights are the maximum seasonal heights reached; all other variables are the seasonal means.

	H _{max}	$H_{\rm s}$	Tp	Tz	Dir	SST	Sea Level	Surge (Residual)
Season	(m)	(m)	(s)	(s)	(°)	(°C)	(m)	(m)
Winter 05	6.07	3.37	6.26	3.69	197.6	7.96	3.56	-0.06
Spring 05	3.81	2.09	6.78	3.69	194.9	8.57	3.58	-0.01
Summer 05	4.13	2.42	5.21	3.36	199.7	17.75	3.62	0.02
Autumn 05	5.90	3.64	6.34	3.68	193.3	15.94	3.69	-0.01
Winter 06	6.63	3.84	7.54	3.90	185.3	7.69	3.56	-0.06

5.2.5 Measurement of CDS Assemblages

The assemblages colonising the rock faces on the CDSs were sampled photographically; this enabled the extensive sampling design chosen to be carried out, enabling large amounts of data to be collected quickly. In contrast, taxonomic resolution was sacrificed; species identification was more difficult for individuals smaller than 0.1 cm, as the images were only 2-dimensional. Quadrats (0.24 x 0.24 cm²) were photographed using a Canon 300D camera (6 mega pixels), which was attached to a tripod with a fixed distance from the quadrat; this ensured the accurate positioning of the camera over the plots, and kept the focal distance and sample area fixed. The photographic equipment allowed monitoring of areas 610 cm². All mobile fauna were measured as number of individuals per unit area (610 cm²); they were identified and the abundance counted from each photograph. Sessile species, algal cover and bare rock were identified and quantified using a 64-point method for each quadrat (Glasby

1999a, 2000, Connell 2001, Glasby & Connell 2001), then converted to percentage cover after correction for points that could not be sampled (e.g. they lay over a large limpet).

5.2.6 Analysis of Data

5.2.6.1 Differences in assemblages

Non-parametric multivariate techniques (PRIMER software package, version 6; Plymouth Marine Laboratory, U.K.) were used to assess differences in assemblages between and within the two sites, and determine which spatial and temporal variables were the most influential factors. For multivariate analyses, sessile cover data and motile species abundance count data were transformed using a square root transformation. Square root transformation was chosen for the analysis as this study did not focus on rare species, but rather the overall assemblage patterns. The assemblages at Felpham and Elmer were examined separately due to the different sampling designs; in addition, it was not possible to pool the vertical shore levels from Felpham as they were at different vertical shore levels (i.e. tidal heights) and the communities were different due to tidal height zonation patterns.

A matrix of similarities between each replicate was first calculated for each site using the Bray Curtis similarity matrices (Bray & Curtis 1957). Multivariate community structure was compared using 2-way crossed analyses of similarities (ANOSIM). These similarity matrices were then used to construct non-metric multidimensional scaling (nMDS, Clarke 1993) plots to visually evaluate variation in community structure. MDS plots were two-dimensional ordinations of the rank orders of similarity within each site across all structures, sides of structures and sampling occasion. Further nMDS ordinations were performed on data averaged for each time period at each site and a trajectory plot added to show the chronological changes in assemblages. The percentage contribution of each taxon to patterns of similarity and dissimilarity within and between structures, sides of structures, sampling occasion and vertical shore levels within each habitat was calculated using SIMPER (Clarke, 1993). Taxa contributing at least 10% to dissimilarity were considered important differentiators.

5.2.6.2 Abundances of dominant taxa

Analysis of variance (ANOVA) was used to test for differences in the following community variables: i) total number of taxa, ii) total number of individuals, iii) total cover of sessile taxa, iv) total cover of bare rock, and v) cover or number of the dominant taxa between and within different spatial scales for different times of the year. Firstly, a 3-way fixed-factor split plot analysis of variance (SPANOVA, SPSS 2005), was used to test for differences in community variables between structures, sides of structures and time at each site (Elmer and Felpham). There was one between subjects factor, 'Site' with two levels (Elmer and Felpham) and three within subjects factors: Factor 1 (Structure) had four levels for Elmer (2, 4, 6 and 8) and two levels for Felpham (A and B); Factor 2 (Sides of Structures) had four levels for Elmer (seawards, landwards, and westward and eastward ends) and three levels for Felpham (seawards, westward and eastward sides); Factor 3 (Time) had five levels (March 2005, May 2005, July 2005, November 2005 and February 2006) for both Elmer and Felpham. Secondly, a 2-way fixed-factor ANOVA was used to test for differences in community variables between vertical shore levels and sampling occasion at Felpham, where Factor 1 (Vertical Shore Level) had four levels (1 (MLW), 2, 3 and 4 (MHW)) and Factor 2 (Time) had five levels (March 2005, May 2005, July 2005, November 2005 and February 2006).

All the analyses were done on $\log (x + 1)$ transformed (apart from percentage data, which were transformed using arcsine percentage square root transformation). Prior to analysis, data were tested for homogeneity of variances using Kolmogorov-Smirnov and Shapiro-Wilks normality tests and homogeneity of inter-correlations using Box's M statistic. Where data remained non-normal following transformations, the more stringent criterion of p = 0.01 was used to reject null hypotheses, since ANOVA is robust for the departure from this assumption when there are many independent replicates and sizes of samples are equal (Underwood 1997). Significant results were, however, interpreted with caution. When ANOVA indicated significant differences among means, the Tukey's HSD *post hoc* test was used to distinguish between them (at p = 0.01). All parametric ANOVAs were done using SPSS (SPSS 2005).

5.2.6.3 Correlation with environmental variables

The BIOENV procedure (PRIMER v6.0, Clarke & Warwick 2001) was used to assess and distinguish which, if any, engineering design features influenced the structure and composition of assemblages on the CDSs at Elmer Beach, and also which the environmental variables were influencing factors on the assemblages at Elmer and Felpham beaches. A matrix of similarities between each replicate for the design and environmental variables was calculated for each site using the Euclidean distance similarity matrices (Bray & Curtis 1957), where data was square root transformed and normalised. These matrices along with the Bray-Curtis matrices for biotic data were used to produce dendrogram and MDS plots for visual assessment of dissimilarities in the structures of assemblages by the optimum combination of variables from the BIO-ENV procedure.

5.3 Results

A total of 15 taxa were found on the breakwaters and groynes (Table 5.4).

Table 5.4 Taxa sampled on the breakwaters (Elmer) and groynes (Felpham)

	Phylum	Class	Family	Species	Species groupings
Animal	Molluscs	Gastropoda	Murididae	Nucella lapillus (Linnaeus)	
			Trochidae	Gibbula umbilicalis (da Costa)	
			Littorinidae	Littorina obtusata (Linnaeus)	
				Littorina saxatilis (Olivia)}	Littorina saxatilis
				Littorina neglecta (Linnaeus)}	group
				Littorina littorea (Linnaeus)	
				Patella vulgata Linnaeus	
		Bivalvia	Mytilidae	Mytilus edulis Linnaeus	
	Crustacea	Cirripedia	Balanidae	Elminius modestus Darwin	Balanidae spp.
				Semibalanus balanoides (Linnaeus)	Datantaae spp.
	Cnidaria	Anthozoa	Actiniidae	Actinia equine (Linnaeus)	
Algae	Chlorophyta		Ulvaceae	Ulva lactuca Linnaeus	
				Ulva enteromorpha var. intestinalis	Ulva spp.
				(Linaeus) Le Jolis	
	Phaeophyta		Fucaceae	Fucus spiralis Linnaeus	
	Rhodophyta		Bangiaceae	Porphyra spp.	

(Blue = motile species; yellow = sessile).

5.3.1 Spatial Patterns of Assemblages on Different CDSs

5.3.1.1 Assemblages on the breakwaters at Elmer

A two-way crossed ANOSIM performed on assemblage data at Elmer for between structures and structure sides showed that the assemblages were significantly (p < 0.001) very similar (R = 0.11). The difference between assemblages on different sides of the structures was greater (R = 0.31, p < 0.001), but still with around 70 % overlap between assemblages. Assemblages differed the most between the eastward ends and landward sides of the breakwaters (R = 0.61, p < 0.001) (Fig. 5.2), with more differences than similarities, followed by landward and seaward assemblages (R = 0.46, p < 0.001), with as many similarities as differences.

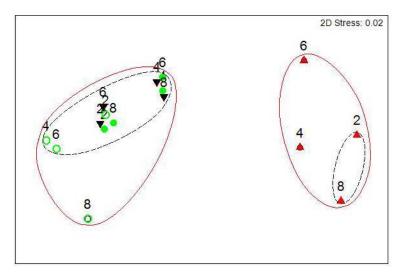


Figure 5.2 MDS ordination of the assemblages on different sides (∇ = seaward side, ○ = eastward end, • = westward end, • = landward side) of the four breakwaters (2 (western end of the scheme), 4, 6 and 8 (eastern end of the scheme)) at Elmer. Data dispersion weighted and $\sqrt{}$ transformed (Stress = 0.02). Contour line from cluster analysis: 60% (red solid line) and 80% (black dotted line).

The assemblages on the westward ends and seaward sides were the most similar (R = 0.05). The landward assemblages showed the most assemblage structure differences compared to the other sides of the breakwaters (Table 5.5). There was no single contributor to these differences in between assemblages from different sides of the breakwaters, although barnacle cover accounted for more than 20 % of the dissimilarities. Overall, the two grazing species, *Littorina saxatilis* species complex and *Patella vulgata* were the only species accountable for approximately 10 % of the dissimilarities between assemblages on the four structure sides (Table 5.5). *F. spiralis* accounted for more than 10 % of the dissimilarities

observed for between westward and landward, and seaward and landward sides.

Table 5.5 Average dissimilarity (%) and variables that contributed to measures of dissimilarity between pairings of assemblages between structure sides (LW = landward, EW = eastward, SW = seaward, WW = westward) at Elmer. Data are the percentage contributions a species contributed to measures of dissimilarity (SIMPER). Greatest contributor (underlined) and important contributor (> 10 %) (bold).

			Structur	e Sides		
	WW v SW	WW v EW	SW v EW	WW v LW	SW v LW	EW v LW
Av. Dissimilarity (%)	37.87	43.08	42.4	61.63	61.2	69.4
Bare rock	18	<u>19</u>	<u>21</u>	14	15	15
Barnacle	<u>20</u>	16	17	<u>23</u>	<u>25</u>	<u>23</u>
Dead barnacles	17	19	20	11	12	17
Detritus						
Ulva spp.				5	5	4
Fucus spiralis		3	2	12	12	9
Littorina saxatilis complex	19	18	16	14	11	12
Littorina littorea	3	4	2			3
Patella vulgata	16	14	14	13	12	10
Porphyra spp.						

Within the assemblages on the eastward, seaward and westward sides of the breakwaters (62, 65 and 64 % similarity, respectively) there were more similarities than differences, this was the opposite for landward assemblages (38 % similarity). The landward assemblages were different from the other sides because of the amount of bare rock (> 70 %) and barnacle cover (< 5 %), and furthermore, it was the only community with a contribution of more than 10 % from *F. spiralis* (Fig. 5.3).

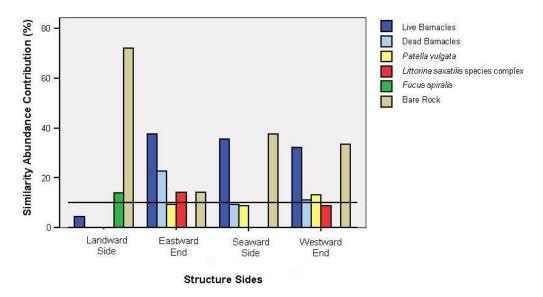


Figure 5.3 Percentage contributions (>90%) from the dominant taxa and bare rock for average similarity (SIMPER) tests within assemblages on different structures sides of the breakwaters at Elmer. (X axis line = 10 % contribution).

The within assemblage structure for each of the other breakwater sides showed similarities, where *P. vulgata* contributed to the similarity in all assemblages (> 10 %) and *L. saxatilis* species complex only accounted for similarities between assemblages on the eastward end (> 10 %) but not particularly to the westward ends (< 10 %). Barnacles contributed more to the within assemblage similarities on the eastward ends of the breakwaters than the westward or seaward sides and less contribution from bare rock (Fig. 5.3).

5.3.1.2 Assemblages on the groynes at Felpham

There were no significant differences (p > 0.05) in the assemblages between the two groynes at Felpham, and a significant similarity (R = 0.08, p < 0.001) in the assemblages occurred between the different sides (westward, seaward and eastward), with 98.12% overlap in the assemblage composition. The assemblages at the different vertical shore levels showed overlap in their composition (R = 0.43, p < 0.001), with slightly more similarities (57 %) than dissimilarities (43 %), there is a gradient of change in the assemblage patterns with vertical shore level, with level 1 and 2 grouped together at 80% similarity (Fig. 5.4).

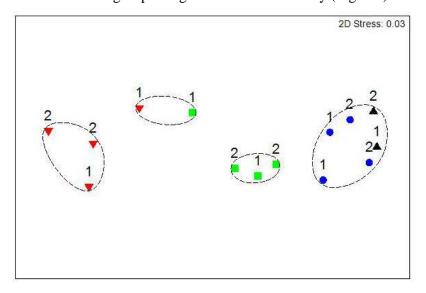


Figure 5.4 MDS ordination of the assemblages at different vertical shore levels (\blacktriangle = level 1 (lower shore), • = level 2, ■ = level 3, ▼ = level 4 (upper shore)) averaged for the different sides of the two breakwaters (1 (western groyne) and 2 (eastern groyne)) at Felpham. Data dispersion weighted and $\sqrt{}$ transformed. Contour line from cluster analysis: 80% (black dotted line). Level 1 is equivalent to mean low water (MLW) and level 4 is equivalent to mean high water (MHW) (Stress = 0.03).

The greatest assemblage differences between the vertical shore levels at Felpham were between vertical level MLW (level 1) and MHW (level 4) (R = 0.70), and 2 and 4 (R = 0.66),

and the least were between vertical shore levels that were adjacent (e.g. levels 1 and 2; R = 0.112). This was because there was a gradual change in the assemblage composition from the low water end of the groynes to the high water end near the shore.

Rock cover was dominated by barnacles (> 35 % similarity) on vertical shore levels 1, 2 and 3 (Fig. 5.5). In contrast, assemblages in shore level 4 were dominated by *F. spiralis* and bare rock (> 80 % similarity), and not by barnacles (> 10 % similarity). *P. vulgata* abundances contributed to 23 % of the assemblage similarity on the low water end of the groynes (level 1) and had decreasing contributions (< 10 %) towards the upper shore (Fig. 5.5). The amount of bare rock increased towards the upper shore, contributing to only 11 % of the assemblage similarity on the low shore (level 1) but 27 % on the upper shore (level 4); whilst the contribution from barnacles and dead barnacles decreased (Fig. 5.5). *L. saxatilis* species complex only made a small abundance contribution (9 %) towards the assemblage similarity in level 3. This was the most abundant motile species found on the groynes at Felpham, but level 3 was the only area that it has made a noticeable abundance contribution in comparison with other sessile cover and motile species.

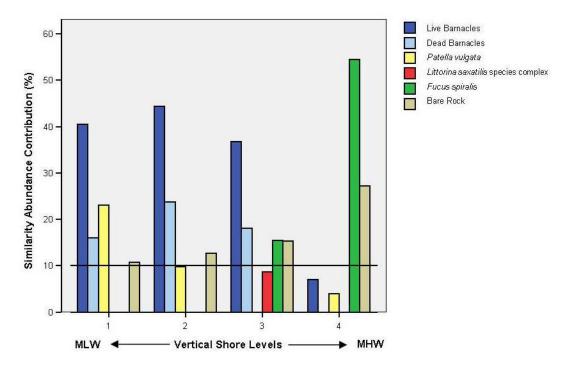


Figure 5.5 Abundance contributions (>90%) of the dominant species and bare rock to average similarity (SIMPER) within vertical shore level assemblages at Felpham (MLW = mean low water; MHW = mean high water). (X axis line = 10% contribution).

There were 6 taxa that were responsible for these differences and overlaps in vertical shore assemblages on the groynes at Felpham Beach (Table 5.6). The sessile taxa of barnacle cover was the most influential on the lower shore (level 1 and 2) and algae (*F. spiralis*) on the upper shore (level 4). The influence of bare rock overlaps the entire vertical shore sampled and accounts most for the spread seen in the MDS plot (Fig. 5.4) for levels 2, 3 and 4. Grazers were not as influential to the similarities and dissimilarities in assemblages along the vertical shore as sessile cover was; only the most abundant species, *L. saxatilis* species complex and *P. vulgata* made significant contributions. *P. vulgata* contributed most to patterns in the lowest shore level (1 and 2), whilst *L. saxatilis* species complex contributed to the assemblage structure higher on the shore in level 3 (Fig. 5.5).

Table 5.6 Variables that contributed > 10 % to measures of dissimilarity between pairings of assemblages at different shore levels (1 = MLW; 4 = MHW) on the groynes at Felpham Beach. Data are the number of times (months: out of five) a species contributed to more than 10% of the dissimilarity. The range of values of dissimilarity is reported in brackets; greatest contributor (*italics*); consistency over time (<u>underline</u>); important contributor (**bold**)

			Vertical Sl	ore Level						
Variables	1 vs. 2	1 vs. 3	2 vs. 3	1vs. 4	2 vs. 4	3 vs. 4				
Bare Rock	4 (8-19)	3 (8-15)	<u>5 (10-16)</u>	1 (4-15)	3 (5-15)	4 (6-17)				
Dead Barnacles	<u>5 (11-19)</u>	3 (9-13)	<u>5 (15-18)</u>	<u>5 (10-16)</u>	<u>5 (13-19)</u>	4 (9-18)				
Detritus	0 (4-8)	0 (5.7-6.3)	0 (2-5)	0 (3-4)	0 (2.8)	0 (5-7)				
Ulva spp.	0 (4-9)	0 (5-7)	1 (8-11)	0 (3-8)	0 (4-9)	1 (4-11)				
Fucus spiralis	0 (3-7)	4 (11-16)	4 (12-18)	<u>5 (11-16)</u>	<u>5 (11-20)</u>	<u>5 (15-21)</u>				
Littorina littorea	0 (2-4)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)				
L. saxatilis species complex	3 (14-22)	3 (10-17)	3 (12-15)	2 (6-17)	3 (11-13)	1 (7-13)				
Barnacles	4 (6-17)	4 (5-23)	<u>5 (10-24)</u>	<u>5 (19-27)</u>	<u>5 (19-26)</u>	<u>5 (20-29)</u>				
Nucella lapillus	0 (5.27)	0 (4.44)	0 (0)	0 (2.42)	0 (0)	0 (0)				
Patella vulgata	<u>5 (20-23)</u>	<u>5 (15-26)</u>	4 (8-16)	<u>5 (14-21)</u>	4 (8-23)	1 (4-21)				
Porphyra spp.	0 (4)	0 (5-6)	0 (7-9)	0 (5.33)	0 (4.98)	0 (1-7)				

5.3.2 Temporal Patterns of Assemblages on Different CDSs

5.3.2.1 Temporal change in assemblages on the Elmer breakwaters

There were significant temporal differences (p < 0.001) in the composition of assemblages on the breakwaters at Elmer between the five months (March 2005, May 2005, July 2005, November 2005 and February 2006). Overall, the assemblages showed more differences than similarities (R = 0.658); the change in the amount of unoccupied rock mainly caused the

observed temporal differences in the assemblages, followed by the amount of live and dead barnacle cover (Table 5.7). The greatest difference in progression over time was between March 2005 and May 2005 (R = 0.76, p < 0.05) (Fig 5.6). This was due to the change in percentage cover of bare rock and barnacles (Fig. 5.7); where bare rock decreased (53 to 25% contribution, respectively) and barnacle cover increased (21 to 43% contribution, respectively).

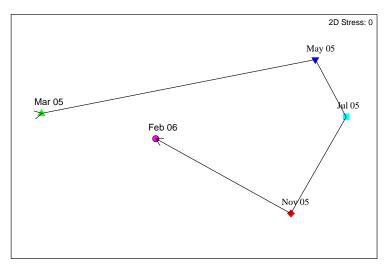


Figure 5.6 MDS ordination plot of average monthly changes in assemblages on the breakwaters at Elmer. Data $\sqrt{\text{transformed (Stress} = 0)}$.

Analysis of the assemblages on the breakwaters at Elmer during May, July and November 2005 showed that the composition did change over time, with an average *R* statistic of 0.5, showing that there were as many similarities as dissimilarities in the changing assemblages (Fig 5.6). The species composition of the assemblages were similar for each sampling occasion, it was the abundances of the dominant taxa that changed with time (Fig. 5.7).

The large differences observed between the sampling times was because the assemblages in both winter periods (March 2005 and February 2006) were very different from the other months; combinations with the other sampling occasions showed dissimilarities ranging from R = 0.635 for between November 2005 and February 2006, to R = 0.865 for between March 2005 and February 2006. This was because the average abundances of the L. saxatilis species complex were the lowest in March 2005 (2.7 ind/quadrat \pm 0.5). The winter sampling times were the only time where there were no significant abundance contributions from L. saxatilis species complex to the assemblages (as defined by SIMPER analysis; Fig. 5.7), and in February 2006, the average abundances were twice that in March 2005 (4.9 ind/quadrat \pm

0.7). Of the grazers, the seasonal change in *P. vulgata* abundances was consistently important (ca. 14 %) in explaining the differences in assemblage structure on the breakwaters (Table 5.7). In contrast, macroalgal species did not contribute a significant (< 10 %) amount to the temporal differences in the assemblages on the breakwaters at Elmer (Table 5.7).

Table 5.7 Average dissimilarity and variables that contributed to measures of dissimilarity between pairings of assemblages between months (Mar = March 2005, May = May 2005, Jul = July 2005, Nov = November 2005, Feb = February 2006) at Elmer. Data are the percentage contributions a species contributed to measures of dissimilarity (SIMPER). Greatest contributor (<u>underline</u>) and important contributor > 10 % (**bold**).

	Mar	Mar	May	Mar	May	Su5	Mar	May	Jul	Nov
57 • 11	VS.									
Variables	May	Jul	Jul	Nov	Nov	Nov	Feb	Feb	Feb	Feb
Av. Dissimilarity (%)	46.3	44.6	42.6	43.2	43.1	39.6	42.4	45.8	43.9	42.6
Bare rock	<u>22</u>	<u>20</u>	<u>19</u>	<u>18</u>	<u>19</u>	<u>18</u>	17	<u>21</u>	<u>19</u>	17
Barnacle	17	18	14	15	13	15	17	17	18	15
Dead barnacles	12	15	15	13	12	13	14	11	15	13
Detritus										
Ulva spp.	5		6	4	6	5		5		4
Fucus spiralis	7	7	8	7	8	9	8	8	8	9
Littorina littorea	6	5	4	5	4					
Littorina saxatilis complex	10	12	12	14	18	16	<u>19</u>	17	16	<u>21</u>
Patella vulgata	13	14	14	14	13	15	15	14	15	14
Porphyra spp.										

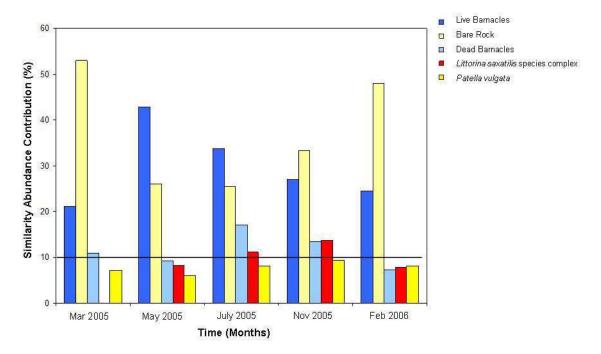


Figure 5.7 Percentage abundance contributions (>90%) of epifaunal species towards average similarity (SIMPER) of assemblages within seasons on granite breakwaters at Elmer Beach. (X axis line = 10% contribution).

5.3.2.2 Temporal change in assemblages on the Felpham groynes

The composition of groyne assemblages showed that there were less temporal changes from March 2005 to February 2006 in the assemblages on the groynes at Felpham (R = 0.233, p < 0.001) than on the breakwaters at Elmer (R = 0.658, < 0.001). Two monthly groupings were observed for the small changes in groyne assemblages (Fig. 5.8). The first consisted of similar assemblages in March and May 2005, and the second in July and November 2005, and February 2006. The greatest change in assemblage structure with progression of time was between May and July (R = 0.345, p < 0.001), and the greatest overall difference was between March and July (R = 0.51, p < 0.001), which shows there was as much the overlap as there was difference in assemblages. There were no significant differences between November and February (p = 0.10).

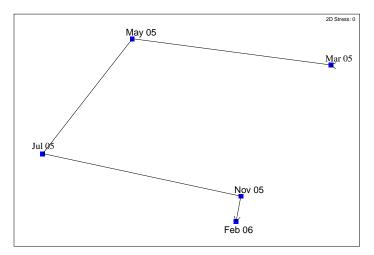


Figure 5.8 MDS ordination of the average monthly changes in assemblages on the groynes at Felpham. Data dispersion weighted, $\sqrt{\text{transformed. Stress}} = 0$.

The average assemblage similarity within each sampling occasion ranged between May (50.4 %) and July (70.9 %), being highest in July and lowest in May. Barnacle cover contributed most to the similarity within all sampling occasions; the highest abundance contribution was in the May (47.3 %). The large average abundance (21.9 ind/quadrat \pm 3.9) of *L. saxatilis* species in July largely accounted for the difference in assemblage structure from the other sampling occasions (Fig. 5.9), as the average abundances were considerably lower (< 9 ind/quadrat) during the other times. The contribution of unoccupied space (bare rock) was also an important factor in determining temporal differences in assemblage structure; the greatest contribution was in March 2005 (27 %), decreasing to 8 % abundance contribution in

July and then increasing again to 17 % in February 2006 (Fig. 5.9). The temporal changes in the amount of barnacle cover, unoccupied space and *F. spiralis* cover were the main differences for the dissimilarities seen between assemblages over the time sampled (Table 5.8). The strong change in assemblage structure from May to July can be accounted for by an increase in average abundances of *L. saxatilis* species (0.13 to 21.9 ind/quadrat).

Table 5.8 Average dissimilarity and variables that contributed to measures of dissimilarity between pairings of assemblages between months (Mar = March 2005, May = May 2005, Jul = July 2005, Nov = November 2005, Feb = February 2006) at Felpham Beach. Data are the percentage contributions a species contributed to measures of dissimilarity (SIMPER). Greatest contributor (<u>underline</u>) and important contributor > 10% (**bold**).

	Mar	Mar	May	Mar	May	Su5	Mar	May	Jul	Nov
Variables	vs. May	vs. Jul	vs. Jul	vs. Nov	vs. Nov	vs. Nov	vs. Feb	vs. Feb	vs. Feb	vs. Feb
Av. Dissimilarity (%)	52.5	57.3	49.9	53.5	49.1	36.7	53.8	50.2	37.9	38.0
Bare rock	18	14	10	14	<u>15</u>	<u>17</u>	16	<u>16</u>	<u>19</u>	<u>20</u>
Barnacle	<u>20</u>	<u>18</u>	14	<u>19</u>	<u>15</u>	10	<u>19</u>	<u>16</u>	12	11
Dead barnacles	12	14	14	13	12	12	15	14	12	13
Detritus	3		4		5	5		4	4	5
Ulva spp.	7	5	9	4	8	8	3	8	8	5
Fucus spiralis	11	11	10	12	13	10	12	12	11	15
L. saxatilis sp. complex	3	18	<u>16</u>	13	13	18	9	9	13	14
Patella vulgata	13	11	8	13	9	8	13	9	8	9
Porphyra spp.	5	4	5	3	4	6	3	4	5	

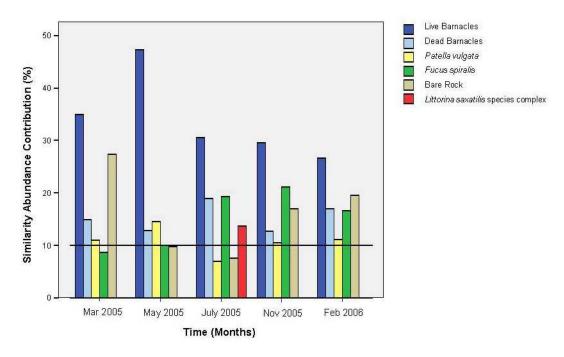


Figure 5.9 Percentage abundance contributions (>90%) of epifaunal species towards average similarity (SIMPER) of assemblages within months on granite groynes at Felpham Beach. (X axis line = 10% contribution).

5.3.3 Spatio-temporal Patterns of Community Measures of CDS Assemblages

5.3.3.1 Differences in assemblage structure between breakwaters and groynes

A 3-factor SPANOVA was performed on the community variables: abundance of motile species, number of taxa, cover of sessile species and unoccupied rock to test for differences between structure types, between structures and within structures (sides of structures) at different times (Table 5.9). Total sessile cover and unoccupied rock mirrored each other, being significantly affected by the same factors to the same degree, so this section will only describe total cover from now on. The abundance of motile species and sessile cover (Table 5.10) were significantly different (p < 0.01) between the two different structure types (Elmer breakwaters and Felpham groynes) (Table 5.10), whilst the number of different taxa did not differ (at p > 0.05).

Table 5.9 Results from a split-plot design analysis of variance for abundance of motile species, number of taxa and also sessile cover. Split-plot design based on sites, Elmer and Felpham with three factors; factor 1, 'structure' had 4 levels at Elmer (2/4/6/8) and 2 levels at Felpham (A/B), both were fixed; factor 2, 'structure sides' had 4 levels at Elmer (landward/eastward/seaward/westward) and 3 levels at Felpham (eastward/seaward/westward), both are fixed; factor 3, 'time' was fixed and had 5 levels (March 05, May 05, July 05, November 05, February 06). Elmer n = 640, Felpham n = 320. *p < 0.05, **p < 0.01, ***p < 0.001, **NS** = not significant (p > 0.05).

		Abund	ances of				
		Motile	Species	Taxa A	bundance	Sessile	e Cover
	df	MS	F	MS	F	MS	F
Site ^a	1	1471.7	7.51**	4.13	2.69	139242.2	136.34***
Elmer							
St	3	564.46	7.48***	9.44	8.09***	5712.66	6.75***
Si	3	2865.65	38.02***	39.07	33.48***	32852.21	38.84***
T	4	1006.78	13.36***	7.88	6.75***	21097.93	24.94***
St * Si	9	173.04	2.3*	4.06	3.48***	6317.52	7.47***
St * T	12	238.49	3.16***	3.74	3.20***	1179.55	1.40 NS
Si * T	12	241.53	3.2***	3.84	3.29***	1190.39	1.41 NS
St * Si * T	36	190.44	2.53***	1.71	1.46*	852.855	1.01 NS
Felpham							
St	1	327.72	1.69 NS	0.15	0.12 NS	353.08	0.71 NS
Si	2	7930.41	40.86***	12.75	10.05***	342.57	0.68 NS
T	4	6958.78	35.85***	9.1	7.18***	6110.38	12.19***
St * Si	2	656.64	3.38*	0.59	0.46 NS	2302.84	4.60**
St * T	4	553.37	2.85*	0.07	0.05 NS	1176.802	2.35*
Si * T	8	2097.34	10.81***	1.6	1.26 NS	305.917	0.61 NS
St * Si * T	8	528.74	2.72**	1.13	0.89 NS	674.455	1.35 NS

^a One-way ANOVA, Factor = site, fixed, 2 levels (Elmer and Felpham) n = 960. St = Structure, Si = Structure Sides, T = Time.

Within sites, the abundance, cover and number of taxa varied, with larger variability on the breakwaters than on the groynes (Table 5.10). The abundances of motile species and number of taxa were overall significantly more variable than total cover. All three community variables at Elmer significantly (p < 0.001) differed between structures, structure sides and season (Table 5.9). Tukey's *post hoc* test showed no differences between structures 4 and 6 at Elmer, but they were both significantly different from the similar pairing of structures 2 and 8 for number of taxa and percentage cover of sessile species (Table 5.10).

Table 5.10 The mean values for the number of motile individuals (per quadrat), cover of sessile species and number of taxa (per quadrat) between two different CDS types (Elmer breakwaters and Felpham groynes), and within the different CDS schemes on the different structures and sides of structures.

_			
	Abundances of	a n a	Taxa
	Motile Species	Sessile Cover	Abundance
Structures			
Elmer	8.1	56.3	2.5
2	7.1	58.8	2.2
4	8.9	53.1	2.7
6	10.4	50.0	2.7
8	6.2	63.4	2.4
Felpham	12.2	81.9	2.7
A	10.1	80.9	2.6
В	11.4	82.8	2.7
Sides of Structures			
Elmer			
Eastward	12.8	76.3	3.1
Seaward	8.6	53.4	2.4
Westward	8.7	53.3	2.7
Landward	2.5	42.2	1.9
Felpham			
Eastward	7.0	82.9	2.5
Seaward	23.0	83.1	3.2
Westward	6.4	80.0	2.5

Structures 2 and 8 had significantly (p < 0.001) less taxa, less motile species and more sessile cover than structures 4 and 6 (Table 5.10). For the structure sides, the eastern end of the breakwaters supported the highest significant (p < 0.001) number of taxa, abundances of motile species and sessile cover and the least on the landward side of the breakwaters, whilst there were no differences between the seaward side and westward end. There were no significant differences (p > 0.05) in abundance of motile species, number of taxa or sessile cover between the two groynes at Felpham, but there were differences for the number of motile individuals and sessile cover between structure sides (Tables 5.9 & 5.10). Tukey's

post hoc test showed significantly (p < 0.001) higher abundances of motile species and taxa on the seaward sides of the groynes at Felpham than the eastward or westward sides; the groyne sides (westward and eastward) had approximately equal mean abundances of motile species (Table 5.10). The abundances of motile species on the seaward sides of the groynes at Felpham were larger than on the breakwaters at Elmer (Table 5.10).

The abundances of motile species, numbers of taxa and sessile cover showed significant monthly differences (p < 0.001) at both Elmer and Felpham (Tables 5.9 & 5.11). The average number of taxa on both structure types on all structure sides was significantly greater in July 2005 (3.35 \pm 0.14) compared to in March 2005 (2.43 \pm 0.14), May 2005 (2.52 \pm 0.14) and February 2006 (2.52 \pm 0.14). In contrast, this pattern was the opposite at Elmer, with significantly (p < 0.001) less taxa in July (2.20 \pm 0.1) compared to in May (2.73 \pm 0.1) and in November (2.78 \pm 0.1). The abundances of motile species at Felpham followed the same pattern as with sessile taxa, with significantly (p < 0.001) larger abundances in July, particularly on the seaward side (Table 5.6). In comparison, Elmer had considerably smaller abundances in July, with peak abundances in November. For both Felpham and Elmer, the largest significant (p < 0.001) incremental difference in sessile cover was between March and May, with a 21 % increase for Felpham and a 29 % increase for Elmer. May and July sessile cover did not differ (p > 0.05) at either site.

5.3.3.2 Spatio-temporal patterns of the dominant species at Elmer

A 3-factor ANOVA (Table 5.12) showed that the factors 'structure' and 'time' were variable in their influence on the distribution of dominant taxa, whereas 'structure sides' was consistent and often the strongest influence. When the factors structure and structure sides were considered together, there were significant (p < 0.001) differences for all dominant taxa at Elmer Beach. The cover of barnacles was only significantly (p < 0.001) different between structure sides and with time (Table 5.12), but not between different structures; whilst dead barnacle cover showed significant (p < 0.001) differences between structures, structure sides, time and all interactions (Table 5.12); common to both was that structure sides had the strongest impact.

Table 5.11 The temporal mean values for the number of motile individuals (per quadrat), cover of sessile species and number of taxa (per quadrat) at two different CDS types (Elmer breakwaters and Felpham groynes) on the different sides of the CDSs. Values in **bold** denote the greatest temporal value.

	Eastward	Seaward	Westward	Landward
Taxa Abundance				
Felpham				
Mar 2005	2.5	2.8	2.0	
May 2005	2.2	2.8	2.5	
Jul 2005	3.0	4.2	2.9	
Nov 2005	2.6	3.2	2.6	
Feb 2006	2.1	2.8	2.5	
Elmer				
Mar 2005	2.8	1.9	2.7	2.1
May 2005	3.3	2.2	3.3	2.2
Jul 2005	2.9	2.6	1.8	1.4
Nov 2005	3.3	2.9	2.9	2.1
Feb 2006	3.3	2.4	2.7	1.8
Abundances of Mo	otile Species			
Felpham				
Mar 2005	3.0	5.5	2.2	
May 2005	1.9	5.1	2.3	
Jul 2005	15.5	61.3	11.1	
Nov 2005	7.0	22.1	7.7	
Feb 2006	7.3	20.8	8.9	
Elmer				
Mar 2005	9.1	3.5	5.3	2.4
May 2005	9.8	4.8	9.8	1.8
Jul 2005	11.0	13.3	6.9	1.5
Nov 2005	20.0	14.8	10.4	4.9
Feb 2006	13.8	6.8	11.1	1.9
Sessile Cover				
Felpham			_	
Mar 2005	76.1	66.6	62.4	
May 2005	90.0	89.6	90.2	
Jul 2005	91.5	95.4	93.1	
Nov 2005	80.5	83.7	76.5	
Feb 2006	76.4	80.1	77.7	
Elmer				
Mar 2005	57.9	32.2	35.7	31.0
May 2005	83.9	59.9	76.8	53.9
Jul 2005	88.7	70.9	59.7	52.9
Nov 2005	83.8	60.8	50.2	36.8
Feb 2006	67.2	43.1	44.0	36.4

The distribution of barnacle cover between structure sides had the same pattern as total sessile cover (Table 5.10), whereby the eastward end had the highest percentage cover (61.2 $\% \pm 1.8$) and the landward sides the least (7.91 $\% \pm 1.8$). Structure and structure sides and their

interaction significantly affected the percentage cover of F. spiralis on the breakwaters at Elmer. Structure 8 (13.5 % \pm 1.5) had significantly (p < 0.001) higher mean percentage cover than on structures 4 (5.1 \pm 1.5) and 6 (4.2 \pm 1.5), whilst there was significantly higher cover on the landward sides of the breakwaters than any of the other sides (Fig. 5.10).

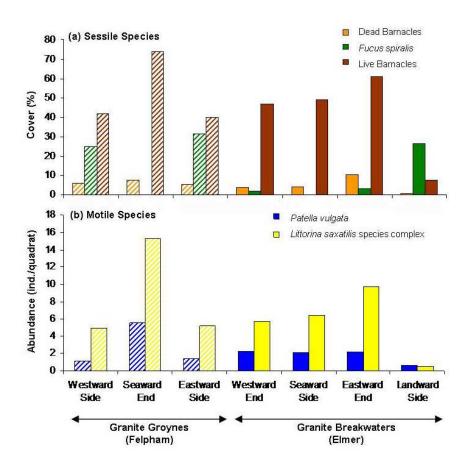


Figure 5.10 Mean (a) cover (%) of sessile and (b) abundance (ind/quadrat) of motile taxa on different sides of the groyne structures at Felpham (diagonal striped bars) and breakwater structures at Elmer (solid bars).

L. saxatilis species complex was influenced by structure sides and time and their interactions but not structure, whereas the abundance of P. vulgata was significantly (p < 0.001) affected by structure and structure sides and their interactions but not time (Table 5.12). The structures at Elmer were separated into 3 significant groups for the abundances of P. vulgata, with structures 2 and 8 having the lowest mean abundances (1.2 ind/quadrat \pm 0.17 and 0.8 ind/quadrat \pm 0.17 respectively), followed by structure 4 (2.2 ind/quadrat \pm 0.17), with the greatest mean abundances on structure 6 (3.0 ind/quadrat \pm 0.17). The eastward ends of the breakwaters harboured significantly (p < 0.001) greater abundances of L. saxatilis species complex than other sides of the breakwaters, with the least on the landward sides (Fig. 5.10).

Overall, there were no differences (p > 0.05) in the abundances of P. vulgata between either breakwater ends (westward or eastward) or the seaward side but were significantly less on the landward sides of the structures.

There were also significant interactions between structure and structure sides for both grazers (Table 5.12); of particular interest, was the circular pattern in *P. vulgata* abundances with relation to structure side across the breakwater scheme at Elmer (Fig. 5.11). On structures 2 and 4 (western end of scheme), there was a clockwise decrease in *P. vulgata* abundances with movement around the breakwaters; the eastward ends had the greatest mean abundances, followed by the seaward sides, then the westward end, and then least on the landward sides. In contrast, on structures 6 and 8 (eastern end of scheme) there was an anti-clockwise decrease in *P. vulgata* abundances with movement round the breakwaters, where the westward end had the highest mean abundances followed by the seaward side, eastward end, and again the least on the landward sides (Fig. 5.11).

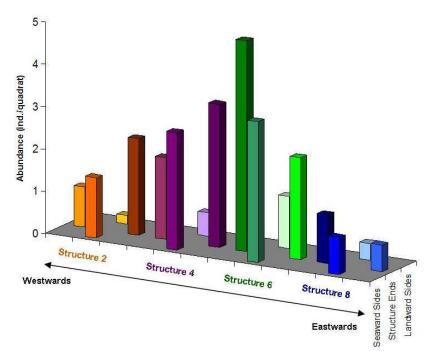


Figure 5.11 *Patella vulgata* mean abundances (ind/quadrat) on different breakwater structures (2, 4, 6 and 8) and structure sides (eastward ends, seaward sides, westward ends and landward sides) at Elmer.

L. saxatilis species complex abundances varied temporally (Fig. 5.12b), with an interaction with structure side (Fig. 5.13b). There was a gradual increase in the abundance from March to peak in November 2005 before declining again to February 2006.

Table 5.12 Results split-plot design analysis of variance F values for species abundances and cover. Split-plot design based on sites, Elmer and Felpham with three factors; factor 1, 'structure' had 4 levels at Elmer (2/4/6/8) and 2 at Felpham (A/B), both were fixed; factor 2, 'structure sides' had 4 levels at Elmer (landward/seaward/westward) and 3 levels at Felpham (eastward/seaward/westward), both were fixed; factor 3, 'time' (sampling occasions) was fixed and had 5 levels (March 05, May 05, July 05, November 05, February 06). Elmer n = 640, Felpham n = 320. *p < 0.05, **p < 0.01, ***p < 0.001, **NS** = not significant (p > 0.05).

		Barnacles		F. sp	F. spiralis		atilis sp. nplex	Patella vulgata	
	df	MS	F	MS	F	MS	F	MS	F
Site ^a	1	13640.54	11.55***	37169.88	48.24***	876.33	5.53 *	60.92	8.04**
Elmer									
St	3	0.00	0.62 NS	0.67	12.04***	0.24	1.63 NS	3.07	38.69***
Si	3	4.36	220.55***	4.21	75.54***	13.90	94.07***	2.52	31.72***
T	4	0.27	26.76***	0.03	0.59 NS	2.84	19.21***	0.16	2.00 NS
St * As	9	0.20	7.81***	0.36	6.40***	0.62	4.22***	0.45	5.69***
St * T	12	0.10	1.43 NS	0.04	0.73 NS	0.17	1.13 NS	0.08	0.95 NS
Si * T	12	0.06	3.19***	0.07	1.23 NS	0.56	3.81***	0.09	1.07 NS
St * Si * T	36	0.03	1.91***	0.05	0.86 NS	0.28	1.88**	0.07	0.88 NS
Felpham									
St	1	0.04	0.02 NS	0.01	0.04 NS	0.55	2.97 NS	1.23	14.14***
Si	2	13.20	28.59***	4.10	23.93***	2.65	14.16***	8.41	96.55***
T	4	1.60	1.76 NS	0.21	1.23 NS	10.97	58.66***	0.07	0.80 NS
St * As	2	0.47	1.29 NS	0.00	0.01 NS	0.90	4.82**	0.13	1.46 NS
St * T	4	0.09	0.67 NS	0.02	0.09 NS	0.41	2.18 NS	0.05	0.55 NS
Si * T	8	0.19	0.40 NS	0.09	0.52 NS	0.92	4.91***	0.25	2.88**
St * Si * T	8	0.11	0.21 NS	0.03	0.15 NS	0.42	2.22*	0.06	0.69 NS

^a One-way ANOVA, Factor = site, fixed, 2 levels (Elmer and Felpham) n = 960.

St = Structure, Si = Structure sides, T = Time.

The temporal pattern was rather variable on different sides of the breakwaters (Fig. 5.13b); individuals on the landward sides showed little variation in abundances temporally, perhaps due to the small abundances that occurred there, whereas abundances on the seaward sides showed an earlier increase in abundances from spring to summer than on the eastward side when it happened between the July and November 2005.

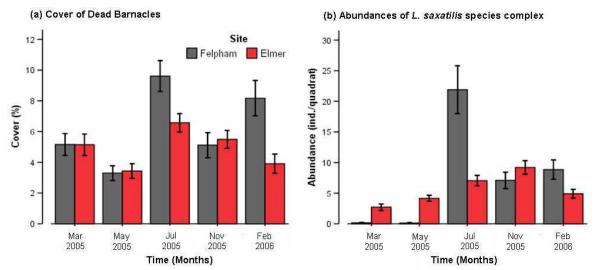


Figure 5.12 Temporal mean (\pm SE) (a) cover (%) of dead barnacles and (b) abundance (ind/quadrat) of *L. saxatilis* species complex on both groynes at Felpham and breakwaters at Elmer. (*Attention*: y-axis scales different).

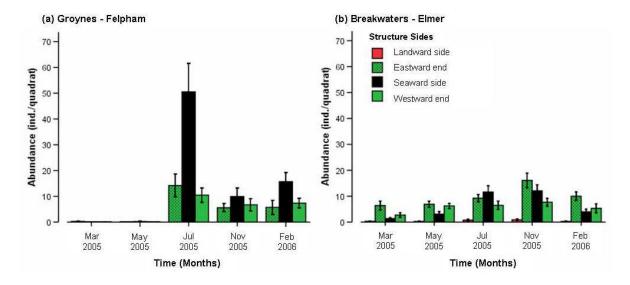


Figure 5.13 Temporal mean (\pm SE) abundances (ind/quadrat) for *Littorina saxatilis* species complex on different sides of the structures on both (a) granite groynes as Felpham and (b) granite breakwaters at Elmer.

5.3.3.3 Spatio-temporal patterns of the dominant species at Felpham

The 3-way fixed-factor ANOVA (Table 5.12) shows that P. vulgata was the only dominant taxa to be significantly (p < 0.001) different between the two groynes at Felpham, whereas the sides of the groynes consistently had significant differences on the abundances and cover of dominant taxa. Statistical differences (p < 0.001) between sampling occasions only occurred in dead barnacles and L. saxatilis species complex (Table 5.12, Fig. 5.10). The factors of structure, structure sides and time had less variability on the groynes at Felpham than at Elmer, although L. saxatilis spp. complex showed the highest variability of the dominant taxa on the groynes (Table 5.12).

The significant differences in the abundances of *P. vulgata* between the two groynes was due to the westerly groyne (B) (3.3 ind/quadrat \pm 0.19) having greater mean abundances than the easterly groyne (1) (2 ind/quadrat \pm 0.19). The seaward sides had higher percentage cover and abundances than either on the eastward or westward sides of the groynes for all taxa (Fig. 5.10). The percentage cover of dead barnacles was highly variable between sampling occasions (Fig. 5.12a): July 2005 had the highest percentage cover (10.1 \pm 0.9 %); this was significantly (p < 0.001) greater than other times but similar (p > 0.05) to February 2006 (8.2 \pm 0.9 %). The mean abundance of *L. saxatilis* spp. complex was similarly (p > 0.05) low in March and May 2005 (< 1 ind/quadrat), but significantly less than in the July (25.1 ind/quadrat \pm 1.7), this high abundance increase was followed by a decrease in November 2005 (7.4 ind/quadrat \pm 1.7). There was a significant (p < 0.001) interaction of spatial patterns of *L. saxatilis* spp. complex over time, with the large increases in July abundances only occurring on the seaward sides of the groynes (Fig. 5.13a).

A two-way ANOVA with vertical shore levels and time as factors was performed (Table 5.13); this was to test if there were differences in the biological measures (abundances of motile species, number of taxa, sessile cover, bare rock) and the dominant species on the groynes at Felpham (Table 5.13). Vertical shore significantly (p < 0.001) affected all biological measures tested with the exception of sessile cover (p > 0.05) and bare rock (p > 0.05); this was also the pattern for the interaction between vertical shore and time, however time alone significantly effected (p < 0.001) sessile cover and the amount of bare rock. The abundance of motile species,

number of taxa, *L. saxatilis* species complex, *P. vulgata*, and barnacles was higher on the low shore (level 1) and decreased with vertical shore level, so on the upper shore (level 4) their abundances and cover was low (Fig. 5.14a). Whereas, the cover of *F. spiralis* was the opposite, with cover increasing further up the shore (Fig. 5.14a).

Table 5.13 ANOVA for total individuals, taxa and cover and species abundances and cover (log transformed) at Felpham with 2 factors: factor 1, 'vertical shore' was fixed and has 4 levels (1 (MLW), 2, 3 and 4 (MHW)); factor 2, 'time' was fixed and has 5 levels (March 05, May05, July 05, November 05, February 06). n = 320. *p < 0.05, **p < 0.01, ***p < 0.001, **p < 0.001, **p < 0.001, **p < 0.001, ***p < 0.001

		Total Individuals		Total taxa		Total Cover	
	df	MS	F	MS	F	MS	F
Vs	3	6975.98	38.58***	21.75	21.88***	94.83	0.18 NS
T	4	5291.83	29.27***	8.145	8.19***	6218.46	11.83***
Vs * T	12	1728.22	9.56***	4.456	4.48***	481.913	0.917 NS

	-	Barnacles		F. spiralis		L. neglecta	
	df	MS	F	MS	F	MS	F
Vs	3	8.223	109.19***	7.944	85.79***	6.533	55.12***
T	4	0.284	3.77**	0.277	2.99*	9.966	84.08***
Vs * T	12	0.602	7.99***	0.6	6.48***	1.501	12.66***

	_	Patel	lla spp.	Bare rock		
	df	MS	F	MS	F	
Vs	3	6.892	104.96***	0.031	0.434 NS	
T	4	0.066	1.004 NS	0.972	13.69***	
Vs * T	12	0.48	7.31***	0.088	1.24 NS	

Vs = Vertical Shore, T = Time.

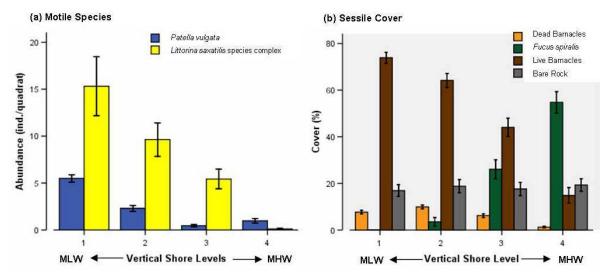


Figure 5.14 Spatial distributions of the mean $(\pm SE)$ dominant taxa on the granite groynes at Felpham along the vertical shore levels from mean low water (MLW: 1) to mean high water (MHW: 4) for (a) motile species and (b) sessile cover.

5.3.4 Influence of Environmental Variables on CDS Assemblages

There were several engineering design features that could have influenced the spatial assemblage variation on the breakwaters at Elmer, including breakwater crest elevation, breakwater length and distance from the shore (MHWS), as well as the hydrodynamic regime (current direction and strength) (Table 5.1). These variables were used in BIO-ENV analysis to determine what degree these variables could explain the observed spatial patterns in assemblages on the breakwaters (Table 5.1). The optimum combination of design features and hydrodynamic (abiotic) variables to match the breakwater assemblages were crest elevation of the structures, current direction and strength ($\rho_{\rm w}=0.07$). These three variables were only able to account for 7 % of the pattern. The assemblage data showed that assemblages on structure 8 were the most dissimilar in comparison with the other three structures, with structure 2 being the closest in similarity. The optimum variables showed a relatively good match to this pattern, ranking structure 8 to be different from 4 and 6, which were in turn were extremely similar. In contrast, the abiotic variables ranked structure 2 as rather more dissimilar to 4 and 6, with the greatest distance in dissimilarity for structure 8 assemblages; 93% of the variation in the assemblages still remained unexplained.

The wave climate changed seasonally, as would be expected (Table 5.3); larger wave height and longer wave periods were experienced in the autumn and winter months, with wave direction varying from 185° to 200° . The average sea surface temperature ranged from 8° C in the winter to 18° C in the summer, with greater sea levels in the summer and less residual surge (Table 5.3). The coastal sea climate could potentially give some explanation of the assemblage patterns (Fig. 5.6). The optimum combination of coastal sea variables to match the temporal assemblage patterns on the breakwaters at Elmer was significant wave height (H_s), sea surface temperature (SST) and maximum surge ($\rho_{\rm w}=0.059$). These three variables only accounted for 6 % of a temporal variation in the assemblage patterns. At Felpham, the matching of the coastal sea climate variables to the temporal assemblage patterns again only accounted for 7 % ($\rho_{\rm w}=0.069$). The optimum combination of variables was slightly different from that at Elmer, with five of the variables; these were H_s, maximum wave height (H_{max}), wave length (T_p), wave direction (dir) and SST.

Overall, the optimum combination of variables to explain the assemblages on the breakwaters at Elmer when all spatial and temporal environmental variables were considered was the angle of the structure sides relative to magnetic north (Table 5.2). This variable accounted for 35 % of the overall match ($\rho_w = 0.354$). There were three environmental variables that explained the spatio-temporal assemblage patterns on the groynes at Felpham, but only 9% of the variation was explained, much lower than that explained at Elmer. The optimum environmental variables were maximum significant wave height, sea surface temperature and the angle the structure sides relative to magnetic north ($\rho_w = 0.090$).

5.4 Discussion

Intertidal assemblages on the defence structures were composed of few species, with only 15 taxa represented. This remarkably low diversity of intertidal assemblages on defence structures has also been confirmed by several studies (e.g. Bacchiocchi & Airoldi 2003, Moschella et al. 2005, Jonsson et al. 2006, Burcharth et al. 2007). Much of the space on the groynes and breakwaters was occupied by sessile filter-feeders: barnacles, *P. vulgata* and *L. saxatilis* spp. complex were the dominant grazers present. One possible explanation for the lack of species diversity is that only the flat boulder faces of the structures were surveyed. These are rather more exposed to desiccation and wave action stress than the small boulders and rockpools at the base of the breakwaters and groynes, which have been shown to have rather more diversity (Burcharth et al. 2007). In addition, the location of the breakwaters and extension of groynes was only on the mid-intertidal foreshore, and those boulder faces surveyed were mid- to upper-intertidal. Diversity can be greatly increased when the CDSs border the intertidal/subtidal boundary, similar to that of the structure on Hurst Spit, Hampshire (Lynas 2005).

5.4.1 Spatial Assemblage Patterns

Generally, there were only small differences in species composition between assemblages among and between different structures at both Elmer and Felpham CDSs. The results of this study are in agreement with those of Underwood and Chapman (1998), who observed that variations at the replicate scale, sites on the shore and among shores were due to the relative importance of a few dominant species rather than changes in the overall composition of the assemblage. This was further confirmed by Bulleri and Chapman (2004), showing that, the mix

of species contributing to differences in man-made structures was consistent from location to location and through time.

In the current study, the small variability in assemblages within and between structures varied differently between groynes and breakwaters; variability being larger and more complex on the breakwaters. The greatest differences were observed between the different sides of the structures (landward and seaward sides, eastward and westward ends) at Elmer, with complex interactions between structures and structure sides; this was mostly attributable to variation in the relative abundances and cover of the dominant species rather than differences in composition of taxa. The magnitude and nature of variations between structure sides through time were different for between breakwaters and groynes. This contrasted to the findings of Bacchiocchi and Airoldi (2003) in the Adriatic, who stated that there were little differences observed in the distribution of species at different positions around groynes and breakwaters. There were indeed little differences in the core species of the assemblages at Elmer, however, the abundances and cover of species were very variable and often specific species were different on different structure sides (e.g. F. spiralis on the sheltered landward sides of breakwaters and nowhere else). It is relatively common for a few components of intertidal assemblages to dominate spatial patterns of variation (Chapman & Underwood 1998, Underwood & Chapman 1998).

There are many explanations in the literature for spatial variations seen in community assemblages associated with man made structures. The majority of the studies have, however, examined the direct and indirect influences of small-scale substratum physical attributes such as complexity, orientation and slope (e.g. Glasby 1999b, Glasby 2000, Glasby & Connell 2001, Chapman & Bulleri 2003, Knott et al. 2004), rather than larger scale abiotic variables such as wave exposure, water flow and sedimentation (e.g. Davis et al. 2002). The orientation to wave attack was shown to be the most important driver measured of assemblages at both Elmer and Felpham.

Wave exposure and patterns of water transport (currents) are potent agents determining species composition, abundance, and distribution of the structure of intertidal epibenthic assemblages on rocky shore (Lewis 1964, Jones & Demetropoulos 1968, Menge 1978, Underwood 1981, Hartnoll & Hawkins 1985) and on man-made surfaces (Southward & Orton 1954, Davis et al. 2002). In very exposed systems, the intensity of wave exposure may be the most important

factor affecting the spatial distribution patterns of assemblages (Underwood 1981, Hawkins 1983, Davis et al. 2002), disabling the identification of clear distribution patterns in relation to shore height or to small-scale spatial variability (Araujo et al. 2005). The sheltered nature of the landward sides of the breakwaters compared to the exposed westward and seaward sides explains the differences between the assemblages they each supported. Exposed conditions generally benefit suspension feeders, like barnacles, since water movement enhances their food supply (Bustamante & Branch 1996, Hammond & Griffiths 2004) and larval supply (Mullineaux & Garland 1993). This trend was also seen in this study, where the low regime of water flow and wave attack on the north sides of the structures at Elmer, and higher up the shore on the groynes at Felpham, compared to other positions, accounted for the low cover in barnacles and presence of macroalgae, whilst no presence of macroalgae was found on the exposed sides (seaward side and westward end), where barnacles dominated (see Jonsson et al. 2006).

One of the most important effects of wave exposure is on the ability of organisms to attach and stay attached. For other more fragile or mobile species, attachment or foraging activities can be compromised by high wave-exposure conditions. As a result, grazers have been found to reach maximal abundances on sheltered and moderately exposed shores; so that species diversity peaks on moderately exposed shores (Bustamante & Branch 1996). In this study, the highest number of taxa, individuals and cover of sessile species were found on the eastward ends of breakwaters at Elmer. In terms of wave exposure, this was moderately exposed, being somewhat sheltered from the dominant prevailing south-westerly wave direction (Fig. 2.1) but still experiencing reasonable water flow from currents (Fig. 5.3).

The assemblages were very similar between the different structures at Elmer, there were a few small interesting differences; these differences may be accounted for by the complex hydrodynamics of the scheme. *P. vulgata* were most abundant on structures 4 and 6, these structures experience increased water flow speeds around the structures during tidal cycles (Plomaritis 2006), and exposure to wave attack; limpets are well known for their presence in exposed areas of rocky shores (Southward & Orton 1954, Lewis 1964, Jenkins & Hartnoll 2001, Pinn et al. 2005). The western end of the breakwater scheme experiences the slowest currents (Fig. 2.4); the interaction of slow currents, greater exposure to wave attack and reduced grazing is apparent as *F. spiralis* is more dominant than on the other breakwaters. McQuaid and Branch

(1985) reported that algae were more abundant at protected sites, as exposed areas present very harsh conditions for algae to settle (Dalhoff & Menge 1996).

In conjunction with wave exposure and water flow speeds, orientation with respect to sunlight may well play an important role in determining the abundance of grazers and sessile species. Animals on intertidal shores have been shown to be affected by shading (Denley & Underwood 1979), with greater recruitment or survival where there is shade (Glasby 1999b, Glasby & Connell 2001). Glasby (1999b) and Blockley (2007) found that the degree of shading may be important in structuring assemblages of epibiota on subtidal pier pilings. The amount of shade can influence the surface temperature of rocky intertidal areas, with unshaded areas having much greater surface temperatures than adjacent shaded areas during low-tide leading to physiological affects (e.g. greater mortality through desiccation or thermal stress) (Blockley 2007). In this study, westward ends and seaward sides of the breakwaters would be subject to more direct sunlight than those on the landward sides and eastward ends, resulting in greater surface temperatures. Blockley (2007) reported that the difference in temperature between shaded and unshaded sections of seawall was up to 10° C in Sydney Harbour. The reduced temperatures experienced on the eastward ends of the breakwaters would reduce the risk of desiccation and can be correlated with the observed higher faunal abundances. However, this theory cannot solely explain the increased abundances of species on the eastward ends, as this was not the case on the groynes at Felpham or at Poole (Pinn et al. 2005); there were no differences between the east and west aspects. Rather, a better explanation is a combination of physical factors influencing the complex variation in communities seen at Elmer.

Vertical shore level was an important factor in determining abundance and distribution patterns on the groynes at Felpham. There were distinct differences between the assemblage species composition at the boundary extremes, with barnacle cover dominating the lower limits and fucoids dominating the upper limits (Fig. 5.21), whilst grazers such as *P. vulgata* and *Littorina littorea* had higher in abundances in the lower half of the groynes. In addition, not only is it risk of desiccation that determines the species zonation, but that the exposure of the upper parts of the groynes to wave attack is also minimal, thereby explaining the high percentage cover of algae, similar to that found on the north (sheltered) sides of the breakwaters.

5.4.2 Temporal Patterns

The temporal results of this study showed that assemblages were complexly variable among sampling occasions on both the groynes and breakwaters. The temporal variability of assemblages on man-made structures, including CDSs, has been somewhat understudied in conjunction with spatial variability; the recent statement by Balata et al. (2006) suggested that temporal variability of these organisms may be more important than previously thought.

Complex patterns were exhibited spatially through time, particularly on the different sides of the breakwaters at Elmer. Of particular interest, were the differences in the number of taxa and individuals, cover, and abundances of dominant species between the two different CDSs types. These spatio-temporal results contradict the findings observed by Bacchiocchi & Airoldi (2003); they compared groynes and offshore breakwater assemblages at different spatial scales, finding that there were fewer differences than expected at different positions on both groynes and breakwaters. The percentage cover of sessile species was highly variable at Elmer on different sides of the structures in comparison with at Felpham. This was also the case for number of taxa. The spatio-temporal pattern in sessile cover observed at Elmer, could be explained through a variety of factors. For example, reduced larval and food supplies on the landward sides of the structures could explain reduced cover of sessile species; scouring from wave action and sedimentation, and increased summer temperatures on the seaward sides and westward ends; whilst, the eastward ends exhibited gradual changes in sessile species cover after an initial increase in May, possibly explained as a result from the shelter from wave attack and high temperatures, added to by the reasonable larval and food supply. It should be noted that the underlying variable for all these factors, are the currents and wave exposure, as mentioned before, with regards to the spatial distribution. The correlation of physical environmental variables of wave height, current speed in relation to the angle of the structure sides was shown to be complex, and the most influential in the temporal changes of the assemblages. The fact that there is high spatio-temporal variability between the two sites, suggests that the complexity of the hydrodynamic regime already shown at Elmer (Plomaritis 2006) is one of the main driving factors in this temporal pattern. In addition, at both sites the percentage cover of sessile organisms was significantly higher in February 2006 than in March 2005. This could be either explained by the increasing age of the structures, or rather the sea surface temperature, which saw significant elevations in temperature between the two years.

At Felpham, the species diversity (number of taxa) on the three sides of the groynes, increased from March to July, and decreased by the following winter in February as expected. In contrast, at Elmer, the species diversity decreased severely in July from the diversity in May, before returning to same diversity in November as in May (Fig. 5.5), with the exception of on the seaward side of the breakwaters, where it slowly increased to a peak in November. This pattern, may potentially be as a result of predation, the abundances of Nucella lapillus inhabiting the crevices and rock pools in the small boulders around the base of the structures at Elmer (these are not present at Felpham) dramatically increased in May and July (author's pers. obs.). This follows the findings of Brown & Swearingen (1998) and Hawkins & Hartnoll (1983), who observed that species recruitment to artificial substrata varied with season, and was also influenced by predation of the recruited individuals. This should be researched further, to see if abundances of predators and this decline are correlated, and preferentially carried out experimentally, as well as observationally. Additionally, this decrease in diversity at Elmer may be due to the combination in the increase in summer temperatures and decrease in wave action, thereby increasing desiccation risk. The more vulnerable motile species (e.g. L. saxatilis species complex) may subsequently move vertically in accordance to height of the splash zone (Underwood 1981, Dalhoff & Menge 1996, Araujo et al. 2005). However, the latter explanation does not explain why this does not occur at Felpham, as the same physical environmental factors are experienced being in the same geographical location.

5.5 Conclusions and Further Research

In conclusion, this study has shown that the angle of structure sides to wave exposure had the strongest influence on differences among assemblages on breakwaters. The breakwaters at Elmer are complex three-dimensional habitats, possibly more multifaceted than the groynes at Felpham due to the complex hydrodynamics that exist there, thus providing a variety of intertidal habitats differing in orientation, complexity and wave exposure.

There is scope for further study into the effects of sedimentation on the assemblages of these structures. A strong correlation between sedimentation and wave exposure and water flow has been observed (Borja et al. 2006), suggesting that sedimentation is an important physical variable to affect community structure. Coarse sediment such as sand and gravel can abrade tissue from organisms or remove them from reefs, thereby affecting community structure. Plomaritis (2006) investigated the sediment transport and hydrodynamics at Elmer, West Sussex and described their complexity within the breakwater scheme; the study site experiences high sediment mobility (author's pers. obs.) with the potential to strongly influence the community structure, through the scouring of rocks. Understanding how sedimentation may affect the early life stages, in particular, of benthic organisms may prove to be crucial in elucidating influences on community structure and the interaction of wave exposure gradients (Schiel 2004). The influence of sedimentation can only be assumed around the breakwaters at Elmer in correlation with wave exposure, and it is an important variable that requires further study in order to understand its impact on CDS. Elmer would be an ideal study site for such research, due to the extensive research into the hydrodynamics and ecology that have been carried out to date. Finally, there are often large deposits of detrital macroalgae on and around the toe of the breakwaters at Elmer, the importance of this allochthonous source to the assemblages has not been studied and may influence the abundances of the dominant taxa on these structures.

Further more, with respect to tidal height on CDS, there is scope for further research into the splash zone and tidal heights on the breakwaters, in order to compare the interactions of wave exposure and tidal height between breakwaters and groynes, with a balanced hierarchical design.

Chapter 6: Macroalgae Decay Processes

6.1 Introduction

6.1.1 Macroalgal Decay

Macroalgal detritus is deposited on shores worldwide (Lavery et al. 1999) and is an important component of energy flow in coastal ecosystems. In intertidal habitats (e.g. sandflats, salt-marshes, beaches), decaying macroalgae can be deposited throughout the entire intertidal range, and is dependent on subtidal sources and environmental variables such as time of the year (e.g. storm frequency, tidal cycle, sea temperature). During this period the decaying macroalgae deposits are subjected to different processes such as: dehydration, ageing, fragmentation, burial by sand, and decomposition. These processes are highly variable and are influenced by both site- and time-specific environmental conditions and in most cases depend on the taxonomic composition of the algae (Colombini & Chelazzi 2003). Macroalgae-derived detritus has been shown to provide food and habitat to a diverse and abundant cross-section of macrofaunal assemblages (Inglis 1989, Colombini et al. 2000, Dugan et al. 2003). Food availability is a potentially important determinant of consumer abundance in natural communities and the densities and growth rates of consumers may be positively associated with food supply (in situ or allochthonous) in a variety of habitats (Dugan et al. 2003).

There is growing evidence that low crested structures (LCSs) influence decaying macroalgae deposition. This has been observed in coastal areas of both Spain (pers. comm. DELOS scientists) and the UK (Elmer, West Sussex: Chapter 3), where large amounts (e.g. 518 t/y of wwt for the 1.75 km beach at Elmer) of decaying macroalgae is seen to be regularly deposited around the LCSs. In this chapter, I aimed to understand the decay processes of some of the dominant macroalgae deposited on the beaches at Elmer, both aerobically and anaerobically, using carbon and nitrogen stable isotope analysis on samples from field and laboratory experiments.

At Elmer, macroalgae are pushed inshore by coastal waves, tidal currents and inshore winds. The constricted circulation of water and varying shore elevation levels within the breakwater scheme results in the majority of algae being deposited and trapped behind the breakwaters on the landward side (see Chapter 3). The results from my study on this phenomenon (Chapter 3) showed that the biomass of decaying macroalgae changed on a daily basis due to the exchange of material between the beach and the surf zone, on a monthly basis due to the influence of the spring neap tidal cycle, and on a seasonal basis due to the influence of sea temperature and storm events. On each receding tide, the algae was deposited and left to decay, removed on the following incoming tide and mechanically broken down, and then deposited again on the next receding tide.

6.1.2 Use of Isotopes for Studying Macroalgal Decay

The understanding of the detailed mechanisms leading to nitrogen fixation in primary producers, especially marine algae, is even less developed than that of the processes involved in carbon fractionation. However, it is understood that macrophyte species show different isotopic values due to differential isotope fractionation according to their photosynthetic pathway (Fry 1996, Wang & Yeh 2003). The carbon isotope values measured in marine algae range between -8.8 and -34.7 ‰ (Raven et al. 1982, Stephenson et al. 1984, Dunton & Schell 1987). Most macrophyte production passes through a detrital phase before it is consumed by animals. If carbon and nitrogen isotope ratios undergo fractionation as the macrophyte tissues decompose, then changes in δ^{13} C and δ^{15} N values of the macrophyte tissue could be reflected in the tissues of consumers, and thus influence the local food web. Fenton and Ritz (1988) investigated the changes in stable isotope ratios in carbon and hydrogen, but not nitrogen, during the decomposition of a representative range of common macroalgae in Southern Tasmania (Australia), both in situ and in the laboratory and suggested that there is little fractionation in the case of carbon. However, a noteworthy fractionation of hydrogen isotopes during decomposition of *Ulva* sp. was reported. Furthermore, studies on higher plants and angiosperms have shown that after decomposition and the breakdown of lignin, the plants become depleted in ¹³C by 2 to 6 ‰ (Benner et al. 1987, Middleburg et al. 1997).

Multiple stable isotope analyses such as δ^{13} C and δ^{15} N have been used in ecological investigations (e.g. Peterson et al. 1986, Currin et al. 1995, Hsieh et al. 2002) as they provide two variables by which to determine differences between primary producers and in resolving food web structures. Studies concerning the flow of organic matter and food web structures in

freshwater and marine ecosystems include papers by DeNiro & Epstein (1978), McConnaughey & McRoy (1979), Rau et al. (1983), Lajtha & Michener (1994), Hobbie et al. (1990), Gartner et al. (2002) and Gauthier et al. (2007). The importance of particulate detritus derived from benthic macrophytes, and its subsequent utilization by consumer organisms as a source of organic carbon and nitrogen in the subtidal region of marine and freshwater habitats was studied by Stuart et al. (1982), Mann et al. (1988) and Fielding & Davis (1989). However, none of these studies used stable isotope analyses as a technique to resolve food web pathways as it was not a widely available technique until more recently. The use of macrophyte detritus in food-webs was investigated using stable isotopes by France (1998), Hsieh et al. (2002) and Adin & Riera (2003); and for example Bustamante & Branch (1996) documented the usage of subtidal kelp detritus by intertidal consumers by using both δ^{13} C and δ^{15} N. As a result, it has been recognized that macroalgal detritus is a significant source of nutrients to grazers, deposit feeders and suspension feeders in food-web linkages in the intertidal region (Stuart et al. 1982, Duggins & Eckman 1997, Adin & Riera 2003, Riera & Hubas 2003). Many food-web studies have focused on the detritus produced by marine angiosperms, such as saltmarsh (Peterson et al. 1986, Middleburg et al. 1997), eel grasses (Zieman et al. 1984, Loneragan et al. 1997, Wainright et al. 2000, Fourqurean & Schrlau 2003) and mangroves (France 1998, Chong et al. 2001, Hsieh et al. 2002) rather than the focus of my study, which is macroalgae.

In my study stable isotope analyses (δ^{13} C and δ^{15} N) obtained values for a range of macroalgal species, with particular emphasis on four dominantly abundant species deposited at Elmer and chosen for the distinct isotope values they exhibited after a period of decay. The general aim of the study was to understand the breakdown and decay processes of the mid-shore deposited decaying macroalgae within the low crested breakwater scheme at Elmer through field and laboratory experiments and the use of stable isotope analysis.

The specific objectives were:

- To study the decay of macroalgae through biomass loss over time, for mixed decaying macroalgae deposited within the bays at Elmer. And, to determine the macrofaunal colonisation of the macroalgae over time;
- 2. To determine the carbon and nitrogen stable isotope values of the dominant seaweed species deposited at Elmer;

- To compare the elemental composition changes during the decay process of different macroalgae species breakdown in both anaerobic and aerobic conditions, as well as the changes in leachate medium (seawater) during anaerobic decay; and
- 4. To compare changes in the stable isotope ratios of degraded macroalgae species over time in both anaerobic and aerobic conditions.

6.2 Methods

6.2.1 Study Sites

The fieldwork was carried out within the coastal defence systems at Elmer and Felpham Beaches in West Sussex (for more details of these locations see Chapter 2). Macroalgae samples were also taken from Poole Harbour training bank in Dorset (Fig. 6.1). The training bank is a 1,500 m long training wall made of stone blocks and situated in the shallow sublittoral (2-5 m). The wall was built to maintain the stability of coastline behind it (Studland Bay) and entrain the water leaving Poole Harbour, so that it scoured a natural channel and minimised the need for dredging. The currents in the channel adjacent are strong because of the exchange of tidal waters between the Bay and the Harbour. It provided an ideal site to collect subtidal seaweeds, particularly, Rhodophyta, due the similarity in seaweed species deposited on the beaches at Elmer and Felpham, and its occasional exposure during extreme spring tides.

6.2.2 Macroalgae Decay Experiments

The decay of deposited macroalgae at Elmer beach was investigated using two experimental designs: the first was a simple field experiment and the second was based on a field and laboratory experiment designed to provide natural aerobic conditions and controlled anaerobic conditions. The field experiments used a 'litterbag method'. The first field experiment was run to quantify the time it took for a set weight of mixed macroalgae species to decay in the field and to determine the colonisation and succession of macrofaunal species associated with the decaying macroalgae. The second set of experiments used stable isotope analysis to investigate how the elemental carbon and nitrogen, and carbon and nitrogen stable isotope values of four dominant algal species, and a mixed batch, changed with progressive tissue decay.

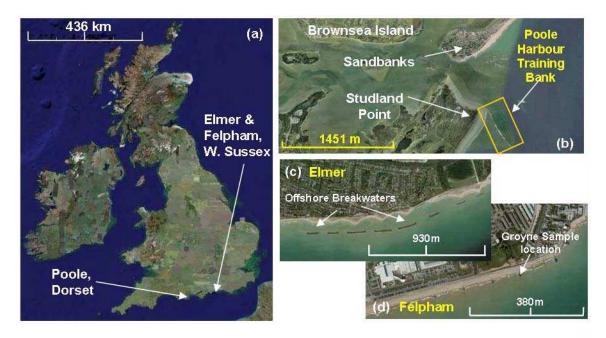


Figure 6.1 Locations of sample sites: (a) Map of the UK; (b) Poole Harbour Training Bank; (c) Elmer Beach; and (d) Felpham Beaches. Maps from Google Earth: Image © 2007 Digital Globe.

6.2.2.1 'Litterbag method'

This method was chosen based upon a study that was carried out in the subtidal zone using a similar method (Thrush 1986). The experimental design consisted of burying 6 concrete breeze blocks in the sediment, so that the top of the blocks lay flush with the sediment (Fig. 6.3). The blocks were laid 10 m apart along a horizontal transect at the mid-intertidal level (~ 50 m from MHWS), across bay 3-4 at Elmer (for location see Fig. 6.1). Each breeze block had 6 pre-drilled holes, so that mesh litterbags could be secured to the blocks with zip ties and left for the desired length of time.

6.2.2.2 Macroalgae decay: rates of decay and macrofaunal colonisation

There is much debate in the literature with regards to terrestrial leaf litter decay experiments and the mesh sizes used (Gartner & Cardon 2004); this is with respect to the accessibility of the leaf litter to mobile detritivores. With this in mind, two mesh sizes were chosen for the field experiments: 5 mm and 10 mm. The aim was to provide for the optional inclusion (10 mm) and exclusion (5 mm) of mobile faunal species (e.g. amphipods and isopods) and observe what

impact this had on the decay time of the macroalgae. The mesh bags measured approximately 200 cm² and could contain up to 500 g of mixed macroalgae.

Ten living specimens of the most dominantly deposited macroalgae species at Elmer (*Ulva lactuca*, *Chondrus crispus*, *Laminaria saccharina*, *Fucus vesiculosus*, *Halopteris* sp., *Cladostephus spongiosus*, *Calliblepharis ciliata*, *Plocamium cartilagineum*, *Halidrys siliquosa* and *Ceramium* sp.) were collected from Poole Harbour Training Bank (Fig. 6.1). The collected macroalgae was cleaned and rinsed of any epifaunal species, so that there were no fauna on the macroalgae when the experiment started. Equal proportions of each algal species, making ca. 500g of macroalgae in total, were put into the experimental mesh bags (n = 24).

The experiment was run over 12 weeks, with collections every two weeks, starting at the beginning of June 2004. For each time period (every 14 days) three 5 mm and three 10 mm mesh sized bags were collected; two of the three were filled with macroalgae (n = 24) and one was filled with shredded inert material (bin liners) for the control bags (n = 12) that controlled for hibernation effects but did not provide nutritional properties (Figs. 6.2 & 6.3). The mesh bags were randomly secured across the six buried concrete blocks. Every 14 days six mesh bags, three 5 mm and three 10 mm mesh size (two macroalgae of each mesh size and one control of each mesh size) were randomly taken from across the six blocks. On collection, each mesh bag was placed in a large plastic bag, to prevent the loss of any faunal species, and returned to the laboratory for analysis (see below).



Figure 6.2 Litterbag experiment design: two different mesh sized (5 and 10 mm) litterbags filled with macroalgae and inert material attached to a buried breeze block.

Sampled bags were brought back to the laboratory in a cool box, and the wet weight (following excess water drainage) of each bag was measured. The contents of the mesh bags were rinsed over a 0.5 mm sieve so that all mobile fauna were retained for species identification and abundance counts. After drying the sample bags for 48 hrs at 60° C, the dry mass of the separated algae was determined.

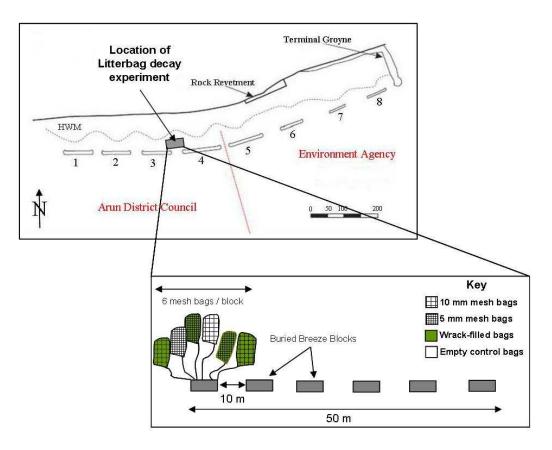


Figure 6.3 Elmer low crested breakwater scheme in West Sussex (UK), with the location (lower landward of bay 3_4) and experimental design of the litterbag field experiment (see section 6.2.2.2).

6.2.2.3 Stable isotope values of macroalgae at Elmer

Initially, eighteen macroalgal species (Table 6.1) were sampled for carbon and nitrogen isotope analysis. These species were chosen from the ten most dominantly observed species from five sampled months (October 2004 to July 2006; see Chapter 3) in the decaying macroalgae deposits at Elmer (sampled in July 2005). Samples (amounting to ca. 1 kg) of deposited decaying macroalgae were collected from randomly chosen locations on Elmer Beach, as part of the spatio-temporal survey of the decaying macroalgae deposits, and assessed for their species

composition (see sections 3.2.2.2 and 3.3.3); excess portions of the samples were kept frozen (ca. -30° C) until they were required for SIA analysis in September 2006.

Table 6.1 The naturally decaying sear	reed species from Elme	r Beach used for stable isotope	analysis
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Chlorophyta	Phaeophyta	Rhodophyta
Cladophera pellucida	Fucus vesiculosus	Calliblepharis ciliata
Ulva intestinalis	Furcellaria lumbricalis	Ceramium sp.
Ulva lactuca	Halidrys siliquosa	Chondrus crispus
	Halopteris filicina	Corallina officinalis
	Laminaria sp. (fragments)	Gracilaria sp.
	Sargassum muticum	Griffithsia sp.
		Mastocarpus stellatus
		Osmundea pinnatifida
		Plocamium cartilagineum

Three months were chosen for their differences in species composition: May 2005, July 2005 and September 2006 (eight 100 g samples for each month). In May 2005, the dominant macroalgae deposited on the beach were *Ectocarpus* sp. (56%), *Ceramium* sp. (13.5%), *Polysiphonia* sp. (13.1%), and *Ulva* sp. (5.9%), the remaining species were subtidal red species such as *Plocamium cartilagineum*, *Griffithsia* sp. and *Cryptopleura ramosa*. In July 2005, an average 67 % of the decaying macroalgae deposits were red macroalgae, 23.5 % brown algae, and 8.7 % green algae. The dominant red alga was *Ceramium* sp. (33.5 %), followed by *Polysiphonia* sp. (19.9 %), *Laminaria* sp. (12.1 %), and *Ulva* sp. (7.3 %). The dominant macroalgal species in September 2006 was *Ectocarpus* sp. (59 \pm 4.5 %), similar to that in May 2005. *Chondrus crispus* (25 \pm 3.8 %), and *Ulva* sp. (3 \pm 0.2 %) were also dominant, whilst the remaining macroalgae were filamentous reds and browns (e.g. *Calliblepharis ciliata*, *Halopteris scoparia*, *Griffithsia* sp.).

6.2.2.4 Isotope values of macroalgae during aerobic decay

A 30-day field decomposition experiment in the field was carried out in February 2005 using four macroalgae species (*Ulva intestinalis*, *Osmundea pinnatifida*, *Sargassum muticum*, and *Chondrus crispus*). These species were chosen based upon their physiological make-up, for example, *C. crispus* is a very tough species, potentially with a slow decay time, whilst, *S. muticum* is the opposite with very soft tissues. Approximately, 500 grams of each of the species was collected from the Poole Training Bank, and immediately stored in plastic bags on ice, and

on return to the laboratory, where they were frozen for 24 hrs to ensure photosynthesis had been stopped so that they would enter a decaying state as they are in the field. Following this, all the macroalgae were rinsed (distilled water) of any attached fauna, stored on ice, transported to Elmer Beach and placed in the 5 mm litterbags (same method as in 6.2.2.1), which were then each attached to a different buried breeze block in the mid-intertidal at Elmer. Initially, the experimental design was for the decaying seaweeds to be sampled every 2 days; this time interval was apparently too short as the decay process in February was slower than anticipated (based on observations made in the summer) because temperatures were lower. The revised sampling collections were made on days 2, 7, 15 and 30.

6.2.2.5 Isotope values of macroalgae during anaerobic decay

The first laboratory decay experiment was designed to clarify the processes which had resulted in changes to the carbon and nitrogen isotope values in the decaying seaweeds of the field study (see section 6.2.2.4), including, variability in the isotope ratios of a single species as sampled over the period of the decay experiment. The same four macroalgal species were chosen as in the field study (*C. crispus*, *O. pinnatifida*, *U. intestinalis*, and *S. muticum*) allowing a comparison to be made between aerobically-decayed macrophytes in the field and anaerobically-decayed macroalgae in the laboratory. In addition, a sample which comprised of a proportional mix of the four algal species was decayed to determine if the mixing of different species affected relative decay rates or the isotope values of individual species. In the laboratory experiment, daily abiotic measurements were made and factors which were thought likely to result in carbon and nitrogen isotope ratio variability (based on field observations) were controlled.

Approximately 1kg of each species was collected from Poole Training Bank, Dorset in May 2006. The experimental design consisted of three replicate quantities (200 g) of each of the four seaweed species (*C. crispus*, *O. pinnatifida*, *U. intestinalis* and *S. muticum*) being placed in a 1L acid-washed container with 800 ml of filtered seawater; resulting in twelve 1L containers (Fig. 6.4). In addition there were three replicates of an equal mixture (50 g each) of the four seaweed species (*C. crispus*, *O. pinnatifida*, *U. intestinalis* and *S. muticum*) and 800 ml of filtered

seawater, and finally three controls: with only 800 ml of filtered seawater (no seaweed). All 18 containers had seal-tight lids and were stored at constant 20.4° C.

Sub-samples of the seaweed and seawater (leachate material) were taken from each container for isotope analysis on days 0, 2, 4, 10, 14, 21, and 30. In addition, the temperature and pH of each container were recorded on these days. The experiment was run in a constant temperature room to allow detection of any temperature change (occurring within the containers) due to bacterially mediated / induced decay. The pH was recorded to determine processes relating to tissue breakdown, leaching of compounds, and bacterial activity. The control containers were used to monitor changes in the pH and temperature of the filtered seawater water and the results were used to calibrate the experimental containers.

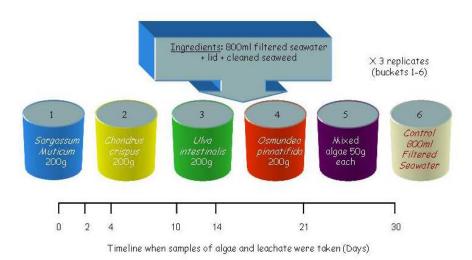


Figure 6.4 The experimental design of the final macroalgae decay experiment for the 4 macroalgal species over a 30-day period.

6.2.3 Collection and Preparation of Samples for Stable Isotope Analysis

6.2.3.1 Macroalgae samples

The samples of mixed decaying macroalgae from Elmer were collected in individual plastic bags and transported back to the laboratory in a cool box. The macroalgae were sifted through for any macrofaunal species present, and subsequently removed. They were then frozen (ca. -30° C) and freeze-dried in separate acidified plastic bags; they were not rinsed in distilled

water, as the samples in the decaying experiment were (see below), as this way they were kept in the state that they are found on the beach, without removing, for example, the bacteria.

Macroalgae samples from the decay experiments were placed in individually sealed plastic bags (acid cleaned) on collection from the field or after experimental manipulation. Where possible the samples were cleaned immediately, if not they were frozen until there was time to do so. The samples were cleaned of all epiphytes and epifauna by adding 50 ml of distilled water to the bag the seaweed had been collected in and then vigorously shaking for 30 seconds, the water was drained off and the process repeated four times. The seaweed sample was then placed under a microscope and any further epiphytes or epifauna were either picked or scraped off. The samples were then placed on pre-combusted Whatman GF/F glass fibre filter, wrapped in a piece of pre-combusted tin foil, placed in a plastic bag and frozen for an hour before being freeze-dried for 48 hours. The samples were then kept in a dessicator until they could be ground up.

6.2.3.2 Leachate medium samples

The leachate mediums from the anaerobic decay experiment were filtered to obtain the particulate organic matter (POM) for SIA. On collection, the water samples were immediately filtered through pre-combusted Whatman GF/F glass fibre filters to collect the POM for SIA. Each of the filters were then acidified with HCl (10 %) in order to remove carbonates, rinsed thoroughly with distilled water, wrapped in tinfoil, frozen for 1 hour, freeze-dried and finally, kept in a dessicator until analysis.

6.2.4 Pulverisation and De-calcification of Samples

The final stage in the preparation was to grind the samples into very small particles to homogenise the samples and to assist combustion in the Elemental Analyser. Then to remove any carbonates present in the samples as they can bias the results of the organic carbon isotope ratios (giving higher values) due to the inclusion of inorganic carbon (as carbonate) which has a distinct isotope signature (Fry 1988). Dried macroalgae samples were pulverized in a ceramic pestle with a mortar and stored in acid washed (4 % HCl) glass vials until analysis. The pestle

and mortar was washed in 10 % ethanol and rinsed twice with distilled water between samples to prevent contamination.

Carbonate-containing samples (e.g. *Corallina officinalis*) were pre-treated to remove the carbonates. Each of the powdered samples was put into a 1.5ml centrifuge tube and treated with 300 ml of hydrochloric acid (10 %) for 24 hours, or until the effervescence stopped. Then 600 ml of MQ water was added to the completely decalcified samples and the samples were then centrifuged in a Sigma 1-15K micro-centrifuge for ten minutes at 2,000 RPM and 8° C. The liquid was then carefully decanted off and another 600 ml was added to each sample and centrifuged again. This procedure was repeated three more times, between each procedure the decanted liquid was tested for acidity with Whatman's pH paper and once the samples were no longer acidic the water was carefully pipetted off with a clean pipette and the sample residue placed in an 60° C oven for 24 hours. The ground samples were then weighed into tin capsules (5 x 3.5 mm) using a Mettler Toledo MX5 micro balance prior to carbon and nitrogen analyses. Table 6.2 shows the weights of powdered material needed for successful SIA (determined by preliminary runs).

Table 6.2 Weight of powdered samples in tin capsules (5 x 3.5 mm) for SIA.

Samples	Weight (mg)
Macroalgae	1.3 - 1.5
Exceptions:	
Fucus vesiculosus	1.95 - 2.25
Corallina officinalis	1.95 - 2.25

6.2.5 Stable Isotope Analysis Technique

Stable isotope analysis on all the samples from the field assessment of decaying macroalgae species and decay experiments were carried out at the East Kilbride node of the Natural Environment Research Council Life Sciences Mass Spectrometry Facility. Carbon and nitrogen isotope measurements were carried out simultaneously using continuous-flow isotope ratio mass spectrometry (CF-IRMS), using a Costech (Milan, Italy) ECS 4010 elemental analyser (EA) combined with a Thermo Finnigan (Bremen, Germany) Delta Plus XP mass spectrometer. Three internal laboratory standards (Sigma-Aldrich gelatine and two Sigma-Aldrich alanine solutions, one of which is labelled with ¹⁵N) were analysed after every 10 samples in each

analytical sequence, assuring good matching of results and allowing for any instrument drift to be corrected. Actual mass, and hence percentage carbon and nitrogen were also recorded. Stable isotope ratios were expressed in δ notation as parts per thousand (‰) deviation from the international standards V-Pee dee belemnite (carbon) and AIR (nitrogen), according to the following equation:

Equation 6.1
$$\delta X = [(R_{sample} / R_{standard}) - 1] \times 1000$$

where, X is ^{15}N or ^{13}C and R is the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$. Where R $_{sample}$ is the ratio in the sample and R $_{standard}$ is the ratio in the corresponding international standards. Measurement precision was estimated to be ≤ 0.2 % for $\delta^{15}N$ and ≤ 0.04 % for $\delta^{13}C$.

6.2.6 Statistical Analysis

Several null hypotheses were tested using five analysis of variance (ANOVA) tests. The first null hypothesis tested that there were no differences in the rate of decay of macroalgae over time nor were there differences in the rate of decay of macroalgae decaying in two different mesh sized bags. A two-way ANOVA was carried out on the percentage initial weight of macroalgae, where factor one (decay time) had three levels (12, 23 and 35 days), and factor two (mesh size) had two levels (5mm and 10mm). All factors were fixed and orthogonal.

The second null hypothesis tested that there were no differences in the number of individuals, number of species and species diversity (Simpson's Index) associated with biomass of decaying macroalgae over time nor were there differences in these faunal measures between the two different mesh sizes (5 mm and 10 mm) of the macroalgae-filled bags. A two-way ANOVA was carried out on three dependent variables (number of faunal individuals, number of species and faunal species diversity) using factor one (decay time), which had three levels (12, 23 and 35 days), and factor two (mesh size), which had two levels (5mm and 10mm). All factors were fixed and orthogonal.

The third null hypothesis tested that there were no differences in the number of amphipods, decapods and isopods associated with biomass of decaying macroalgae nor were there differences in the numbers of these taxa between the two different mesh sizes (5 mm and 10

mm) of the macroalgae-filled bags. A two-way ANOVA was carried out on three dependent variables (number of Amphipoda, Decapoda and Isopoda) using factor one (decay time), which had three levels (12, 23 and 35 days), and factor two (mesh size), which had two levels (5mm and 10mm). All factors were fixed and orthogonal.

The fourth null hypothesis tested that there were no differences in the $\delta^{13}C$ and $\delta^{15}N$ values between three different months of random mixes (as taken from the beach) of algal species in the deposits of decaying macroalgae. A one-way ANOVA was used to test this null hypothesis, with two dependent variables ($\delta^{13}C$ and $\delta^{15}N$ values of mixed decaying macroalgae deposits), using time as the factor, which had three levels (May 2005, July 2005 and September 2006) and was fixed and orthogonal.

The fifth and final null hypothesis tested that there were no differences in the δ^{13} C and δ^{15} N values between living and 30 day anaerobically decomposed *Sargassum muticum*, *Ulva intestinalis*, *Chondrus crispus*, *Osmundea pinnatifida* and mixed species. Again a one-way ANOVA was used to test this null hypothesis, with five dependent variables (δ^{13} C and δ^{15} N values of *S. muticum*, *U. intestinalis*, *C. crispus*, *O. pinnatifida* and mixed species), using decay time as the factor, which had two levels (living and 30-day decayed) and was fixed and orthogonal.

All data were tested for normality using the Kolmogorov-Smirnov test, and where necessary data were $\log (x + 1)$ transformed for abundances and biomasses and arcsine percentage square root transformed for the diversity index data and isotope ratios. When ANOVA indicated significant differences among the means for decay time Tukey's HSD *post hoc* tests was used to distinguish between them (p < 0.05).

6.3 Results

6.3.1 Macroalgae Biomass Decomposition Rates and Faunal Colonisation

6.3.1.1 Macroalgae decomposition rates

There were significant differences (F = 34.36, p < 0.001, Table 6.3) in the amount of decaying macroalgae lost during the course of the litterbag experiment; the weight lost after 12 days was significantly greater than that lost after 23 and 35 days, with no significant differences (p = 0.05) between the latter time points.

Table 6.3 Analysis of the decomposition of macroalgal deposits (percentage of initial weight) in litterbags of different mesh size through time, n = 12, *p < 0.05, **p < 0.001, **NS** = not significant (p > 0.05).

Source	df	MS	F ratio			
DT	2	1591.89	34.356**			
MS	1	331.49	7.154*			
DT x MS	2	97.29	2.1 NS			
DT = Decay Time, MS = Mesh Size.						

The exponential pattern of algae decomposition in the litterbags was similar between the two mesh types (Fig. 6.5), but the rate of algae decomposition was significantly (p < 0.05) different between them (Table 6.3, Fig. 6.5). The 10 mm mesh bags showed a higher rate of decomposition than the 5 mm bags through time.

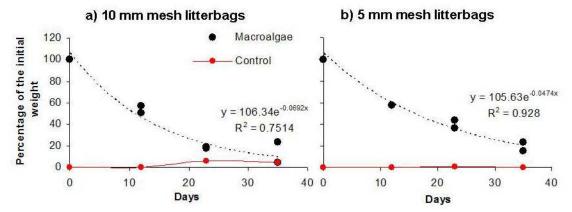


Figure 6.5 Changes in dry weight (g) of mixed decaying macroalgae species in (a) 10 mm and (b) 5 mm mesh litterbags with inert material filled control bags through time. Curves show an exponential decay model.

Decomposition was initially very rapid (i.e. by day 12); following this, the loss slowed more rapidly in the 5 mm rather than the 10 mm bags (Fig. 6.5). By day 12, all the litterbags had lost ~ 50 % of their contents and by day 23, the litterbags were between ~ 80 % and ~ 60 % of their initial dry weight for 10 mm and 5 mm bags, respectively. The control bags (filled with shredded bin liners) remained empty of macroalgae after 12 days, however, after 23 days small quantities (~ 1 g dry weight) of algae debris were found in the litterbags (Fig. 6.5); greater quantities in the 10 mm than the 5 mm bags (Fig. 6.5).

6.3.1.2 Faunal abundances

A total of 4,165 individuals belonging to 27 species/taxa, from 8 orders were collected from litterbags over the course of the decay experiment. *Gammarus locusta* accounted for 89 % of the total abundance (n = 3,656), with *Carcinus maenas* juveniles found in reasonable numbers (n = 379), accounting for 9 % of the abundance, and a further 2 % from six isopod species (Table 6.4). The remaining < 1 % of the total abundance was made up from sporadic occurrences of different species (Table 6.4).

6.3.1.3 Colonisation of decaying macroalgae

The faunal assemblages colonising the litterbags varied between the control and macroalgae-filled litterbags, both among mesh sizes and with time. There were significant variations in the number of species (F $_{(1, 13)} = 5.38$, p < 0.05), individuals (F $_{(1, 13)} = 44.25$, p < 0.001) and species diversity (Simpson's: F $_{(1, 13)} = 7.21$, p < 0.05) across time for assemblages within macroalgae-filled litterbags (Table 6.5). There were more individuals after 12 days than later on in the experiment (Tukey's HSD tests; p < 0.001), with significantly (F = 10.52, p < 0.05) greater abundances in smaller mesh bags (Fig. 6.6ai).

There were significant interactions between mesh size and decay for the average number of species (F $_{(1,13)}$ = 16.13, p < 0.05); species numbers gradually decreased from 6 ± 0 to 2.5 ± 0.5 in 10 mm bags over time, whereas the number of species in 5 mm bags showed an initial decrease from 5.5 ± 0.5 to 2.5 ± 0.5 species for days 12 to 23, respectively, followed by an increase to 6 ± 1 species after 35 days (Fig. 6.6aii). Decay time but not mesh size had a significant effect on Simpson's diversity index (Table 6.5; Fig. 6.7).

Table 6.4 Total number and percentage composition of fauna found in the litterbags

Order	Species	Number of Individuals	% Community
Amphipoda		3,690	88.60
•	¹ Amphithoe sp.	1	0.02
	¹ Bathyporeia sp.	6	0.14
	¹ Corophium arenarium	1	0.02
	Ericthonus sp.	1	0.02
	¹ Gammarus locusta	3,656	87.78
	Unidentifiable species 1	2	0.05
	¹ Unidentifiable species 2	23	0.55
Bivalvia		1	0.02
	¹ Donacidae/Veneridae (Juvenile)	1	0.02
Cumacea		2	0.05
	¹ Bodotria scorpioides	2	0.05
Decapoda		384	9,22
Decupoda	Pisa tetradon (Juvenile)	1	0.02
	¹ Carcinus maenas (Juvenile)	379	9.10
	Decapod (Juvenile)	3	0.07
	Unidentifiable <i>Majidae</i> sp.	1	0.02
Gastropoda	emocianiae o majaane sp.	6	0.14
Gastropoua	Gibbula umbilicalis	3	0.07
	¹ Littorina saxatilis species complex	2	0.04
	¹ Littorina littorea.	1	0.02
	Rissoa guerni	2	0.05
	¹ Rissoa parva	2	0.05
Isopoda	Rissou parva	70	1.68
Isopoda	Gnathia sp. (Pranzo Juvenile)	7 0 1	0.02
	Idotea baltica	9	0.02
	Idotea granulosa	38	0.22
	¹ Idotea neglecta	5	0.91
	¹ Idotea pelagica	17	0.12
	Lekaneshaera sp.	1	0.41
D. I	Lekanesnaera sp.		
Polychaeta	Dhulladaaa	1	0.02
D	Phyllodoce sp.	1	0.02
Pycnogonida	4 1 7: 1 ·	1	0.02
	Achelia longipes	1	0.02
	Unidentified	5	0.12

Numbers are the pooled samples from all litterbags across the course of the experiment. Species found in experimental and control samples.

The diversity of the assemblages found in the decaying macroalgae was initially small (after 12 days), primarily because they were dominated by *Gammarus locusta* and *Carcinus maenas* (Table. 6.4), contributing 78 % and 13.5 %, respectively to the average similarity (82.45) between litterbags (across both mesh sizes; ANOSIM). The diversity of the assemblages increased with time; the 10 mm bags showed to have higher diversity; however, there was considerable variability (Fig. 6.8). The control bags, illustrated an opposite pattern with a high

diversity after 12 days (Fig. 6.8), represented by a small number of individuals (Fig. 6.6a), followed by an increase in individuals, which corresponded to a decrease in diversity.

Table 6.5 Summary of analysis of variance for number of species, number of individuals and species diversity (Simpson's diversity indices). *p < 0.05, **p < 0.001, **NS** = not significant (p > 0.05).

Source	Number	of Species		¹ Number of Ind	ividuals
	df	MS	F ratio	MS	F ratio
DT	2	3.58	5.38*	2.50	44.25**
MS	1	0.00	$0.00~\mathrm{NS}$	0.59	10.52*
DT * MS	2	10.75	16.13*	0.13	2.29 NS
	Simpsor	n's Diversity	Index		
DT	2	0.33	7.21*		
MS	1	0.15	3.35 NS		
DT * MS	2	0.08	1.87 NS		

¹Data transformation required to meet the assumption of normality $[\log (x+1)]$.

Df = degrees of freedom; DT = decay time; MS = mesh size.

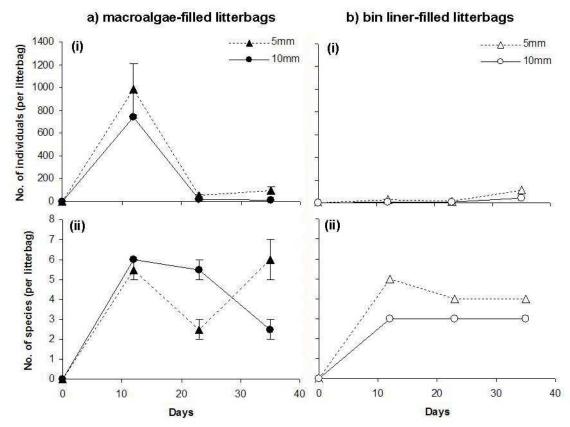


Figure 6.6 Number of (i) faunal individuals and (ii) species colonising the decaying macroalgae in the 5 mm and 10 mm litterbags at different times during the course of the experiment (35 days) for (a) macroalgae-filled litterbags and (b) control litterbags. Error bars represent \pm SE for mean values for (a).

The overall faunal abundance was positively correlated with the wet weight (g) of decaying macroalgae in the litterbags (r = 0.824, p < 0.001, n = 12), whilst dry weight (g) of the macroalgae was not (p > 0.05). There were strong positive correlations between the wet weight of algae (g) in the litterbags and the overall abundances of *G. locusta* (r = 0.797, p < 0.001, n = 12) and isopods (r = 0.893, p < 0.001, n = 12) (Fig. 6.8), but not the juvenile *C. maenas*.

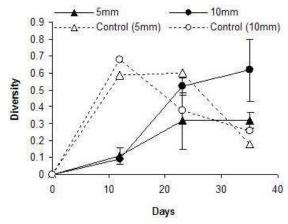


Figure 6.7 Simpson's Diversity Index for the fauna in the macroalgae-filled and bin liner-filled (control) 5 mm and 10mm litterbags during the course of the experiment. Error bars represent \pm SE.

Multiple linear regression was performed with wet (r = 0.797, p < 0.001) and dry weights (r = 0.498, p < 0.05) of decaying macroalgae in the litterbags as predictors of *G. locusta*; together (r = 0.848, p < 0.05) they explained a large amount (71.9 %) of the variation in *G. locusta* abundances, with wet weight explaining most of the variation (63.5 %). There was no significant collinearity between the predictors; therefore, there were measuring different things.

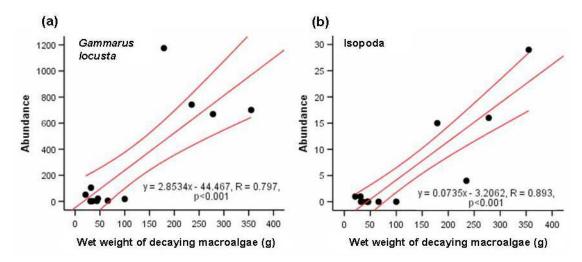


Figure 6.8 Scatter plot and regression with 95 % confidence levels of (a) *Gammarus locusta*, and (b) Isopoda as a function of the wet weight of decaying macroalgae (wrack) in the litterbags. n = 12. **NB**: y axis scales are different.

No relationship between the amount of decaying macroalgae in the litterbags and the number of species was observed, however, there were negative correlations for between wet weight (g) of decaying macroalgae and Simpson's diversity index (r = -0.651, p < 0.05, n = 12). The greater the biomass of macroalgae, the lower the species diversity; this relationship was also shown by the much higher diversity in the control bags, where there was little macroalgae (Fig. 6.7). In general, the macroalgae-filled litterbags were colonised rapidly. The community assemblages colonising the decaying macroalgae showed very strong significant differences (p < 0.05) between decay times (R = 0.944, ANOSIM) and mesh sizes (R = 0.667, ANOSIM). The pattern of colonisation of the most abundant species varied across time.

G. locusta (F $_{(1, 13)}$ = 43.12, p < 0.001), the most abundant species over the course of the experiment (3,656 ind.), and juvenile *C. maenas* (F $_{(1, 13)}$ = 20.49, p < 0.002), the second most abundant species (379 ind.) showed significant differences in abundances with length of time. In addition, the former species was significantly affected by mesh size (F $_{(1, 13)}$ = 6.18, p < 0.047) (Table 6.7). After 12 days, *G. locusta* (94.8 %) were the most dominant taxon (Fig. 6.9a) with small occurrences of juvenile decapods (3.1 %) and isopods (2 %); this corresponded with the largest decrease in macroalgae in the litterbags (Fig. 6.5).

Table 6.6 Summary of analysis of variance for number of individuals of Amphipoda, Decapoda and Isopoda. *p < 0.05, **p < 0.001, **NS** = not significant (p > 0.05).

Source	¹ Amphipod	¹ Amphipoda			
	\overline{df}	MS	F ratio		
DT	2	4.34	43.12**		
MS	1	0.62	6.18*		
DT * MS	2	0.23	2.27 NS		
	¹ Decapoda				
DT	2	0.48	20.49*		
MS	1	0.10	4.45 NS		
DT * MS	2	0.04	1.83 NS		
	Isopods				
DT	2	330.75	11.61*		
MS	1	48.00	1.68 NS		
DT * MS	2	48.25	1.69 NS		
D		.1			

¹Data transformation required to meet the assumption of normality [log(x+1)]. Df = degrees of freedom, DT = Decay Time, MS = Mesh Size.

After 23 days, the dominant species switched to juvenile *C. maenas* (75.3 %) with a fall in abundances of amphipods (21 %) and isopods (0.5 %); by this time the macroalgae in the bags was a fifth of its original biomass. After 35 days, the amphipod abundances increased and the decapod abundances decreased (Fig. 6.9a,b); this corresponded also with an increase in

decaying macroalgae in the 10mm bags after 35 days (Fig. 6.5a). It is also worth noting the large numbers of amphipods found in the controls for that time period (Fig.6.9d).

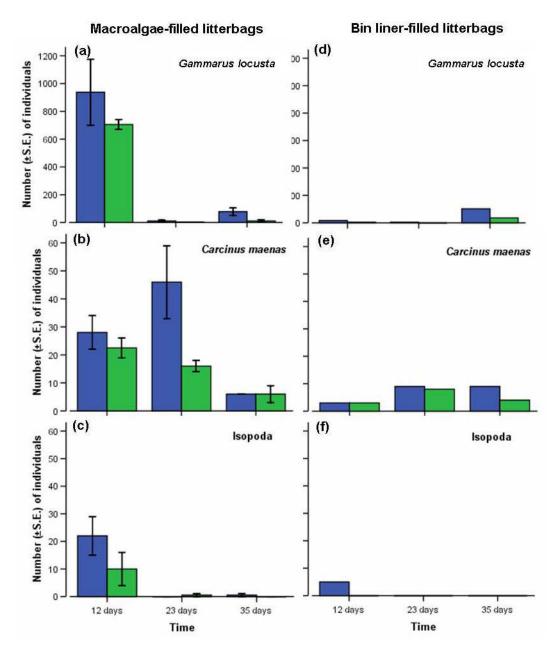


Figure 6.9 The influence of mesh size ($\blacksquare 5$ mm & $\blacksquare 10$ mm) on the mean number (\pm S.E.) of individuals through time. (a) – (c) macroalgae-filled litterbags (n = 2); (d) – (f) control litterbags (n = 1). (a) & (d) *Gammarus locusta*, (b) & (e) Isopoda, (c) & (f) *Carcinus maenas*. **NB**: Scale different in (a) & (d).

6.3.2 Macroalgae Isotope Values

A preliminary study was carried out to determine the isotope values of the consistently dominant species within the decaying macroalgae deposits at Elmer. Their δ^{13} C vs. δ^{15} N values are shown in Figure 6.10, as well as the values of the mixture of decaying macroalgae from deposits in May 2005, July 2005 and September 2006.

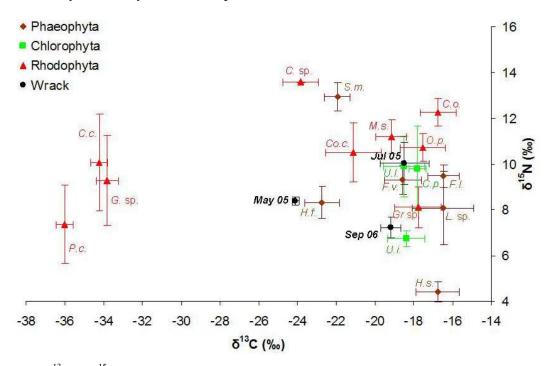


Figure 6.10 δ^{13} C vs. δ^{15} N values (means ± SD) of the dominant decaying macroalgae species deposited on and around the CDS at Elmer beach in July 2005, and the values of mixed decaying macroalgae deposits for May 2005, July 2005 and September 2006. **Chlorophyta**: *U.l.* = *Ulva lactuca*; *U.i.* = *Ulva intestinalis*; *C.p.* = *Cladophera pellucida*; **Phaeophyta**: *S.m.* = *Sargassum muticum*; *L.* sp. = *Laminaria* sp.; *F.l.* = *Furcellaria lumbricalis*; *F.v.* = *Fucus vesiculosus*; *H.s.* = *Halidrys siliquosa*; *H.f.* = *Halopteris filicina*; **Rhodophyta**: *P.c.* = *Plocamium cartilagineum*; *G.*sp. = *Griffithsia* sp.; *C.c.* = *Calliblepharis ciliata*; *C.* sp. = *Ceramium* sp.; *M.s.* = *Mastocarpus stellatus*; *Co.c.* = *Chondrus crispus*; *O.p.* = *Osmundea pinnatifida*; *Gr.* sp. = *Gracilaria* sp.; *C.o.* = *Corallina officinalis*.

There was an extensive range of $\delta^{13}C$ values for the living algal species studied; they ranged from -16.5 to -36.0 ‰. The Chlorophyta (greens) $\delta^{13}C$ values ranged from -17.8 to -18.5 ‰, the Phaeophyta (browns) from -16.5 to -22.8‰, and the Rhodophyta (reds) from -16.7 to -36.0 ‰. The $\delta^{15}N$ and $\delta^{13}C$ values for the red algae extended a very large range ($\delta^{13}C$: 19.5 ‰ and $\delta^{15}N$: 6.2 ‰).

Of particular interest, were the three species that were extremely δ^{13} C depleted: *Calliblepharis* ciliata, *Plocamium cartilagineum*, and *Griffithsia* sp. (-34.2, -36.0, and -33.8 %, respectively),

all were filamentous, small, subtidal red algal species. These species exhibited small withinspecies variation (n = 10) for the δ^{13} C values (Fig. 6.10), however they had a large range of values for $\delta^{15}N$ (ca. ± 2 % S.D.). The other filamentous red algae, Ceramium sp., did not, however, have similar δ^{13} C or δ^{15} N values (-23.8 vs. 13.6 %) to Calliblepharis ciliata, *Plocamium cartilagineum* and *Griffithsia* sp.; the δ^{13} C or δ^{15} N values were instead more enriched. The more robust red algae species Chondrus crispus, Mastocarpus stellatus and Osmundea pinnatifida were in the range of -17.5 to -21.1 %, with similar δ^{15} N values (10.5 to 11.2 ‰). The brown macroalgae group had a smaller range of δ^{13} C values than the red macroalgae group, whereas the values of $\delta^{15}N$ ranged extensively from 4.4 % for Halidrys siliquosa (a large brown tough leathery seaweed), to 13.0 % for Sargassum muticum (an invasive fast growing seaweed). The Chlorophyta were not well represented due to their lack of presence in the decaying macroalgae deposits at Elmer. There was an interesting difference in the $\delta^{15}N$ values of *Ulva intestinalis* (previously *Enteromorpha* genus) and *Ulva lactuca* (6.8 vs. 9.9 ‰, respectively; t-test p < 0.01), considering these two species have received much contention about their taxon classification. These two species, however, had similar $\delta^{13}C$ values (Fig. 6.10).

The mixture of decaying macroalgae species from the three months were significantly different (δ^{13} C: F_{2, 15} = 46.3, p<0.001; δ^{15} N: F_{2, 15} = 21.7, p<0.001). Tukey's HSD *post hoc* tests showed that the δ^{15} N values were different for each of the three months. The decaying macroalgae deposits had similar δ^{13} C values in July and September, but different values in May (Fig. 6.10).

6.3.3 Changes in Elemental Composition during Decomposition

6.3.3.1 Changes in elemental composition of macroalgae species

Experimental anaerobic decay

The C and N content, and Ash Free Dry Weight (AFDW) of the anaerobically decomposed macroalgae *Sargassum muticum*, *Ulva intestinalis*, *Chondrus crispus*, and *Osmundea pinnatifida* decreased significantly in the initial leaching stages of decay (days 0 - 2; Fig. 6.11a-c). *O. pinnatifida* and *U. intestinalis* initially decayed the most rapidly, losing 36 % and 34 % of their original percentage AFDW (91.5 and 74.0 %, respectively), whilst *C. crispus* and *S. muticum* decayed more slowly, losing only 14 % and 20 %, respectively (84.6 and 88.2 %,

respectively). The loss of carbon followed very similar patterns to the loss of AFDW. This pattern of AFDW loss in the initial stages of anaerobic decay was also seen for the C and N content; for example, *O. pinnatifida* exhibited the greatest loss of C and N from the living macrophyte specimens to two day leached specimens, with a 38 and 25 % respective loss (Table 6.7). The least net loss of N was from *S. muticum*, losing only 7 %. The decay of the C and N content of the macrophytes was not of the same magnitude; this can be seen by the significant decrease in the C: N ratios during the initial stages of decay (Fig. 6.11f); this indicates that a large amount of N remained in relation to structural C after decomposition.

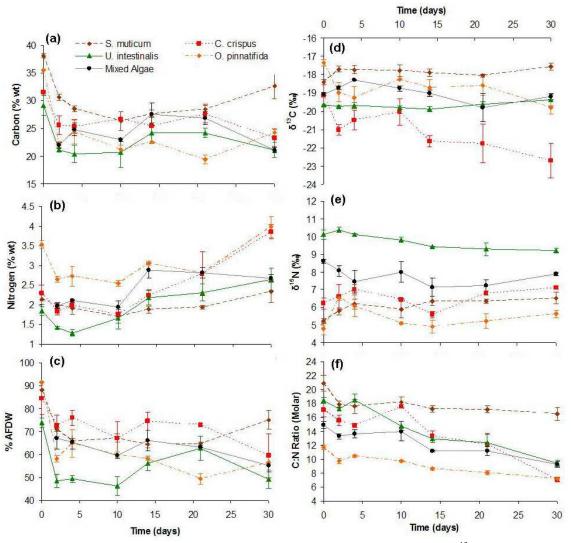


Figure 6.11 Changes in a) carbon, b) nitrogen, c) ash free dry weight (AFDW), d) δ^{13} C isotope values, e) δ^{15} N isotope values and carbon: nitrogen ratio (molar) during anaerobic macroalgae decay for four different species (*Sargassum muticum*, *Ulva intestinalis*, *Chondrus crispus* and *Osmundea pinnatifida*) and the mixture of these four species. **NB**: y axis scales are different.

Experimental aerobic decay

The initial aerobic decay processes of the decaying macrophytes in the field showed some similarities to the anaerobic decay process. With the exception of *U. intestinalis*, all macrophyte species experienced leaching of C and N, although not to the same degree as the anaerobically-decayed detritus. *S. muticum* experienced the greatest loss of C and N content (10 and 40 %, respectively); however, this and the increase in C: N ratio (Table 6.7) showed that in comparison to the anaerobically-decayed macroalgae there was a large initial loss of N, whilst the majority of the structural C remained. This trend was also seen for *C. crispus* and *O. pinnatifida* but to a lesser degree. In contrast, *U. intestinalis* exhibited a very small increase in C content (1 %) and a large increase in N content (26 %).

Table 6.7 Fluxes of percentage AFDW, carbon, nitrogen (from the original content), and C: N Ratio, δ^{13} C and δ^{15} N values (depletion or enrichment fluxes) during anaerobic (laboratory decay) and aerobic (field decay) leaching (0-2 days) and ageing (2-30 days) phases of macrophyte detritus decomposition¹. Mean values for the anaerobic decay experiment (n = 3).

-	Anaerobic Laboratory Decay					Aerobic Field Decay			
	C conte	nt (%)	N conte	N content (%)		C content (%)		N content (%)	
	Leachin	Agein				Agein			
	g	g	Leaching	Ageing	Leaching	g	Leaching	Ageing	
S. muticum	-20	+7	– 7	+17	-10	+9	-40	+102	
C. crispus	-19	-9	-20	+111	-8	+23	-14	+14	
U. intestinalis	-28	0	-23	+85	+1	+11	+26	+10	
O. pinnatifida	-38	+10	-25	+50	-4	+21	-10	+1	
Mixed Algae	-30	-4	-10	+35	-	-	-	-	
	$\delta^{13}C$	(‰)	$\delta^{15}N$	(‰)	$\delta^{13}C$	(‰)	$\delta^{15}N$	(‰)	
	Leachin	Agein				Agein			
	g	g	Leaching	Ageing	Leaching	g	Leaching	Ageing	
S. muticum	+0.71	+0.13	+0.56	+0.74	+0.74	-0.12	-1.32	+0.97	
C. crispus	-1.87	-1.67	+0.37	+0.51	-2.74	+0.11	+0.98	-2.35	
U. intestinalis	-0.07	+0.35	+0.28	-1.16	-0.25	+0.51	-0.32	-0.87	
O. pinnatifida	-1.38	-0.83	+1.76	-0.92	-0.62	-0.48	+0.97	-1.77	
Mixed Algae	+0.35	-0.48	-0.53	-0.18	-	-	-	-	
	AFDW	7 (%)	C:N Ratio	(Molar)	AFDV	V (%)	C:N Ratio	(Molar)	
	Leachin	Agein				Agein			
-	g	g	Leaching	Ageing	Leaching	g	Leaching	Ageing	
S. muticum	-20	+6	-2.99	-1.43	-	-	+7.46	-10.20	
C. crispus	-14	-18	-1.49	-8.51	-	-	+0.56	+0.70	
U. intestinalis	-34	+2	-1.20	-7.83	-	-	-2.46	+0.08	
O. pinnatifida	-36	-5	-2.00	-2.59	-	-	+0.57	+1.78	
Mixed Algae	-25	-18	-1.60	-4.06	-	-	-	-	

¹ (–) indicates net loss/depletion from detritus, (+) indicates net gain/enrichment by detritus, (-) indicates no samples.

During the ageing stage (after 2 days, following the initial leaching stage of decay), the C flux varied in both magnitude and direction (influx or efflux) from one macrophyte species to another (Fig. 6.11). *C. crispus* and the mixed algae exhibited a net loss of C during the ageing stage of decay (days 2 - 30), losing 9 and 4 %, respectively. *S. muticum* showed a net loss until day 10, following this there was a net gain (Fig. 6.11), eventually gaining 7 % more C than after the leaching stage. *O. pinnatifida* experienced a series of influxes and effluxes in C and in the last 9 days noticeably increased in C gaining 10 % more C than after 2 days (22.1 % content). *U. intestinalis* exhibited a gain in C after 10 days and maintained this until after 21 days there was a loss of C, so overall there was no net change during the ageing process (Table 6.8). The mixed algae followed a general trend of increasing C after leaching until day 21 when the C content noticeably reduced to only having a net gain of 4 % during the ageing stage.

In contrast, the macroalgae showed an increasing trend in the N content during the ageing stage of decay (Fig. 6.11, Table 6.7), with *C. crispus* and *U. intestinalis* experiencing the greatest influxes (111 and 85 %) since day 2, when there had been an overall efflux during leaching. The aerobically-decayed macroalgae experienced an overall trend of net gain of both N and C content during the ageing stage (Table 6.7).

Experimental anaerobic vs. aerobic decay

There were differences though in the magnitude of net gain from the anaerobically to the aerobically-decayed algae; for example, where *S. muticum* experienced the least gain in N in the former decay process (17 %), there was the most gain in N content in the latter decay process (102 %).

During the ageing stage of anaerobic macrophyte decomposition the C: N ratios continued to show a decreasing trend for all the macrophytes (Fig. 6.11f), showing that C was lost at a greater rate than N. The decay of the C and N content for *S. muticum* was almost of the same magnitude (1.4:1 molar), with C being lost marginally quicker than the N (Table 6.7), whereas for *U. intestinalis* and *C. crispus* the C content was lost ca. 8 times faster than the N content (Table 6.7). A different trend was seen for the aerobically-decayed algae; the C: N ratio increased marginally after the leaching stage for all the species, indicating a slightly greater N loss to C loss. The exception was *S. muticum*, which exhibited a large decrease in C: N ratios

over time, indicating that a large amount of N remained in relation to structural C after decomposition.

6.3.3.2 Elemental changes of the anaerobic decay medium

Within the first two days (leaching period) of the anaerobic macroalgae decay there was leaching of soluble components; the C and N of these leached soluble components were assessed by using the filtered soluble material in the seawater medium that the macroalgae species were decayed in (referred to as medium or media from hereon in). The seawater medium showed an initial increase in elemental component concentrations compared to the starting concentrations (0 days; Fig. 6.12). The *S. muticum* medium exhibited the largest initial increase in C (19.9%) and N (3.6 %) contents, whilst *O. pinnatifida* and the mixed algae medium had values of half this (Table 6.8) for both elements.

Table 6.8 The changes in percentage weight of carbon (C) and nitrogen (N) in the medium during decay of *S. muticum*, *C. crispus*, *U. intestinalis*, *O. pinnatifida*, and a mixture of these four species.

				Macrophyte	s	_
-	Time					
_	(days)	S. muticum	C. crispus	U. intestinalus	O. pinnatifida	Mixed algae
C	0	1.4	1.4	1.4	1.4	1.4
(% wt)	2	19.9	14.2	12.6	7.4	7.5
	4	16.3	14.0	4.1	13.2	9.8
	10	24.9	9.5	7.6	9.1	8.2
	14	23.5	15.1	13.4	13.5	18.0
	21	10.9	16.1	13.3	16.2	19.8
_	30	16.3	8.7	13.6	3.7	21.4
_						
N	0	0.1	0.1	0.1	0.1	0.1
(% wt)	2	3.6	3.3	3.2	1.9	1.6
	4	2.6	3.6	0.8	2.6	2.0
	10	3.6	2.1	1.7	1.8	1.8
	14	3.3	2.8	2.7	3.2	4.1
	21	1.9	3.2	2.4	3.1	4.1
	30	2.7	1.4	2.3	25.3	4.1

These leachate values were the opposite to the C and N content of the detritus, where the former macroalgae species had a low initial loss of both elements and the latter species a high loss (Table 6.7). In the first two days, the C content of the macrophytes leached out of the macrophytes and into the medium more rapidly than the N, thus explaining the sharp increase seen in the C: N ratios (Fig. 6.13). The pattern of C: N ratio change of the leachate medium and

the macrophytes reflect each other reasonably well (Fig. 6.13), being mostly negatively correlated; the C: N ratios of the medium and detritus for *S. muticum* and the mixed algae were however not correlated.

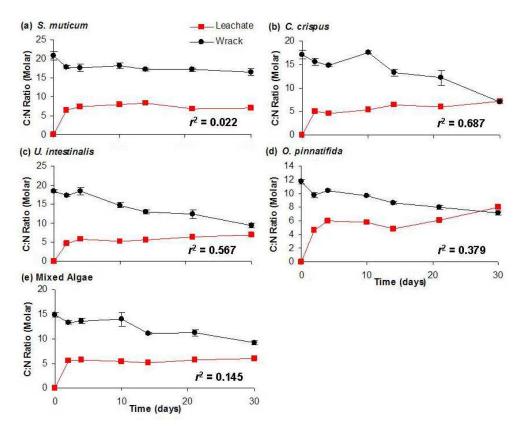


Figure 6.12 The changes in the C: N ratios (molar) of the remaining macroalgae detritus and medium (leachate) over time for a) *Sargassum muticum*, b) *Chondrus crispus*, c) *Ulva intestinalis*, d) *Osmundea pinnatifida* and e) the mixture of these four macroalgae. Values are mean (\pm SD) for the macroalgae (n = 3). r^2 equations show the correlation between the C: N Ratio of each the macroalgae species and their respective leachate material. **NB**: y axis scales are different.

Over the rest of the course of the ageing stage the magnitude of C gain and loss varied between the species. The red algae medium for *C. crispus* and *O. pinnatifida* exhibited similar gains and losses; the C content of the mediums peaked (gained) after 4 days, followed by a sharp reduction (loss) by 10 days of decay, the C then increased to similar values again by day 21, and finally the C content decreased by 30 days. The gains and losses of C in the seawater medium of the brown alga *S. muticum* was the complete opposite to this. The medium for the mixed algae and *U. intestinalis* decreased in C after the initial leaching stage (days 0 - 2) and then slowly increased the amount of C (Table 6.8). The same patterns of gains and losses exhibited in the C content of all the macrophyte mediums were also observed for the N content (Table 6.8), with

the exception of the extreme increase in N between 21 and 30 days of decay for *Osmundea pinnatifida* (3.1 to 25.3 %, respectively).

The temperature of the seawater media exhibited a significant increase (ca. 1.25° C) for all the macroalgae in the first 48 hours (Fig, 6.13a) from a starting temperature of 17.2° C. The temperature then levelled out around 18.8°C for the rest of the decay process, with the exception of *C. crispus*, *U. intestinalis* and the mixed algae.

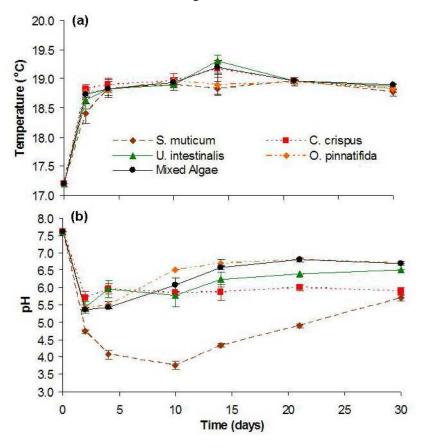


Figure 6.13 The a) temperature and b) pH changes over time of decay in the seawater medium for *S. muticum*, *C. crispus*, *U. intestinalis*, *O. pinnatifida* and the mixture of these four macroalgae. Values are mean $(\pm SD)$ (n = 3).

A positive temperature flux was exhibited at 14 days decay of ca. 19.2° C, this then fell again by day 21 to ca. 19.0° C (Fig. 6.13a). The pH of the filtered seawater was slightly alkaline (7.6) at the beginning of the experiment (Fig. 6.13b). During the initial leaching period (days 0 - 2) the pH of the media rapidly became more acidic, decreasing to an average of 5.5 ± 0.2 for all the species except *S. muticum*, where the media decreased further to 4.7 ± 0.1 . Following this leaching period, the pH of all the algae (except *S. muticum*) gradually became less acidic over time, returning to an almost neutral environment by 30 days (pH 6.7; Fig. 6.13b). The *C. crispus*

media remained more acidic than the other species maintaining an environment just below pH 6. In contrast, the *S. muticum* environment continued to become more acidic during the course of decomposition, only after the pH reached a low of 3.8 around 10 days did the environment begin to increase in pH until it reached a similar value to that of *C. crispus*.

6.3.5 Changes in Stable Isotope Values during Decomposition

Experimental aerobic and anaerobic decay

The responses of the δ^{13} C and δ^{15} N values to the decaying of the macrophytes showed complex patterns (Fig. 6.11); there was within-species consistency for the anaerobically-decayed macroalgae as there were no significant differences in δ^{13} C or δ^{15} N values between replicate experiments (n = 3; p > 0.05). In the initial anaerobic decay stage C. crispus, O. pinnatifida and U. intestinalis exhibited lower δ^{13} C values (Table 6.7) than living plants, C. crispus experienced the largest ¹³C depletion (loss by -1.87 ‰) and *U. intestinalis* only by a small increment (-0.07 ‰) (Fig. 6.14b). In contrast, S. muticum and the mixed algae experienced ¹³C enrichment (0.71 and 0.35 %, respectively). The same flux patterns were also seen in the aerobically-decayed macroalgae. All four anaerobically-decayed species exhibited δ¹⁵N enrichment during the leaching stage, whilst the mixed algae experienced ¹⁵N depletion (-0.53 %; Fig. 6.14b). Whereas in the field (aerobic), S. muticum and U. intestinalis exhibited lower $\delta^{15}N$ values and O. pinnatifida and S. muticum higher $\delta^{15}N$ values than seen for anaerobic decay (Fig. 6.11). The δ^{13} C values of anaerobically-decayed S. muticum, U. intestinalis and mixed algae did not change greatly during the ageing stage (> 2 days) (Table 6.6, Fig. 6.14b). The former species exhibited a marginal but significant (p < 0.05) enrichment by 0.8 % (Table 6.8), whereas the latter two species were similar to their initial values (-18.4 and -19.7 ‰, respectively; Table 6.9).

The red algae *C. crispus* showed the largest significant change in δ^{13} C during decomposition, from the initial value of –19.2 to –22.7 ‰ (3.5 ‰ 13 C depletion, p < 0.05); followed by the other red algae, *O. pinnatifida*, which was significantly lower than the initial mean value of –17.6 ‰ to –19.8‰ (2.2 ‰ 13 C depletion, p < 0.01; Fig. 6.14b). A similar situation occurred for the aerobically-decayed macroalgae, where the red algal species showed reasonably large changes in δ^{13} C. *C. crispus* was depleted of 13 C by 2.7 ‰ from its initial δ^{13} C value of –20.3 ‰; the majority of this depletion occurred in the leaching stages (Fig. 6.11; Table 6.7). Whilst *O. pinnatifida* was 13 C depleted by 1.1 ‰ from its initial δ^{13} C value of –16.6 ‰; 40 % of this

depletion occurred in the ageing stages (days 2 - 30) of decomposition. Overall, the alteration in δ^{13} C values for the aerobically-decayed algae during the ageing stage only changed marginally (≤ 0.5 ‰ increment; Table 6.8), *O. pinnatifida* and *U. intestinalis* were ¹³C depleted and enriched respectively, in the same order of magnitude as the anaerobically-decayed algae (Table 6.9). On the other hand, the changes seen for *S. muticum* and *C. crispus* were very marginal (-0.1 and +0.1 ‰, respectively), but the overall change (+ or -) in δ^{13} C values between the anaerobically and aerobically after 30 days decay was in the same order of magnitude (*S. muticum*: +0.8 vs. +0.6 ‰, *C. crispus*: -3.5 vs. -2.6 ‰, respectively; Table 6.9).

The δ^{15} N values of all the macroalgae also did not change greatly during the anaerobic ageing stage (days 2 - 30) (Fig. 6.11e). The largest change was exhibited by *U. intestinalis* with a ¹⁵N depletion of 1.2 % (Fig. 6.14). Overall, the red algae showed net ¹⁵N enrichment during the decay of the initial living algae to that of the decomposed material, but only ca. 0.8 % (Table 6.8), and these were not significant changes (Table 6.10). There were significant differences between the initial δ^{15} N values and the 30-day decomposed algae for S. muticum, U. intestinalis and the mixed algae (Table 6.8). The former experienced a 1.3 % ¹⁵N enrichment, whilst the latter two ^{15}N depletions (-0.9 and -0.7 ‰, respectively). The $\delta^{15}N$ values of the aerobicallydecayed macroalgae changed generally more than in the initial leaching stage (days 0 - 2) (Table 6.9). All but S. muticum experienced net depletion of ¹⁵N, more than in the first two days. C. crispus experienced the largest ¹⁵N depletion of 2.3 ‰, giving an end signature of 10.1 ‰; however this was only 1.5 % less than the original signature due to the enrichment of ¹⁵N in the leaching stage. S. muticum experienced a 1 % enrichment of ¹⁵N during the ageing stage, a similar order to the anaerobically-decayed individuals; there was a net ¹⁵N depletion of 0.3 % from the living specimen, this contrasted to the net ¹⁵N enrichment of 1.3 ‰ in the laboratory (Table 6.8).

Table 6.9 One-way ANOVA (degrees of freedom: 1, 5) results for the statistical comparison of δ^{13} C and δ^{15} N values (n = 3) for between living and 30-day anaerobically decomposed macroalgae. *p < 0.05, **p < 0.01, **NS** = not significant (p > 0.05).

	δ	¹³ C		6 ¹⁵ N
Anaerobic Decay	MS	F	MS	F
S. muticum	1.08	13.00*	2.52	13.30*
C. crispus	18.83	10.21*	1.17	7.05 NS
U. intestinalis	0.11	0.69 NS	1.17	10.11*
O. pinnatifida	9.00	38.85**	1.06	4.38 NS
Mixed Algae	0.03	0.52 NS	0.75	25.68**

Naturally-decayed vs. experimentally-decayed macroalgae

The C and N elemental composition of the living and anaerobically-decayed macroalgae were significantly higher than the naturally-decayed algae from Elmer beach for the same time period (July 2006; Fig. 6.14a). The elemental composition of the naturally-decayed macroalgae was very low, with a C value of 11.8 % \pm 3 and a N value of 0.96 % \pm 0.2. During the initial leaching stages (0 - 2 days) of decay all anaerobically-decayed macroalgae exhibited a combined depletion in N and C towards that of the naturally-decayed macroalgae. Then during the ageing process (2 to 30 days), there were gains in the elemental composition of the anaerobically-decayed macroalgae, which was not similar to the naturally-decayed macroalgae's elemental composition.

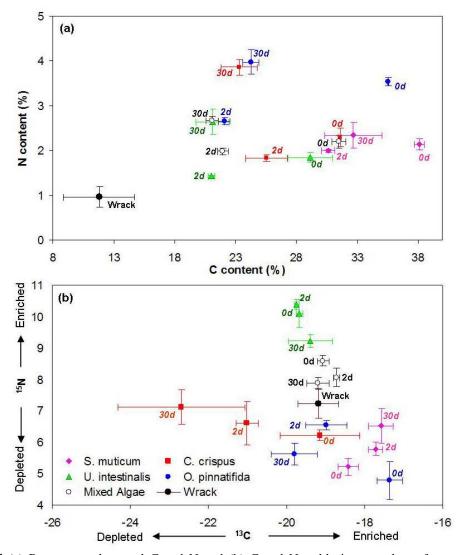


Figure 6.14 (a) Percentage elemental C and N and (b) C and N stable isotope plots of naturally decayed macroalgae at Elmer, living macroalgae (0d), initial detritus (2d) and end detritus (30d) during the anaerobic decay of *S. muticum*, *C. crispus*, *U. intestinalis*, *O. pinnatifida*, and mixed macroalgae. Values are means \pm SD.

6.4 Discussion

6.4.1 Processes of Macroalgae Decay

A variety of macroalgal species, including *Sargassum muticum*, *Ulva intestinalis*, *Chondrus crispus*, and *Osmundea pinnatifida*, form large quantities of decaying macroalgae deposits on the beach at Elmer. Aerobic field and anaerobic laboratory experiments were conducted with these four species to study the changes in elemental and stable isotope composition of the plant matter and surrounding medium during the leaching and ageing processes of decay. This study has shown that the processes of deposited macroalgae decomposition to be complex and highly variable, and could depend on the composition and mix of the macroalgae, interactions between water chemistry (pH, C and N leachate material), microbial activity (via temperature changes) and detritivorous macrofauna. Furthermore, the site-specific environmental conditions such as: anaerobic (e.g. strandline and sediment buried decaying macroalgae) and aerobic conditions (e.g. mobile decaying macroalgae on the mid-shore), as well as the time of year (influences of temperature) will dictate the rate of decay.

Carbon and nitrogen isotope ratios were measured for the most dominant macroalgae species in the beach deposits. The results showed that the macroalgae isotope values were very variable and although there were some distinctively different species (e.g. Halidrys siliquosa, Ceramium sp.), it would be hard to infer which detritivores are feeding on which species of macroalgae if this were to be investigated. The filamentous subtidal red seaweeds appeared to be distinctively depleted in 13 C values. Any species feeding off these would show a low δ^{13} C value reflecting their diet, for example, Dauby et al. (1998) showed that Aplysia depilans (Cuvier) fed off ¹³C depleted subtidal seaweeds and exhibited a δ^{13} C isotopic value of -29.0 %. The bulk mixture of decaying macroalgae from the three months sampled varied in their taxonomic composition and had distinct δ^{13} C and δ^{15} N isotopic values. The δ^{13} C and δ^{15} N values did not appear to represent the values of the most dominant algae in the samples (that were determined for the eighteen most dominant species; see Fig. 6.10), suggesting that when macroalgae decays together, different processes occur and may result in a different δ^{13} C and δ^{15} N values. The seasonal change in isotope composition of the mixed macroalgae samples illustrates a temporal variation in isotope values of likely detrital inputs to the diet of local herbivores and detritivores, which compounds the difficulty of assessing the food web contribution derived from the macroalgae. The taxonomic composition changed over time, but it was not possible to link the bulk isotope values with the percentage portions of species. This suggests that when a mixture of macroalgae decays together the breakdown of individual algae will be affected by slightly different processes. It is likely that it will be dependent on the decay stages of each algal species in the mixture, as they will not all be in the same stage.

The decomposition of macrophyte detritus is principally a function of the chemical composition of the initial source material (Rice & Tenore 1981). Sargassum muticum and Osmundea pinnatifida had the highest C content (38.1 and 35.6 %, respectively) of the four species, with Ulva intestinalis the lowest (29.1 %). The latter species also had the lowest N levels (1.9 %), whilst Osmundea pinnatifida had the highest (3.5 %). The nitrogen content is dependent on several factors such as age of the plant, light availability, nutrient conditions and plays a major influence on the processes and rates of detrital decomposition (Tenore et al. 1984, Buchsbaum et al. 1991). Plant material high in soluble ash, organic nitrogen and other hydrolysable components are easily degraded (Rice & Tenore 1981). The observed rapid loss of mass and carbon early in the decomposition process of these experiments has been attributed in previous studies to the simple leaching of hydrolysable organic and inorganic substances (Kucera 1959, Boyd 1970, Koop et al. 1982), such as carbohydrates (agar, carageenan) and lipids. The lability of detrital carbon is largely a function of the quantity and quality of lignocellulose detrital walls (Benner et al. 1984, Wilson et al. 1985). Most of the carbon lost from the macroalgae detritus during the laboratory and field experiments were lost within the first 2 weeks.

After simple leaching ceased (i.e. about 2 days, Machas et al. 2006), the algal detritus becomes more suitable for microbes to colonise. Koop et al. (1982) and Robertson & Hansen (1982) found that dissolved organic carbon released from decomposing aquatic macroalgae, declines to less than 10-20 % of the initial value, owing to microbial uptake. Blum & Mills (1991) illustrated the direct rapid response between microbial abundances and productivity, and the loss of seagrass detritus. They calculated a carbon budget, suggesting that during the first 14 days of seagrass decay that the detritus-associated bacterial activity accounted for less than 10 % of the detrital carbon, in comparison with later stages of decay, where ca. 53 % of the detrital carbon flowed through the bacterial loop. Thus, microbial biomass rich in proteins can be assumed to account for the carbon influxes observed in the latter stages of decay, particularly in aerobic decay, where oxygen is not a limiting factor for microbial communities.

Nitrogen is clearly gained and lost from the detrital system. Following the initial leaching of nitrogen from the cell walls in the first few days, the concentrations increased in all macroalgae types during the ageing stage (days 2 - 30) of both anaerobic and aerobic decay; this has previously been observed in other studies (Tenore et al. 1984). In conjunction with this nitrogen increase, the temperature rapidly increased during the leaching stage and was maintained for the duration of the decay process. Furthermore, the pH of the decay medium became noticeably acidic (in particular for *Sargassum muticum*) before returning to a more neutral environment after a month. These observations could be attributed to either the microbial colonization of the decomposing material through extracellular microbial excretions (Hobbie & Lee 1980), such as the binding of carbohydrates and phenolic plant constituents to microbial proteins (Tenore & Hanson 1980), or the bio-chemical immobilization of protein into non-soluble complexes (Buchsbaum et al. 1991). Similar pH changes were observed by (Pellikaan 1984) for decaying seagrasses; it was suggested that the probable cause was the formation of organic acids by microbial action in anaerobic micro-sites within the damaged cells, followed by a gradual pH increase from the uptake of these organic acids by the bacteria.

The detritus derived from Sargassum muticum, Chondrus crispus, Ulva intestinalis, Osmundea pinnatifida and the mix of all four macroalgae obviously gained more nitrogen by production of microbial biomass than they lost to the seawater medium. The fixation of nitrogen reduces the mineralization rate of nitrogen in relation to that of carbon, causing the nitrogen concentrations in the detritus to increase, thus explaining the decreasing C: N ratio. Rice & Tenore (1981) found similar results in vascular plant detritus but the opposite response in easily decomposed macroalgal detritus. However, contrasting to this, but in concurrence with the findings of this study, Stuart et al. (1982) observed a decrease in the C:N ratio of Laminaria pallida Greville detritus caused by microbial enrichment, and furthermore, Robinson et al. (1982) observed a decrease in C:N ratios of decomposing Laminaria longicruris detritus and attributed it to a preferential use of more easily digestible nitrogen compounds. Changes in the N content and the C:N ratio are held to difficult to interpret because leaching of soluble components, nutrient enrichment of the particulate detritus by microbial colonization and formation of structural protein-like compounds can occur simultaneously (Pellikaan 1984).

The observed differences in N and C fluxes during the decay process for the different macroalgae species may indicate a difference in the size of the microbial populations. For

example, *Sargassum muticum* experienced the lowest leaching of nitrogen in anaerobic decay, as well as a slow and gradual increase in nitrogen levels during the ageing stage and extremely acidic conditions in the surrounding media. For aerobic decay the large amount of nitrogen initially leached and the subsequently large increase would suggest that this species provides unfavourable conditions for anaerobic microbes due to the potentially slow colonization of the detritus in comparison with aerobic conditions. It was the opposite story for *Chondrus crispus*, *Ulva intestinalis*, and *Osmundea pinnatifida*, for these species the decay was quicker in anaerobic conditions, also observed by Tenore et al. (1984). This may have been due in part to the low levels of phenolic constituents (Buchsbaum et al. 1991).

These results indicate that for certain algal species anaerobic conditions cause the bacterial growth and activity in decomposing macroalgae to be much lower than under aerobic conditions. This has been confirmed by Godschalk & Wetzel (1978) who stated that the presence of oxygen assured a rapid removal of labile *Zostera* leachates, but in part, it has been shown that under anaerobic conditions the metabolism of available carbon is exhausted more quickly than under aerobic conditions (Tenore et al. 1984). The dissimilarity between aerobic and anaerobic conditions may be attributed to differences in the type, timing and degree of microbial activity and preferential degradation (Lehmann et al. 2002). The difference found in decay rates and processes for the different types of macroalgae, have potentially significant consequences for the ecosystem. In summer periods, high temperatures induce faster decay rates (Jedrzejczak 2002), and if the dominant macroalgae are filamentous reds and greens (as observed in summer 2004 at Elmer) the detritus will be nutrient rich and experience fast release of carbon and growth of microbial populations, thus attracting detritivores (Danovaro et al. 1999, Manini et al. 2003). However, at other times of the year when there are lower, temperatures and the decaying macroalgae deposits are dominated by tough algae (e.g. Chondrus crispus), the nutrient availability will be lower, except for the strandline, where more anaerobic decay occurs, speeding up the decay of species such as Chondrus crispus. The limiting factor of the transfer of carbon to higher trophic levels is the source and quality of the organic inputs, the capability of the system to mobilise organic matter pools, and the ability of the benthic bacteria to convert the mobilised carbon into bacterial biomass (Danovaro 1999).

The size and direction of $\delta^{13}C$ and $\delta^{15}N$ changes during decay for the macroalgae species studied were shown to be very variable. There was no predictable ^{13}C or ^{15}N depletion in

association with the amount of C and N in the detritus. Furthermore, the variation in δ^{13} C and δ^{15} N values for the four species was often large (e.g. *Chondrus crispus*) and unpredictable. There was however, within species consistency in the decay response for the δ^{13} C and δ^{15} N isotopes, providing evidence that the responses that were observed were reproducible for these species. In addition, both the red algae *Chondrus crispus* and *Osmundea pinnatifida* exhibited similar patterns of δ^{13} C and δ^{15} N changes during decay; both being 13 C depleted and 15 N enriched, suggesting that species from the major algal groupings respond in a similar manner.

Studies of the changes in δ^{13} C and δ^{15} N values during decomposition, for vascular plants, have shown that mangroves show little δ^{13} C change but a marked reduction in δ^{15} N (Zieman et al. 1984); the salt marsh species *Spartina alterniflora* showed declines in both δ^{13} C values (Benner et al. 1987) and δ^{15} N values (Currin et al. 1995); and seagrass *Zostera noltii* showed little change in either δ^{13} C or δ^{15} N values during the initial stages of decay (Machas et al. 2006). The differences in the changes between each of the macroalgae in this study and vascular plants in other studies could perhaps be explained by the species-specific differences in plant tissue and different microbial utilization of detritus.

The changes in δ^{13} C values during algal decomposition may result from the differential decay of polysaccharide and lignocellulose components of the original material (Machas et al. 2006). A decline in the δ^{13} C value of an algal species with decay time can either be explained by the preferential removal of an organic matter fraction enriched in ¹³C or the gain of components depleted in ¹³C (Fenton & Ritz 1988). Lignin has depleted ¹³C values and when it decomposes results in a lower δ^{13} C value in plants with higher lignin content. Although macroalgae lack true lignin (Siegel & Siegel 1973, Swain 1979, Ragan & Glombitza 1986), it was suggested that those vascular plants that had slow-growing leaves with higher amounts of lignin should show significant shifts in δ^{13} C values during decomposition (Cebrian & Duarte 1998). The theory by Cebrian & Duarte (1998) may also apply to the more complex structured red macroalgae species. Furthermore, carbohydrates and proteins are generally enriched, and lipids are depleted in ¹³C compared to total plant tissue (Degens 1969, Deines 1980). Selective loss of carbohydrates and proteins, which are particularly susceptible to microbial degradation (Hedges et al. 1988, Harvey et al. 1995), would lead to a decrease in the δ^{13} C value of residual organic matter. Ulva intestinalis did not show a significant change in δ^{13} C after decay, perhaps because of its relatively simple cell wall structure that lacks phenolics (Siegel & Siegel 1973). In contrast, *Chondrus crispus* and *Osmundea pinnatifida* showed the largest change and variation in δ^{13} C values; this may have been for a number of reasons, for example because of their composite cartilaginous structure (Swain 1979), and the fact that red algae decays faster than brown and green algae (Rice & Tenore 1981). When leaching and microbial breakdown occurs, and complex carbohydrates and proteins are lost, the residual matter should become considerably depleted in 13 C.

The changes in $\delta^{15}N$ values reported during the decomposition of vascular plants were accounted for by the microbial immobilization of N from environmental sources (Zieman et al. 1984, Wilson et al. 1986, Fourqurean & Schrlau 2003). The isotopic shift in $\delta^{15}N$ values depends on several factors: the initial N content (Zieman et al. 1984), the nature of the microbial community (Lehmann et al. 2002) and the isotopic composition of the dissolved inorganic nitrogen (DIN) assimilated by the microbial community (Caraco et al. 1998). The N content of the macroalgae species in this study were initially small (1.9 to 3.5 %), and even lower than those small amounts found in seagrasses (ca. 3.7 %; (Machas et al. 2006). Therefore, the growth of microbes may be enough to change the $\delta^{15}N$ values during decomposition (Zieman et al. 1984, Wilson et al. 1986). During the first two days of anaerobic incubation, the $\delta^{15}N$ values of the algal species increased (with the exception of the mixed batch), whilst relatively large losses of N were observed. After 30 days decay, only the *Ulva intestinalis* and the mixed batch had depleted ¹⁵N values, of about 0.84 and 0.71 ‰ (respectively) below the initial values, whereas the Chondrus crispus, Osmundea pinnatifida, and Sargassum muticum had enriched ¹⁵N values (by 0.89, 0.84, and 1.3 ‰, respectively). These results indicate that N loss and gain does not necessarily coincide with large changes in isotopic composition. The nitrogen increases and decreases probably relate to the type of bacterial growth that is occurring, resulting in the addition of ¹⁵N-enriched and/or ¹⁵N-depleted biomass to the remaining material. In addition, the mixed batch responded differently from the individual species, showing that when algae decay together, the decay process may be changed to the mix of nutrients, microbes and release of constituents.

Sargassum muticum was the only species that had significantly different $\delta^{13}C$ and $\delta^{15}N$ values when fresh, to that of 30 day decayed samples; however, it was enriched in both ^{13}C and ^{15}N after decay, which was not as predicted. Species differences in the patterns of isotope decomposition may be partially due to their differing abilities to resist desiccation in the

environment. These results clarify the need for more detailed analyses of potential sources of variability when stable carbon and nitrogen isotopes of decayed macroalgae are used in food web studies. Most macrophyte production passes through a detrital phase before it is consumed by animals. Hence, it is of great interest to know whether any change in stable isotope values accompanies the decomposition of macrophyte tissue. Nevertheless, it has often been used without any recognition of potential variability. Although there was no overlap in carbon and nitrogen isotope values between the species investigated in detail here, there may have been overlap with other macroalgae. As also shown in this study, if the composition of decaying macroalgae pool is very variable (the range of values is large) then the values of each species may not be significantly different, thus limiting the use δ^{13} C and δ^{15} N isotope analyses in tracing mixed detritus through the foodweb. However, δ^{13} C and δ^{15} N analysis still represents a useful tool for tracing the movement of detritus in coastal food webs, providing attention is given to the magnitude and causes of isotopic variability.

6.4.2 Role of Fauna in Decomposition

The findings of the biomass decay field-study clearly indicate differential mass loss of decaying macroalgae deposits due to decay, mechanical loss from the mesh bags and the role of colonizing fauna in the decomposition processes. Greater biomass loss was exhibited in the initial stages of decay with a 50 % reduction in decaying macroalgae deposits after 12 days, and on average only a further 30 % after 23 days. The experiments on the loss of nutrients during decomposition in both the field and laboratory illustrated that approximately 10 to 40 %, depending on the macroalgae composition, of the macroalgae carbon content was lost in the first two days due to leaching, microbial growth, fragmentation and loss. Studies on the decomposition of strandline decaying macroalgae at high shore levels have found shorter decay cycles (ranging from 10 to 14 days) than this study, which was 30 days (McLachlan 1980, Griffiths & Stenton-Dozey 1981, Koop et al. 1982). The difference in the speed of decay between previous strandline studies and the results of this study could be because of the presence of increased anaerobic conditions in strandline conditions in comparison with aerated and mechanically decaying floating macroalgae.

Another contributory factor to this differential biomass loss over time was the rapid colonization by the detritivorous amphipod *Gammarus locusta* found in the mid-intertidal zone, which was

seen in large numbers after the initial stage of decay but was then only present in negligible numbers following this. Fresh deposits attract amphipods and isopods, followed by predatory species (Colombini et al. 2000). The number of *Gammarus locusta* processing the macroalgae (shredding and grazing) declined after the biomass had been reduced to ca. 50 %, to be replaced by species consuming fine particulate matter (e.g. juvenile *Carcinus maenas*) as the study advanced, which reflects the increasing fragmentation of the decomposing material. Estimates of ingestion rates for *G. locusta* have also been shown that when approximately 50 % of the total available macroalgae deposits are consumed they are succeeded by other grazing species (Moore & Francis 1985, Créacha et al. 1997). The large mesh size (10 mm) permitted slightly larger abundance of macrofauna, especially amphipods to invade the decaying macroalgae deposits. Mann (1972) showed that the larger the abundance of macrofauna associated with decaying macroalgae, the more accelerated the level of microbial activity and more importantly the increased grazing activity increases the rate of mechanical breakdown of particles. This and the loss of greater proportions of smaller fragments from the larger mesh size (10 mm), could explain the faster decay rates seen in comparison with the smaller mesh bags (5 mm).

6.5 Conclusions and Future Recommendations

This study of isotopic variability within and between different species of decaying macroalgae was initiated to test the hypothesis that the assumption that the isotopic composition of fresh source plant carbon and nitrogen becomes depleted in ¹³C and ¹⁵N on decay, thus providing significantly different isotope composition, which could be used for foodweb analysis. The results showed that the isotopic value of a macroalgal species does change during decomposition for carbon and nitrogen, but is both species and time dependent, and there appears to be no obvious overall predictable change. In terms of food web analysis the results so far indicate that carbon and nitrogen isotopes alone could not be used to determine which state the plant was in when consumed, due to the complexity involved during the process of decay. However, this does not preclude further investigation into this topic.

Future studies should study the decay of macroalgae over longer periods, to see if depleted ¹³C and ¹⁵N values are eventually reached, and particularly to link the depletion of ¹⁵N with that shown by POM, so that the trophic position of the decaying macroalgae in the detrital pool is understood. Furthermore, it is necessary to understand the role that bacteria and fungi play in

the decay of macroalgae, as there are still unanswered questions, such as: How bacteria and fungi change the δ^{13} C and δ^{15} N values of macroalgae during decay? When faunal species ingest macroalgae detritus, do they assimilate the isotopic value of the bacteria and fungi or a combination of the macroalgae and bacteria? Experimental study is ideally required to answer these questions. In addition, culturing anaerobic and aerobic bacteria, and understanding the differences between and within these populations during the decay of different macroalgae groups should be determined, and if possible their carbon and nitrogen isotope signatures.

Chapter 7: Algal Detritus in Food Webs around CDSs

7.1 Introduction

Macrofaunal species associated with decaying macroalgae occupy a range of trophic levels, including primary consumers, scavengers, and predators (Griffiths et al. 1983). Primary consumers include deposit feeders, such as spionid polychaetes and amphipods such as *Bathyporeia* spp., which utilise phytoplankton and associated particulate organic material; and herbivores / detritivores, such as talitrid amphipods, isopods, and insects, which consume drift macrophytes and other stranded material (Dugan et al. 2003). Secondary consumers include crabs, isopods, polychaetes, and beetles, which prey upon primary consumers of both types and feed on drift carrion. Vertebrate predators, such as shorebirds and fish, utilize all of the trophic levels in both branches of this food web as prey (Dugan et al. 2003). Changes in the availability and input of macrophytes could shift the faunal community structure and alter energy flow for consumers and prey availability to higher trophic levels (Dugan et al. 2003).

Earlier in this study, it was shown that the influx of decaying macroalgae deposits into the intertidal zone at Elmer was correlated with the population abundances of some sediment infaunal deposit feeders (e.g. *Arenicola marina*, *Bathyporeia sarsi* and *Bathyporeia pilosa*); however, the structure and composition of these communities appeared to be unrelated (Chapter 4). Furthermore, the presence of the decaying macroalgae in the surf zone has been shown to benefit the surf-zone fauna by providing a food source and increasing habitat complexity (Robertson & Lenanton 1984, Van der Merwe & McLachlan 1987, Crawley et al. 2006, Crawley & Hyndes 2007). These findings suggest that this allocthonous food supply could influence the food chain around the Elmer breakwater system. Indeed, this may be of particular importance to the juvenile mobile fauna in this tidal zone, such as commercially important fish and crustaceans (see Airoldi et al. 2005, Martin et al. 2005). In this chapter, the aim was to determine, directly, using carbon and nitrogen stable isotope ratios, the impact of the decayed detrital material on the foodwebs around the low-crested breakwaters at Elmer and the groynes at Felpham.

The significance of macrophyte-derived detritus as a source of organic carbon and nitrogen for subtidal consumers was illustrated by Stuart et al. (1982), Mann (1988), Fielding & Davis (1989) and for rocky shore consumers e.g. Bustamante & Branch (1996). There have also been studies on the decomposition of high-shore macrophyte debris (strandline) for sandy beaches (e.g. Backlund 1945, Griffiths & Stenton-Dozey 1981, Koop et al. 1982, Stenton-Dozey & Griffiths 1983, Hansen 1985). Food web dynamics in the intertidal zone were studied by Adin & Riera (2003), Dugan et al. (2003), Mews et al. (2006) and Olabarria et al. (2007). But only Gauthier et al. (2007) have considered the nutritional importance of decaying macroalgae deposits on the mid-intertidal area of beaches and the role artificial structures play in this process. However, Gauthier et al. 2007 did not investigate detrital decay processes, which is an important aspect of ecosystem functioning and thus requires further consideration.

7.1.1 Use of Isotopes for Studying Food Webs

Stable isotopes can be used to understand food webs and the flux of organic matter through ecosystems by comparing the carbon and nitrogen isotope ratios of consumers to their likely food resources, or primary producers, during trophic interactions. The abundance and the variability in naturally occurring carbon (C) and nitrogen (N) stable isotopes make these elements well-suited for such ecological studies. The basis of stable isotope analysis in food web studies can be summarised thus: organisms reflect the stable isotope signals of the food they assimilate (i.e. 'they are what they eat' plus a few per mil), a phenomenon demonstrated almost thirty years ago by DeNiro & Epstein (1978). For nitrogen isotope values, the difference between the tissues of the producer and the consumer is controlled by excretion of urine (by the consumer), which contains less ¹⁵N than dietary material (producer's tissues), leaving the assimilated nitrogen relatively enriched in ^{15}N compared with diet (a $\delta^{15}N$ difference of 2-3 ‰). The ¹³C:¹²C ratios in organisms higher up the food web will reflect that of their food resources and the stable isotope ratios in the primary producers at the bottom of the food web. Dietary carbon isotope fractionation is less predictable and often not measurable in comparison to nitrogen, and depends on the tissue being analysed. There is no measurable δ^{13} C fractionation from producer to consumer for muscle tissue, but fractionation ca. 0.5 - 1.5 % is observed in other tissues (DeNiro & Epstein 1978, Peterson & Fry 1987). This process of carbon or nitrogen isotope fractionation between producers and consumers leads to increasing enrichment with increasing trophic level and thus food web studies can determine trophic interactions (DeNiro &

Epstein 1978, McConnaughey & McRoy 1979, Rau et al. 1983, Fry & Sherr 1984, Minagawa & Wada 1984).

Using stable isotopes it is possible to resolve trophic pathways in detrital systems. To be able to identify the carbon or nitrogen contribution of decaying macroalgae to CDS foodwebs, it is necessary for this material to be isotopically distinct from living macroalgae. The information gathered on the changes in the $\delta^{13}C$ and $\delta^{15}N$ for decaying macroalgae in Chapter 6 was used to infer the importance of decayed algae in the food web around breakwaters at Elmer and groynes at Felpham beach, by studying if a range of consumers were enriched with naturally-decaying algal isotope values.

The general aim of this study was to see if it was possible to determine which macrofaunal species utilised macroalgae detritus as a food source for ecosystems on and around two different coastal defence systems: Elmer Beach, a beach with a low crested breakwater scheme, which at certain times of the year receives decaying macroalgae deposits in large (> 60 % beach cover) quantities, and Felpham Beach, a groyne field covered beach, which receives less (< 20 % beach cover) decaying macroalgae deposits than at Elmer. Similarities and differences that were found between these two ecosystems are also discussed. The specific objectives were:

- 1. To test the hypotheses, that there were differences in carbon and nitrogen stable isotope values:
 - i. Between comparable food sources and macrofaunal species at Felpham and Elmer (see Table 7.1);
 - ii. Between rockpool and rockface species present on the LCSs at Elmer;
 - iii. Between rockpool and rockface species present on the groynes at Felpham
 - iv. Between Elmer and Felpham rockpool and rockface species; and
 - v. Among deposits of decaying macroalgae at different times of the year.
- To determine whether the dominant species found colonising the decaying macroalgae (e.g. grazers and detritivores), as well as sediment surface deposit feeders and rocky shore grazers were using decaying macroalgae as a food source.

 To establish how far stable isotope analysis can be used in the understanding of detrital pathways in ecosystems with complex compositional sources of macroalgae-derived detritus.

Table 7.1 Samples taken for the food web survey at Elmer and Felpham Beaches in September 2006 for SIA. Grey boxes denote samples not taken; as not present at the relevant site at time of sampling.

			of replicate nples
		Elmer	Felpham
	Water Particulate Organic Matter (POM) Sedimentary Organic Matter	6	6
	(SOM)	6	6
	Green Surface SOM	6	6
Potential food sources	Bulk Decaying Macroalgae	8	8
	Biofilm	6	6
	Strandline Bank - Surface	6	
	Strandline Bank - Bottom	6	
	Enteromorpha spp.		6
	Porphyra spp.		6
	Juvenile Fucus spiralis.		6
	P. vulgata - Rockface	6	6
	P. vulgata - Rockpool	6	6
Breakwater hard substrata	L. littorea - Rockface	6	6
species	L. littorea - Rockpool	6	6
	G. umbilicalis - Rockface	6	
	G. umbilicalis - Rockpool	6	
Deposited macroalgae	Gammarus locusta	6	
species	Idotea	6	
High-water strandline	Dipteran fly larvae	6	
species	Orchestia gammarellus	6	
Sediment infaunal species	Arenicola marina	6	6

7.2 Methods

7.2.1 Study Sites

The study locations for the foodweb surveys were Elmer Beach and Felpham Beach, on the West Sussex coastline near Bognor Regis on south coast of England (Fig. 7.1). The beach at Elmer, with its low crested breakwater scheme, has been the main focus of this thesis, and Felpham, with its groyne field, one of the comparative sites. The environmental setting of these

beaches is discussed in detail in Chapters 1 and 2. Elmer Beach received deposits of decaying macroalgae throughout the year (2005-2006), estimated at 600-2,300 kg / m² / yr (see section 3.4), overall this was three times the amount as at Felpham, which was estimated at 200-800 kg / m² / yr. At Elmer, deposits were found to be larger in the summer months (800-2,700 kg / m² / yr) than in the winter months (400-1,500 kg / m² / yr). The potential importance of this dominant allochthonous source for the food web at Elmer Beach (incorporating the CDSs and the surrounding sediments), in comparison with at Felpham Beach, was the reasoning behind the following investigation.

7.2.2 Field Foodweb Survey

A foodweb survey was carried out to test the hypothesis that the faunal species both on the breakwaters and in the environment surrounding them utilise the decaying macroalgae that is deposited regularly throughout the scheme at Elmer (see Chapter 3 for dominant deposit timings). The survey incorporated all available food sources and representative macrofaunal species from (i) on and within the sediment of the beach surrounding the CDSs, (ii) on the CDSs, and (iii) the high water mark strandline (Fig. 7.1).

Table 7.1 shows the species sampled from Elmer and Felpham. Six replicate samples were taken for each food source (except for the decaying macroalgae deposits, where n=8) and eight samples for each macrofaunal species. There were some differences in the food resources and faunal species showed between the two sites. At Felpham there were smaller quantities of deposited decaying macroalgae and no strandline in comparison to that recorded at Elmer. In addition, no *Gibbula umbilicalis* were found on either of the two rock groynes at Felpham so, this species was omitted from this site. However, there were additional food sources found on the boulders at Felpham did not occur within the sample area at Elmer (Table 7.1). Three sediment infaunal species were chosen for the survey: *Arenicola marina*, *Bathyporeia sarsi* and *Spio filicornis*. However, after collecting and sieving half a tonne of sediment from both Elmer and Felpham, the latter two species were found to occur in limited numbers; not enough for this survey, therefore, *Arenicola marina* was the only species analysed from the sediment communities.



Figure 7.1 Aerial maps of (a) Elmer Beach and (b) Felpham Beach on the West Sussex coast with the areas from which the food sources and macrofaunal species were sampled.

It was hypothesised that there would be differences in the isotope values between rockface and rockpool fauna due to availability of different food sources. Rockface species refers to species found on the flat boulder faces that make up the majority of the breakwaters, whilst the rockpool species refers the small boulders around the toe of the breakwaters, where there are numerous rock pools. From field observations it appeared that different foods were available to these species; on the rockfaces gastropods appear to be reliant on biofilm as a food source, whereas in the toe of the breakwaters, macrofauna could utilise decaying macroalgae which was deposited and trapped forming thick layers in crevices (Fig. 7.2).

Seasonal variation in macroalgal species composition was observed throughout the duration of the ecological surveys (Chapter 3); whereby the macroalgal deposits of one season can be dominated by ephemeral green algae (> 60 %) and at other times it would comprise of more

than 70 % of red algae (see section 3.3.2). Preliminary carbon isotope values results differentiated (with only a small overlap) between Chlorophyta (greens), Phaeophyta (browns) and Rhodophyta (reds) macroalgal groupings. Consequently, it was hypothesised that carbon and nitrogen isotope ratios would permit the tracing of trapped decaying macroalgae through the foodweb. Based on seasonal variation, the species composition of the macroalgae deposited was tested by measuring the isotope values of the mixed batches of macroalgae (May 2005, July 2005 and September 2006; see Chapter 6), controlling for the combined percentage combination of greens to browns to reds.



Figure 7.2 Decaying macroalgae deposits around the base of the breakwaters at Elmer (23rd July 2005).

7.2.3 Collection and Preparation of Samples for Stable Isotope Analysis

7.2.3.1 Macroalgal samples

Eight samples of approximately 100 g of deposited decaying macroalgae were collected from randomly chosen locations on both Elmer and Felpham beaches on 21st of September 2006 (Fig. 7.1). Samples of approximately 100 g of strandline decaying macroalgae were also collected from Elmer; six samples from the upper strandline, and six from the lower strandline (Table 7.1). The samples were collected in individual plastic bags and transported back to the laboratory in a cool box. Samples of decaying macroalgae had also been collected in the same manner from May and July 2005 (kept frozen at ca. –30° C). The macroalgae were sifted through for any macrofaunal species present, and subsequently removed. They were then frozen (ca. –30° C) and freeze-dried in separate acidified plastic bags; they were not rinsed in distilled water, as the samples had been in the decaying experiment had (see section 6.2.4.1), as this way

they were kept in the state that they are found on the beach, without removing, for example, the bacteria.

7.2.3.2 Biofilm samples

Small rock samples or chippings of rocks were collected from the CDSs from both Elmer and Felpham. These were brought back to the laboratory where they were flushed with filtered seawater to remove any excess sediment and then the biofilm was brushed off with an acidified soft brush. The seawater containing the scraped biofilm was then filtered and processed using the procedure in section 6.2.4.3.

7.2.3.3 Particulate organic matter

Seawater samples were collected from the field in 2 L acid (4 % HCl) washed glass bottles from a depth of ca. 20 cm below the water's surface to analyse the suspended particulate organic matter (POM). Within 2 hours of collection, the water samples were filtered through precombusted Whatman GF/F glass fibre filters to collect the POM for stable isotope analysis (SIA). Each of the filters were then acidified with HCl (10 %) in order to remove carbonates, rinsed thoroughly with distilled water, wrapped in tinfoil, frozen for 1 hour, freeze-dried and finally, kept in a dessicator until analysis.

7.2.3.4 Sedimentary organic matter

Sedimentary organic matter (SOM) samples were collected from the field by taking sediment cores (1 cm diameter, 10 cm depth) and the benthic diatoms on the sediment surface were collected by scraping the top 1 mm. These samples were then brought back to the lab where they were dried at 60° C for 24 to 48 hours and sieved using the Wentworth procedure and the grain size analysis recorded. The < 63 μ m portion was then retained as the SOM sample (as this portion is closely correlated with the organic matter content (Riera & Hubas 2003), and excluded any large fragments of macroalgae) and stored in glass vials in a dessicator for further preparation (see section 7.2.4).

7.2.3.5 Macrofaunal samples

Macrofaunal samples for the foodweb survey were collected from Elmer and Felpham (Table 7.1). The gastropods: *Littorina littorea*, *Gibbula umbilicalis* and *Patella vulgata* were collected from the rockfaces and rockpools on the east end of breakwater 4 at Elmer, and the former two species from the east facing side of groyne 1 (see Fig. 7.1), so that the aspect to wave exposure was kept the same. The tidal height for each level (rockface and rockpool) was kept comparable between the replicate samples from each site and between the different sites. They were transported back in buckets of filtered seawater. Sediment fauna were collected from the midintertidal shore level (lower landward) by taking 50 randomly chosen cores (surface area: 57 cm²; depth: 10 cm) from each beach, and stored in plastic buckets. Large macroalgae samples were collected at Elmer Beach: (i) from the mid-intertidal for the freshly deposited decaying macroalgae, and (ii) from the HWSM strandline; these were stored in plastic bags in a cool box until return to the laboratory. *Gammarus locusta* specimens were picked out of the midintertidal decaying macroalgae, and *Orchestia gammarellus* and dipteran fly larvae from the strandline decaying macroalgae.

All the fauna were starved for 24 hours so that the gut contents were cleared. The soft body tissues for *L. littorea*, *Gibbula umbilicalis* and *P. vulgata* species were removed from their shells for the analysis. All samples were then rinsed and any remaining debris was manually removed under a dissecting microscope. The fauna were individually placed on precombusted Whatman GF/F glass fibre filters, with the exception of the dipteran fly larvae and *Gammarus locusta*, which were pooled, 3 individuals per filter, because of their small size. They were briefly rinsed with distilled water, frozen (ca. –30° C), freeze-dried and stored in a dessicator until further preparation (see section 7.2.4).

7.2.4 Homogenisation and De-calcification of Samples

The final stage in the preparation was to grind the samples to a homogenous powder and remove any carbonates present in samples containing carbonates (e.g. sediments and crustacean samples) (see section 6.2.4 for further details). Dried macroalgae, macrofaunal, and sediment samples were pulverized in a ceramic pestle with a mortar and stored in acid washed (4 % HCl) glass vials until analysis. The dried filtrate on the glass fibre filters for the POM, leachate and

biofilm samples was scraped off and then was also ground and stored in glass vials. The pestle and mortar was washed in 10 % ethanol and rinsed twice with distilled water between samples to prevent contamination. The ground samples were then weighed into a tin capsules (5 x 3.5 mm) using a Mettler Toledo micro balance prior to carbon and nitrogen isotope analyses by CF-IRMS (see sections 6.2.4 and 6.2.5 in Chapter 6 for further details). Table 7.2 shows the weights of powdered material needed for successful SIA (determined by preliminary runs).

Table 7.2 Weight of powdered samples in tin capsules (5 x 3.5 mm) for SIA.

Samples	Weight (mg)
Macrofauna	0.7 - 0.8
Macroalgae	1.3 - 1.5
Sediments	60
Filtrate samples (POM,	1.5 - 2 (dark-colour)
biofilm, leachate)	2.5 - 3 (light-colour)

7.2.5 Stable Isotope Analysis Technique

Carbon and nitrogen isotope ratios of all the samples for the food web survey were measured simultaneously by CF-IRMS (for a detailed description, please refer to section 6.2.5).

7.2.6 Data Analyses

The differences in the $\delta^{15}N$ and $\delta^{13}C$ values of food sources and macrofaunal species between Elmer and Felpham beaches were tested using one-way analysis of variance (ANOVA), as were the differences between species found on the rockfaces and in the rockpools of the CDS at these two sites (Table 7.3). Furthermore, the differences in values between different months of bulk decayed macroalgae were tested using one-way analysis of variance (Table 7.3). All data were tested for normality using the Kolmogorov-Smirnov test, and where necessary data were arcsine percentage square root transformed. When ANOVA indicated significant differences among means, SNK *post hoc* test was used to distinguish between them. All parametric ANOVAs used SPSS (SPSS 2005).

Table 7.3 Four hypotheses (see section 7.1) were tested using a series of one-way analysis of variances (ANOVA).

1) Food Sources & Species: Elmer vs. Felpham Foodweb

Benthic microalgae

POM

Deposited decaying macroalgae

Biofilm

Patella vulgata

Littorina littorea

Arenicola marina

2) Elmer: Rockpool vs. Rockface CDS Species

Patella vulgata

Littorina littorea

Gibbula umbilicalis

3) Felpham: Rockpool vs. Rockface CDS Species

Patella vulgata

Littorina littorea

4) **Decaying Macroalgae Deposits:** Temporal Differences

May 2005

July 2005

September 2006

7.2.7 ISOSOURCE modelling

Mixing models can be used to determine the isotopic contribution of food sources in a consumer's tissues and thus determine the relative contributions to the consumer's diet. The ISOSOURCE model (Phillips & Gregg 2003) allows the possible contribution of a range of sources using an iterative approach to calculate all possible feasible solutions for any given sources and isotopic mixtures, generating a distribution of feasible solutions. The mean δ^{13} C and δ^{15} N values for the macrofaunal species (Table 7.1) sampled at both Felpham and Elmer beaches in September 2006 were used in the analysis. Values were first adjusted for trophic fractionation (1.5 for δ^{13} C and 3.4 δ^{15} N) using accredited fractionation values determined from literature sources (DeNiro & Epstein 1978, Rau et al. 1983, Peterson & Fry 1987, Inger et al. 2006) before input to ISOSOURCE. The δ^{13} C and δ^{15} N values for the potential food sources (Table 7.1) were input as sources. Source increments of 1 % and a mass balance tolerance of \pm 0.1 were set (with the exception of *O. gammarellus*: 2 % and \pm 0.5, respectively). The results from ISOSOURCE enable the quantification (in percent) of the proportion of different food sources in the macrofaunal species' diets for the two different beaches.

7.3 Results

7.3.1 Foodweb Survey

The range of δ^{13} C and δ^{15} N values of the available food sources on and around the CDS at Elmer and Felpham Beaches for the CDS fauna, macroalgae-associated fauna and sediment fauna are presented in Table 7.4. The primary producers at the Elmer and Felpham were similar; however, there was some macroalgae species growing on the rocks in the areas sampled on the CDSs at Felpham and not at Elmer, whereas there was no established strandline at Felpham that was present at Elmer (Table 7.4).

Table 7.4 δ^{13} C and δ^{15} N (range of values) of the available food sources on and around the CDS at Elmer and Felpham Beaches for the CDS fauna, macroalgae-associated fauna and sediment fauna in September 2006.

	Elmer			Felpham		
Samples	δ ¹³ C	$\delta^{15}N$	n	δ^{13} C	$\delta^{15} N$	n
Food Sources						
SOM	−88.5 to −2.7	7.8 to 12.0	6	−23.5 to −21.6	5.8 to 8.3	6
Surface Benthic Algae	-20.2 to -17.2	3.9 to 6.0	6	−22.5 to −21.9	4.9 to 6.8	6
POM	-21.1 to -20.8	7.2 to 8.4	6	-21.9 to -19.7	7.8 to 9.4	6
Deposited Decaying						
Macroalgae	-20.6 to -16.6	9.0 to 11.5	8	-27.7 to -16.8	8.2 to 13.4	8
Biofilm	-21.9 to -18.1	5.7 to 8.0	6	-20.5 to -19.2	8.6 to 12.4	6
Top of Strandline	-21.7 to -19.3	9.4 to 10.0	6	-	-	-
Bottom of Strandline	-21.2 to -20.3	8.8 to 9.7	6	-	-	-
Enteromorpha sp.	-	-	-	-18.1 to -17.7	16.5 to 17.2	6
Porphyra sp.	-	-	-	-22.6 to -21.4	16.3 to 17.9	6
Fucus sp. (Juv)	-	-	-	-17.8 to -17.0	13.9 to 14.6	6
CDS Species						
P. vulgata - Rockface	-16.8 to -14.4	10.8 to 11.8	8	-18.8 to -17.1	12.8 to 14.6	8
P. vulgata - Rockpool	-17.1 to -15.1	9.5 to 11.1	8	-16.5 to -14.9	11.2 to 12.5	8
L. littorea - Rockface	-18.6 to -16.4	10.0 to 11.4	8	-18.7 to -17.8	13.3 to 15.1	8
L. littorea - Rockpool	-18.6 to -17.8	11.0 to 11.9	8	-18.8 to -17.8	12.1 to 14.4	8
G. umbilicalis - Rockface	-18.1 to -17.1	9.9 to 11.3	8	-	-	-
G. umbilicalis - Rockpool	-17.3 to -16.6	9.1 to 10.7	8	-	-	-
Algae -Associated						
Gammarus locusta	−20.4 to −19.2	9.5 to 11.6	8	-	-	-
Idotea baltica	−20.2 to −19.2	10.3 to 12.5	8	-	-	-
Dipteran Fly Larvae	-20.7 to -20.3	9.6 to 10.7	8	-	-	-
Orchestia gammarellus	−19.5 to −18.5	10.8 to 12.8	8	-	-	-
Sediment Species						
Arenicola marina	-18.2 to -16.6	11.4 to 13.6	8	−18.2 to −17.1	11.4 to 12.8	8

7.3.1.1 Water column POM $\delta^{13}C$ and $\delta^{15}N$ values

The δ^{13} C values of the water column POM did not differ between the Elmer and Felpham beaches (-21.0 vs. -20.1‰, p = 0.15; Table 7.5), even though the range of δ^{13} C values were larger at Felpham beach (2.2 ‰) that at Elmer (0.3 ‰); this can be seen in Table 7.4 and Figure 7.3. There were however, significant differences in the δ^{15} N values of the POM between the two beaches (7.6 vs. 8.9 ‰, p = 0.003); the δ^{15} N value of the POM in the water column at Felpham beach was 1.3 ‰ higher than at Elmer (Fig. 7.3 & 7.5).

7.3.1.2 Sedimentary organic matter (SOM) δ^{13} C and δ^{15} N values

The average δ^{13} C value of the SOM at Felpham was -22.3 ‰, whereas the value at Elmer was -25.0 ‰. These results would not have been significantly different if analysed, as the δ^{13} C range for the SOM samples at Elmer were extremely large from -88.5 ‰ to -2.7 ‰ (Table 7.4) overlapping the range at Felpham. The results from the SOM samples (n = 6) at Elmer were obviously not correct. The extreme δ^{13} C values at Elmer may have been because the samples were too large, with higher carbon content than the largest standard gel, and were therefore, outside the linearity corrections. In contrast, there were significant differences ($F_{1, 11} = 9.95$, p = 0.01) in the δ^{15} N values between the beaches at Elmer and Felpham (9.1 vs. 6.8 ‰), with the sediments being more enriched at Elmer by 2.3 ‰ (Fig. 7.6).

Table 7.5 Results from a series of one-way analysis of variance testing differences in the δ^{13} C and δ^{15} N values between Elmer and Felpham beaches. *p < 0.05, **p < 0.01, ***p < 0.001, **NS** = not significant (p > 0.05). n = 8 for each species and n = 6 for each food source. df = 1 for all (total 11 for n = 6 and 15 for n = 8).

	δ ¹³ C		$\delta^{15}N$	
Elmer vs. Felpham	\overline{F}	p	F	р
Benthic micro algae	17.90	0.05**	9.60	0.21*
POM	2.46	0.148 NS	15.72	0.003***
Decaying Macroalgae Deposits	7.02	0.19*	0.58	0.457 NS
Biofilm	0.17	0.692 NS	11.37	0.12*

7.3.1.3 Primary producer $\delta^{13}C$ and $\delta^{15}N$ values

On the seaward sides of the CDS at Felpham there were three macroalgae taxa (*Enteromorpha* sp., *Fucus* sp., and *Porphyra* sp.) present. The average δ^{13} C values for the juvenile *Fucus* plants

and *Enteromorpha* sp. (now named *Ulva* sp.) were similar (-17.4 and -17.9 ‰, respectively), whilst the δ^{13} C values for the red alga *Porphyra* sp. were lower (-21.9 ‰; Fig. 7.4). The δ^{13} C values of these three algae were significantly different from each other (F_{2, 17} = 387.2, p < 0.001) because of the small range of values for each species (see Table 7.4). The δ^{15} N values also differed significantly (F_{2, 17} = 115.0, p < 0.001), with the values for the juvenile *Fucus* plants being lower in δ^{15} N (14.2 ‰; Fig. 7.4) than for *Enteromorpha* sp. and *Porphyra* sp., which did not differ from each other (16.98 and 17.00 ‰, respectively) (Fig. 7.5).

Both the δ^{13} C and δ^{15} N values recorded for the benthic microalgae differed between Elmer and Felpham beaches (–19.1 vs. –22.2 ‰ and 4.3 vs. 5.8 ‰, respectively; Table 7.5 and Figure 7.3). The benthic microalgae at Elmer had higher δ^{13} C values in comparison to that at Felpham, but a lower δ^{15} N value (Fig. 7.3). The range of δ^{13} C values for the benthic microalgae was much larger at Elmer than at Felpham (3.0 vs. 0.6 ‰; Table 7.4), whilst the δ^{13} C and δ^{15} N values of the latter were similar to the SOM value (Table 7.4; Fig. 7.4). The surface sediment at Elmer was noticeably discoloured with green benthic microalgae at the time of sampling; this was not the case at Felpham.

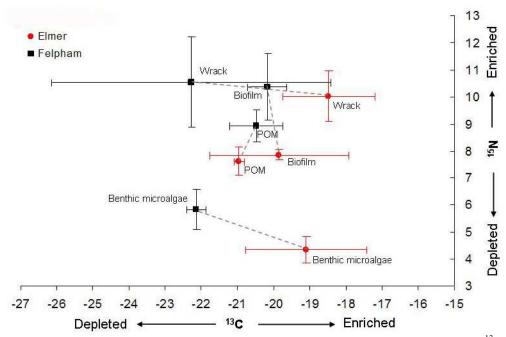


Figure 7.3 The differences between Elmer and Felpham beaches in the available food source $\delta^{13}C$ vs. $\delta^{15}N$ (‰; means \pm SD) values for September 2006. (- - -) marks the difference between the two sites in $\delta^{13}C$ and $\delta^{15}N$ values.

7.3.1.4 Decaying macroalgae deposit δ^{13} C and δ^{15} N values

At Elmer, decaying macroalgae deposits are left on the beach on a receding tide (see Chapter 3), and at the time of sampling (21^{st} September 2006) the beach had received relatively large quantities (ca. 60 % beach coverage; Chapter 3). The dominant species were *Ectocarpus* sp. (59 \pm 4.5 %), *Chondrus crispus* (25 ± 3.8 %), and *Ulva* sp. (3 ± 0.2 %) and the remaining macroalgae were filamentous reds and browns (e.g. *Calliblepharis ciliata*, *Halidrys scoparia*, *Griffithsia* sp.); this gave the decaying macroalgae deposits an intermediate δ^{13} C value of -18.5 %. The small range of δ^{13} C values (-20.6 to -16.6 %) demonstrate the domination of brown algae in the deposits. The overall δ^{15} N value of the decaying macroalgae deposits at Elmer was 10.0 %, again the range of values exhibited was small (2.5 %).

At Felpham on the other hand, the amount of decaying macroalgae deposits on the beach was extremely small (ca. < 1 % beach coverage; author's pers. obs.), with only enough decaying macroalgae deposits for eight samples (ca. 20 g dry weight). The composition in comparison with that at Elmer was very variable, resulting in a wide range of δ^{13} C values, from a low value of -27.7 % (95 % red, 5 % brown) to a high value of -16.8 % (80 % brown, 20 % red). The range of δ^{13} C values shown in Table 7.3 was large because of the large variation in the ratio of brown to red macroalgae for the eight samples. *Griffithsia* sp. was the most consistently dominant algae (dominated 70 % of the samples); in a couple of the samples used in the analysis *Laminaria* sp. and *Fucus spiralis* were dominant. The decaying macroalgae deposits composition on average comprised of 66 % red and 34 % brown macroalgae, giving an average δ^{13} C value of -22.3 % (Table 7.4), which was significantly different from that at Elmer (F_{1,11} = 7.02, p = 0.019). The δ^{15} N values of the decaying macroalgae at Felpham did not differ from those δ^{15} N values for the algae at Elmer (10.6 %, Table 7.4), though there was a greater range, from a low value of 8.2 % to a high value of 13.5 % (Fig. 7.6).

There was an established decaying macroalgae bank (strandline) at the HWSM at Elmer but not at Felpham. The δ^{13} C and δ^{15} N values of the strandline did not differ between the top and bottom of the strandline (δ^{13} C: -20.4 vs. -20.7 ‰, p = 0.45; δ^{15} N: 9.6 vs. 9.2 ‰, p = 0.058). The ranges of values shown in Table 7.4 suggest that the top of the strandline had higher δ^{13} C and δ^{15} N values, with these values perhaps becoming lower with depth. The δ^{13} C values of the strandline macroalgae were significantly ($F_{2, 19} = 11.14$, p = 0.001) lower (by ca. 1 ‰) than the

values of the recently deposited decaying macroalgae on the rest of the shore. By contrast, there were no significant differences in the $\delta^{15}N$ values (p=0.08), though the range was largest for the fresher beach decaying macroalgae deposits (2.5 ‰) and smallest in the bottom of the strandline (0.9 ‰; Table 7.3, Fig. 7.5).

7.3.1.5 CDS macrofaunal δ^{13} C and δ^{15} N values

The respective $\delta^{13}C$ and $\delta^{15}N$ values from both Elmer and Felpham beaches for the gastropods on the CDS rockfaces and in the rockpools were plotted against each other and are shown in Figure 7.4. Overall, the $\delta^{15}N$ values showed significant differences between rockpool and rockface locations for each of the gastropods at both sites (Table 7.6, Fig. 7.5). Whereas, the $\delta^{13}C$ values did not demonstrate as many differences, this can be seen from Figure 7.3; where there was much overlap between species from the different tidal zones, it shows that there was much overlap in their food resources.

Table 7.6 Results from a series of one-way analysis of variances testing differences in the δ^{13} C and δ^{15} N values for firstly between rockpool and rockface macrofauna at each site, and secondly between macrofauna at Elmer and Felpham beaches in rockpools, on rockfaces and in the sediment. *p < 0.05, **p < 0.01, ***p < 0.001, **NS** = not significant (p > 0.05).

	δ	5 ¹³ C	δ	$\delta^{15}N$		
	F	p	F	p		
Rockpool vs. Rockface						
Elmer	0.062	0.81 NS	3.39	0.073 NS		
P. vulgata	0.03	0.86 NS	14.49	0.02**		
L. littorea	2.97	0.11 NS	9.59	0.08***		
G. umbilicalis	27.58	0.0001***	5.76	0.031*		
Felpham	10.697	0.03**	46.43	0.0001***		
P. vulgata	95.00	0.0001***	49.35	0.0001***		
L. littorea	0.97	0.34 NS	8.95	0.01**		
G. umbilicalis	-	-	-	-		
Elmer vs. Felpham	3.73	0.067	180.25	0.0001***		
P. vulgata (RF)	33.39	0.0001***	122.13	0.0001***		
P. vulgata (RP)	1.66	0.218 NS	34.51	0.0001***		
L. littorea (RF)	6.83	0.020*	166.99	0.0001***		
L. littorea (RP)	0.20	0.658 NS	58.08	0.0001***		
Arenicola marina	7.93	0.14*	12.42	0.003**		

At Elmer, the gastropods *Patella vulgata* and *Littorina littorea* living on the rockfaces and in the rockpools exhibited no differences in δ^{13} C values (*P. vulgata*: –15.7 vs. –15.8 ‰, p = 0.86; *L. littorea*: –17.8 vs. –18.2 ‰, p = 0.11, respectively; Table 7.6), whereas the gastropod *Gibbula*

umbilicalis on the rockfaces had a δ^{13} C value statistically greater than that recorded in the rockpools (-17.6 vs. -16.8 ‰, p < 0.001). Regarding their δ^{15} N values, all three gastropods exhibited significant differences between the rockfaces and the rockpools (Table 7.6); *Gibbula umbilicalis* and *Patella vulgata* in the rockpools were more ¹⁵N depleted than those on the rockfaces (10.1 vs. 10.7 ‰, p < 0.001; 10.4 vs. 11.2 ‰, p = 0.002, respectively; Fig. 7.5), but this between tidal height difference was reversed for *Littorina littorea*, where individuals living in the rockpools exhibited more enriched ¹⁵N values than on the rockfaces (-18.2 vs. -18.0 ‰, p = 0.008). However, this small discrepancy is likely to be biologically insignificant (Fig. 7.4).

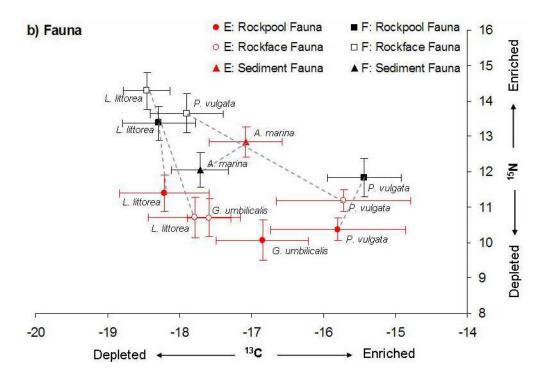


Figure 7.4 The differences in macrofaunal $\delta^{13}C$ vs. $\delta^{15}N$ (‰; means \pm SD) values between Elmer (red) and Felpham (black) beaches for the CDSs (rockpool and rockface specimens) and sediment fauna for September 2006 (---) marks the difference between the two sites in $\delta^{13}C$ and $\delta^{15}N$ values.

On the whole, the fauna at Felpham showed significant differences in the δ^{15} N values between the rockfaces and rockpools (14.0 vs. 12.6 ‰, p < 0.001); individuals on the rockfaces were more 15 N enriched than in the rockpools (Fig. 7.5). Only *Patella vulgata* exhibited a significant difference in both δ^{13} C and δ^{15} N values between those individuals living on the rockfaces and those in the rockpools (δ^{13} C: -17.9 vs. -15.4 ‰, p < 0.001; δ^{15} N: 13.6 vs. 11.8 ‰, p < 0.001). This species showed the largest tidal zone food resource partitioning for any of the gastropods at either site (Fig. 7.4), with individuals living in the rockpools being more 13 C enriched and 15 N depleted. Although *Littorina littorea* showed an overlap in δ^{13} C values for between the rockface

and rockpool individuals (-18.6 vs. -18.3 ‰, p = 0.34), zonal differences were exhibited in the δ^{15} N values (14.3 vs. 13.4 ‰, p = 0.01); with the rockface individuals again being more ¹⁵N enriched. *Littorina littorea* individuals from both tidal zones also overlapped food resources with rockface dwelling *Patella vulgata* (Fig. 7.4).

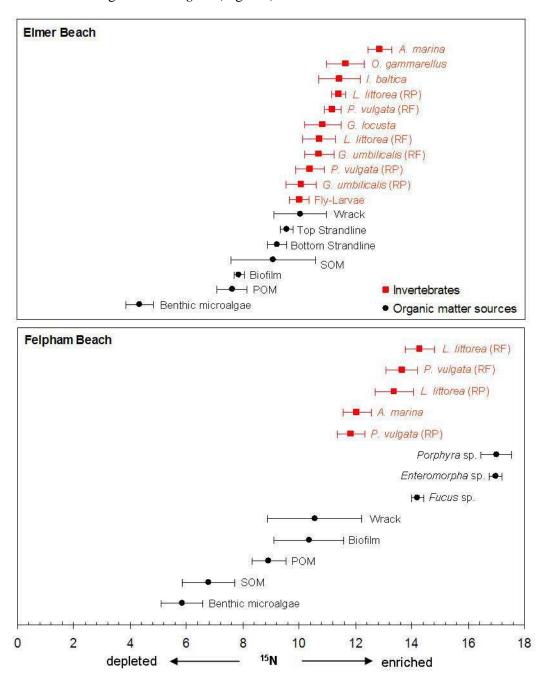


Figure 7.5 Sources of organic matter and invertebrates' $\delta^{15}N$ (‰) values (mean \pm SD) in the foodwebs around the coastal defence structures at Elmer and Felpham beaches for September 2007.

The gastropods on the groynes at Felpham were significantly more 15 N enriched than those on the breakwaters at Elmer (13.3 vs. 10.7 ‰, p < 0.001; Table 7.6). The largest difference was seen between *Littorina littorea* individuals on the rockfaces of the CDSs; where those at Felpham were 15 N enriched by 3.6 ‰, a whole trophic level. In contrast, there was no statistical difference in the overall δ^{13} C values of gastropods between the two sites; however, Figure 7.6 shows that there are more complex patterns to be explained.

There were no differences between the two sites in the δ^{13} C values for *Patella vulgata* and *Littorina littorea* individuals living in the rockpools (Table 7.6), there were however, for those living on the rockfaces. *Patella vulgata* individuals on rockfaces at Elmer exhibited a marked 2.2‰ enrichment in 13 C over those at Felpham (Fig. 7.4); whilst although statistical differences (p < 0.05) were seen for *Littorina littorea* individuals, the range of values in Table 7.3 show that there is much overlap (also seen in Fig. 7.4), but may not be biologically significant. There were, however, significant differences in the δ^{15} N values between Felpham and Elmer (Table 7.6, Fig. 7.5). The biggest differences were seen for the rockface *Patella vulgata* and *Littorina littorea* specimens, which were 2.5 and 3.6 ‰ more 15 N enriched at Felpham than Elmer; whilst those in the rockpools were still more enriched at Felpham but not to the same degree (1.5 and 2.0 ‰, respectively).

7.3.1.6 Sediment and algae-associated macrofaunal $\delta^{13}C$ and $\delta^{15}N$ values

The polychaete *Arenicola marina* was significantly more 13 C and 15 N enriched at Elmer than at Felpham (δ^{13} C: -17.1 vs. -17.7 ‰, p = 0.014; δ^{15} N: 12.8 vs. 12.0 ‰, p = 0.003; Fig. 7.4), though there appears to be some resource overlap (Table 7.4). The patterns seen for the gastropods between Elmer and Felpham (see Section 7.3.1.5) were not see for *Arenicola marina*; instead those at Elmer were more enriched than at Felpham but to a lesser degree than the gastropods (0.8 ‰).

The amphipod *Gammarus locusta* and isopod *Idotea baltica* found living in the deposited decaying macroalgae at Elmer exhibited the same δ^{13} C value (-19.8 %; Fig. 7.6a) and had very similar δ^{15} N values (10.8 vs. 11.4 %, p = 0.11), though the range of δ^{15} N values indicates that *Idotea baltica* was slightly more enriched (Fig. 7.5 & 7.6). The talitrid amphipod found living in the strandline macroalgae at Elmer was trophically similar to *Idotea baltica*, with a δ^{15} N value

of 11.6 ‰, whereas δ^{13} C was significantly more enriched (by 0.8 ‰), with the δ^{13} C values of the individuals ranging from –19.5 to –18.5 ‰; showing small resource range (Fig. 7.6a). The dipteran fly larvae differed from the amphipods and isopod in having more 13 C and 15 N depleted values (δ^{13} C: by –0.7 to –1.5 ‰, p < 0.001; δ^{15} N: by 0.8 to 1.6 ‰, p < 0.001; Fig. 7.6a).

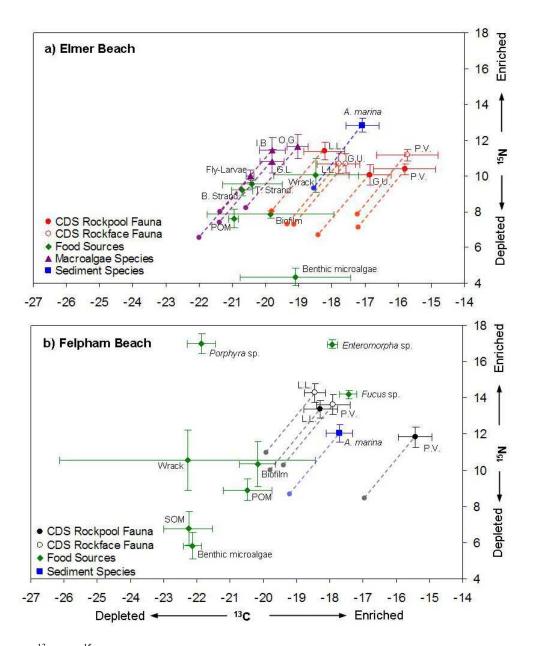


Figure 7.6 δ^{13} C vs. δ^{15} N (means \pm SD) for the available food sources on and around the CDS at (a) Elmer and (b) Felpham beaches for the CDS fauna, macroalgae-associated fauna and sediment fauna for September 2006. (--- and ---) Lines of trophic enrichment of δ^{13} C and δ^{15} N resulting in • and •, which are the average δ^{13} C and δ^{15} N values corresponding to the theoretical food source for each of the faunal species taking into account the trophic enrichment of 1.5 and 3.4 % for δ^{13} C and δ^{15} N, respectively. L.L. = *Littorina littorea*; P.V. = *Patella vulgata*; G.U. = *Gibbula umbilicalis*; O.G. = *Orchestia gammarellus*; G.L. = *Gammarus locusta*; I.B. = *Idotea baltica*; T. Strand. = Top layer of the strandline; B. Strand. = Bottom layer of the strandline; SOM = Sedimentary organic matter; POM = Particulate organic matter.

7.3.2 ISOSOURCE Analysis of the Foodwebs at Elmer and Felpham Beaches

At first glance, the trophically enriched isotope values of the gastropods on the CDS rockfaces at both sites (Fig. 7.6) appear to indicate a primary contribution of biofilm to the diet, with the exception of *Patella vulgata*. However, the results from the linear mixing equations (Phillips 2001) estimated a more mixed diet (Table 7.7, Fig. 7.7). POM appeared to constitute the majority of the diet for *Littorina littorea* both on the rockfaces (RF) and in the rockpools (RP) at both Felpham (1 - 99th percentile: 2 - 71 % and 39 - 86 %, respectively) and Elmer (RF: 30 - 70 % and RP: 62 - 72 %), although contribution to those on the rockfaces were less precise and is perhaps more variable with time than in the rockpools.

Table 7.7 Contribution of food sources to the diets of *Arenicola marina*, *Littorina littorea* (RF¹ & RP²), *Gibbula umbilicalis* (RF & RP) and *Orchestia gammarellus* at Elmer beach, and *A. marina*, *Patella vulgata* (RF), *L. littorea* (RF & RP) at Felpham beach. Values are shown as 1 - 99 percentiles for the corresponding distributions. The sampled food sources at Elmer beach could not account for any diet contributions for *P. vulgata* (RF & RP), *Gammarellus. locusta*, *Idotea baltica* and the kelp fly larvae, and neither at Felpham for *P. vulgata* (RP).

- 10							
Food Source		Contribution to the diet 1-99 percentiles (%)					
Elmer	A. marina	L. littorea (RF)	L. littorea (RP)	G. umbilicalis (RF)	G. umbilicalis (RP)	O. gammarellus	
Benthic microalgae	0-50	0-11	0-11	15-36	36-61	0-4	
POM Decaying	20-28	30-70	62-72	29-40	0-4	18-54	
Macroalgae	71-78	2-25	5-25	0-31	0-39	0-2	
Biofilm	-	0-67	0-31	0-53	0-62	-	
Top Strandline	-	-	-	-	-	0-12	
Bottom Strandline	-	-	-	-	-	0-20	

Felpham	A. marina	P. vulgata (RF)	L. littorea (RF)	L. littorea (RP)
SOM	0-12	-	-	-
Benthic microalgae	0-12	0-0	0-0	0-0
POM	86-98	48-80	2-71	39-86
Decaying				
Macroalgae	0-10	0-7	0-24	0-13
Biofilm	-	0-38	0-34	0-57
Enteromorpha sp.	-	0-9	0-4	0-10
Porphyra sp.	-	0-3	0-5	0-6
Fucus sp.	-	8-22	0-6	0-13

¹RF = rockface; ²RP = rockpool

Biofilm was calculated to be an important secondary food source (Table 7.7), along with decaying macroalgae, which appeared to be a reasonably important food source, contributing up to a quarter of their diet at times. At Felpham, the macroalgae living on the CDSs were

definitely minor components (< 13 %) in the littorinids' diet; this was not the case for rockface *P. vulgata* at Felpham, where instead there was an increased contribution from young *Fucus* sp. plants (8 - 22 %) and a reduced significance of the decaying macroalgae (0 - 7 %). Similarly though, POM was the main contributor to their diet (48 - 80 %), with biofilm an important secondary contributor.

The food sources for *Gibbula umbilicalis* were different from those of the littorinids, in that those on the rockfaces of the breakwaters at Elmer appeared to obtain the majority of their diet from a more proportional mixture of POM (29 - 40 %), biofilm (0 - 53 %), benthic microalgae (15 - 36 %) and decaying macroalgae (0 - 31 %), rather than feeding specifically on a single food source; the average estimated diet was dominated by benthic microalgae, followed by POM (Fig. 7.7). The diets of *G. umbilicalis* in the rockpools around the base of the breakwaters were predicted to comprise: (1) of benthic microalgae (36 - 61 %), twice the magnitude of those on the rockfaces, and (2) although more variably, from biofilm (0 - 62 %). Noticeably, POM was only a minor component (0-4 %), but decaying macroalgae was still of a similar order of importance and variability as for those on the rockfaces (0 - 39 %).

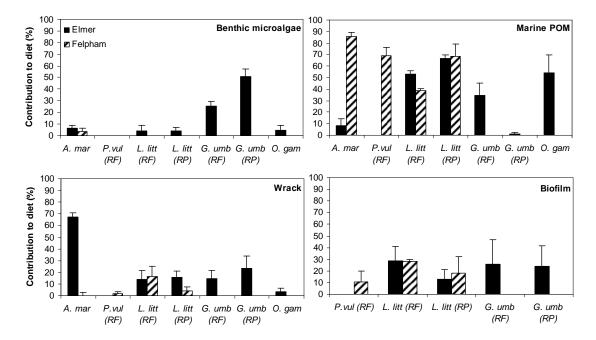


Figure 7.7 The differences in contribution of benthic microalgae, marine POM, decaying macroalgae (wrack) and biofilm to the diets of fauna sampled at Elmer (block) and Felpham (striped). Data from ISOSOURCE analysis (linear mixing equations could not be used on all species because there were no available food sources sampled). A. mar = A. marina, P. vul = P. vulgata, L. litt = L. littorea, G. umb. = G. umbilicalis, O. gam = O. gammarellus. RF = rockfaces and RP = rockpools.

For *Arenicola marina* the mean isotopic values for the dietary material exploited were predicted to be -19.1 and 9.4 % for δ^{13} C and δ^{15} N, respectively, at Elmer (Fig. 7.6a) and -19.7 and 8.6 % for δ^{13} C and δ^{15} N, respectively, at Felpham (Fig. 7.6b). With all the available food sources for each beach included in ISOSOURCE analysis (Table 7.6), the deposited decaying macroalgae appeared to be the primary food source for *A. marina* at Elmer (1 - 99th percentile: 71 - 78 %), whereas at Felpham, it was POM (86 - 98 %, also see Fig. 7.7). The benthic microalgae also contributed more to the diet at Elmer (0 - 50 %) than at Felpham (0 - 12 %), although it showed a larger range of variability.

At Elmer, for the diet of *Orchestia gammarellus* and dipteran fly larvae the predicted mean isotopic values were both more 13 C and 15 N depleted than the δ^{13} C and δ^{15} N values of the strandline (Fig. 7.6a), which is not as would have been expected. Instead, the expected δ^{13} C and δ^{15} N values for *O. gammarellus* were similar to the δ^{13} C and δ^{15} N values of the POM, and for the larvae there were no suggestible food resources sampled (Fig. 7.6a). In addition, the calculated isotopic mean values for both *Gammarellus locusta* and *Idotea baltica* were considerably more 13 C and 15 N depleted than that of the macroalgae deposits on the beach where they were found to be living. Their likely δ^{13} C and δ^{15} N values were instead close to the outside boundaries of the biofilm (ca. -22 and 8 ‰, respectively). ISOSOURCE analysis resulted in no suggestions of a mixing diet for *G. locusta*, *I. baltica*, or the kelp fly larvae. There was however, a modelled mixed diet for *O. gammarellus*, with primary contributions from POM (18 - 54 %) and not, as was expected, the freshly deposited decaying macroalgae (0 - 2 %). However, the decaying macroalgae in the strandline appeared to contribute a small but variable amount (0 - 32 %).

7.4 Discussion

In general, the δ^{13} C value of a tissue sample from an organism gives information on the primary energy source, while the δ^{15} N ratio allows the discrimination of trophic levels and can provide information about processing of nitrogen and therefore sources of nitrogen (Peterson and Fry, 1987). The main sources of organic matter at both Elmer and Felpham had relatively distinct δ^{13} C and δ^{15} N values, which enabled me to make inferences regarding the food sources used by the macrofauna investigated (Fig. 7.6). The potential stable isotope ratio of the diet of a consumer can be predicted by using a mean trophic δ^{13} C enrichment of 0.5 to 1.5 ‰ (Peterson

& Fry 1987, Inger et al. 2006) and a mean trophic 15 N enrichment of 3.4 ‰ (DeNiro & Epstein 1978), a fractionation effect which occurs between diet and consumer tissue as a result of the assimilation of food. The trophic enrichments in 13 C and 15 N for each macrofaunal species are shown in Figure 7.6 (dashed grey line). The closer the theoretical δ^{13} C and δ^{15} N values of a consumer's food is to that one of a single food source, the higher the proportion of that source in the diet of the consumer, as compared to other sources (Riera & Hubas 2003).

7.4.1 $\delta^{13}C$ and $\delta^{15}N$ Values of the Available Food Sources at Elmer and Felpham

The δ^{13} C values of the marine POM at both Felpham and Elmer were similar, and were close to the values given in the literature for oceanic phytoplankton. Gearing et al. (1984) compiled data for temperate regions and gave a mean value of -21.3 \(\infty\) within a range from -23.8 to -19.3 \(\infty\). The δ^{13} C values of the decaying macroalgae deposited on both beaches fell across this range, and it cannot therefore be suggested that this allochthonous source was excluded from the particulate organic carbon (POC) pool, as previously done in other studies e.g. Gauthier et al. (2007), Abreu et al. (2007). The range of δ^{13} C values for the biofilm at Elmer was large in comparison with Felpham and this may be because the makeup of the biofilm differed between the two sites. The angle of the CDSs to the approaching waves was the same for the two sites, so this can not be considered a significant causal factor. The diversity of the biofilm microorganism composition may have been more diverse (e.g. cyanobacteria, pinnate diatoms, ciliates and nematodes, microalgae; Thompson et al. 2005) because of the additional carbon influx to Elmer from the decaying macroalgae, as the carbon isotope values for diatoms have been shown to be dependent on dissolved inorganic carbon levels (Fry 1994). Another reason may be that the extreme small-scale variability of environmental conditions, surface properties and/or biological interactions influences the structuring of the biofilm communities, resulting in more diverse δ^{13} C isotope values. This is supported by culture studies that have found δ^{13} C differences both within and between species of microalgae in biofilms (Wong & Sackett 1978, Hinga et al. 1994). The δ^{13} C and δ^{15} N values of the deposited decaying macroalgae were more diverse at Felpham than Elmer. This was because of the differences in the composition of decaying macroalgae deposits; in comparison with at Felpham, Elmer showed greater species consistency due to the magnitude of macroalgae biomass deposited, therefore explaining the reduced variability in isotope values.

The SOM and POM had lower $\delta^{15}N$ values compared with the macroalgae primary producers (both living and decaying). These primary producers eventually contribute to the detrital organic matter pool, and must therefore become ¹⁵N depleted during decomposition; this theory was also suggested by McClelland and Valiela (1998). This assumption of ¹⁵N depletion during anaerobic decomposition was seen in this study for the anaerobically-decayed Ulva intestinalis and the mixed macroalgae, and aerobically-decayed Chondrus crispus, Ulva intestinalis, and Osmundea pinnatifida. However, in the samples an overall ¹⁵N enrichment was observed after 30 days (more so for anaerobic decay), it was interpreted to be because of microbial activity and assumed that over a longer period, after further decomposition, there would be a loss of ¹⁵N. This process can further be seen in the δ^{13} C and δ^{15} N values of the strandline, which were slightly more depleted in both ¹³C and ¹⁵N than the freshly deposited decaying algae on the rest of the beach, with the bottom of the strandline being more depleted than the top. The $\delta^{15}N$ values if this dietary material may help to determine which decay stage is most important in foodwebs. Interestingly, the $\delta^{15}N$ value of the SOM at Elmer was more ^{15}N enriched than at Felpham, with an overlap in the range of values with that of the decaying macroalgae both on the beach and in the strandline. This was not the case at Felpham, where the SOM was considerably more depleted in ¹⁵N than the macroalgae. A possible explanation for this difference is the large input of ¹⁵N from the decaying macroalgae at Elmer, and there will be ¹⁵N enrichment in sediments where POM has not been completely organically broken down. In comparison, Felpham does not receive the same degree of macroalgae deposits and therefore explain the lack of significant ¹⁵N enrichment in sediments.

The enriched 15 N values observed for the biofilm, benthic microalgae, and POM at Felpham, in comparison with those at Elmer, as well as the excessively high δ^{15} N values for the macroalgal species *Fucus* sp., *Porphyra* sp., and *Enteromorpha* sp. (14.2, 17.0, and 16.9 ‰, respectively) growing on the groynes at Felpham, was likely because of the close proximity to a sewage outfall (ca. 200m). Studies carried out on the influence of sewage effluent on the δ^{15} N signatures of macroalgae by Hobbie et al. (1990) and Gartner et al. (2002) support the theory that Felpham is a nitrogen-enriched ecosystem because of sewage outfall. Both studies measured increasing δ^{15} N values in macroalgae as a result of increasing incorporation of 15 N-rich NH₄ and NO₃ delivered by discharges of sewage treatment plants. The reason for slightly lower δ^{15} N values for the *Fucus* sp. in comparison with *Porphyra* sp. and *Enteromorpha* sp. may have been because it has lower nitrogen uptake, therefore requiring longer periods of exposure to

assimilate new nitrogen to alter the $\delta^{15}N$ value, especially as these were young plants. The latter two species are opportunistic fast growing species and respond more quickly to nitrogen availability (Gartner et al. 2002). It should be noted that the SOM at Felpham did not seem to be influenced by this discharge, as the $\delta^{15}N$ values were lower at Felpham than at Elmer where there was no sewage outfall. The higher $\delta^{15}N$ values at Elmer were probably due to the large quantities of decaying macroalgae. The difference in the source of nitrogen input into the two ecosystems at the two beaches is certainly reflected differently in the $\delta^{15}N$ values of the primary producers and consequently the consumers through nutrient assimilation. Thus, these results confirm that the local sewage effluent has an impact on the primary producers and grazers at Felpham, whereas the macroalgae deposits and POM are the sources of nitrogen entering the ecosystem at Elmer.

The absence of visible benthic microalgae mats at the surface of the sediment at Felpham beach in comparison with Elmer beach during sampling was not due to a lack of nitrogen, because this has been shown not to be a limiting factor because of the nearby sewage effluent. The CDSs is one possible factor contributing to this ecosystem variation, resulting in differences in the local hydrodynamics between Felpham and Elmer. Felpham does not retain the same quantities of decaying macroalgae and coarse particulate matter as at Elmer. Elmer also exhibits greater water retention and sediment temperatures in the summer during low tide because of its changed beach profile, a direct result of the CDS design. This difference in nutrient availability and residual water during low tide may have been the reason for the growth of benthic microalgae at Elmer and not Felpham. The δ^{13} C and δ^{15} N values of the benthic microalgae are therefore very similar to the SOM at Felpham. This could not be concluded for δ^{13} C values at Elmer because of the distortion in the SOM because of high quantities of carbon in the samples (data were not useable for analysis for SOM δ^{13} C values); however, the δ^{15} N values were considerably more different between the SOM and benthic microalgae at Elmer than at Felpham, suggesting that it would be the same for the δ^{13} C values.

7.4.2 Faunal Diets at Elmer and Felpham

The stronger ¹³C enrichment observed for *Patella vulgata* in the rockpools at both sites and on the rockfaces on the Elmer breakwaters could not be explained by a consumption of the sources sampled; Gauthier et al. (2007) found similarly high δ^{13} C values for *P. vulgata* on an artificial

rocky shore (-15.1 ‰) that could not be explained by POM, SOM or biofilm. There were also differing $\delta^{15}N$ values for this species between the rockfaces and rockpools at Elmer, with those in the latter location feeding on a source that was more ^{15}N depleted (ca. 1 ‰). One suggestion could be that more detrital material is being fed on, which is in the later stages of decay than found in the beach deposited macroalgae. This would explain the depletion in ^{15}N . In support of this, Bustamante and Branch (1996) observed two patellid species to predominantly feed on kelp-derived detritus rather than that of the intertidal algae or biofilm. Furthermore, specialist food selection may be exhibited for a specific species, e.g. *Fucus* sp.

Gibbula umbilicalis are known to have a mixed diet composed of microalgae and miscellaneous organic detritus (Dauby et al. 1998). Currin et al. (1995) estimated that benthic microalgae and dead *Spartina alterniflora* were the primary dietary components of *Littorina irrorata*, and ruled out contributions from phytoplankton and living macroalgae in a salt marsh in North Carolina. Gastropods have enzymes capable of degrading the resistant structural components of seaweeds such as cellulose (Owen 1966); thus the refractory nitrogen, which has been described as unavailable to decomposing organisms (Rice & Tenore 1981), may be assimilated by these organisms. However, it is possible that the benthic microalgae have similar δ^{13} C and δ^{15} N values to the microalgae in the biofilm on the rocks, which would also explain this result. *G. umbilicalis* may specifically ingest this proportion of the biofilm through the adherence of microalgae to their mucus trails, which some gastropods are known to re-ingest, whereas littorinids are not such specialists in ingesting microalgae (Edwards & Davies 2002).

Based on studies of gut content analysis, biofilm has always been considered the primary source of food for the gastropods sampled (Hawkins et al. 1989, Hill & Hawkins 1991, Thompson et al. 2005), but these results show differently, as did those of Gauthier et al. (2007). A possible explanation for these differences in diet may be related to differences in dietary specialisation of these three gastropods (*P. vulgata*, *Littorina littorea* and *G. umbilicalis*), as these species occur in the similar areas in the presence of the similar biofilms and suspended organic matter pool. Dittel (1997) and Abreu (2007) suggested that ingestion of specific food items from the biofilm is possible. If this is the case, these individual components may have different δ^{13} C values that are difficult to detect, as it was not within the scope of this study to separate the biofilm out to individual components for SIA. In addition it is known that the microbiota of biofilm show seasonal patterns with decreased abundances in the summer in comparison with the winter (Hill

& Hawkins 1991, Thompson et al. 2000, Jenkins & Hartnoll 2001). Therefore it is possible that the biofilm on these structures is a limiting resource and at certain times of the year the gastropods feeding patterns may change (this study only represents a single sample point in the year so potential seasonality in diets is not reflected in this data set).

Furthermore, the biofilm may be limited because of accumulation and scouring by the suspended sediments that were observed on both the breakwaters and groynes (pers. obs.); this is likely to prevent the rocky surfaces from being extensively colonized by biofilms (Gauthier et al. 2007). According to Levins (1968), the breadth of a species niche can be evaluated in terms of the availability of an important resource. Therefore, macro-detritus, micro-detritus, and phytoplankton may be more readily abundant at times and possibly of better nutritional value (Wilson 2002) resulting in an increased contribution to gastropod diets. Availability of detritus has been shown to exceed that of diatoms in the summer months making it a seasonally favourable food resource (Smith & Foreman 1984). These results show the broad niche-breadth of these gastropods, suggesting they utilize a wide variety of the available food resources. Gastropods, particularly limpets are known to feed off the propagules of macroalgae (e.g. *Fucus* sp.) that settle on rocky shores (Southward 1964, Hawkins & Hartnoll 1983, Thompson et al. 2000). The values of these young plants may not resemble those of adult plants, which has been something observed in kelp species (Duggins & Eckman 1997), and would have been mixed in with the biofilm values; the δ^{13} C of *P. vulgata* lie within the δ^{13} C range of *Fucus* sp.

The difference in food resource partitioning for *Arenicola marina* between Elmer and Felpham is most probably because of the availability of food resources; Elmer is rich in detrital allochthonous input where Felpham is not. It would be interesting to further investigate the seasonality of *A. marina*'s diet at these two beaches in accordance with the availability of deposited decaying macroalgae. It was shown in Chapter 4, that there was a correlation between amount of macroalgae deposited and the abundance of this species at Elmer; this foodweb analysis has further clarified the importance of the macroalgal detritus in the diet of this large surface deposit feeder in the sediments around the breakwaters at Elmer.

The macroalgae-associated species *Orchestia gammarellus*, *Gammarus locusta*, *Idotea baltica* and dipteran fly larvae sampled in this study are generally considered to be opportunistic consumers feeding mainly on living and dead macroalgae and occasionally small animals

(Backlund 1945, Moore & Francis 1985). Similar to findings by Dauby et al. (1998), the predicted δ^{13} C and δ^{15} N values for *O. gammarellus* were similar to the δ^{13} C and δ^{15} N values of the POM, instead of the decaying macroalgae. Gauthier et al. (2007) found considerable ¹⁵N depletion in *O. gammarellus* and *Chaetogammarus marinus* that excluded any significant dietary contribution from living macroalgae, comparable to the results of this study. One reason behind this may be that *O. gammarellus* was feeding on parts of the macroalgae, which had undergone more decay, and that are therefore more ¹⁵N depleted than those sampled, more like the macroalgal material found in the POM. An omnivorous feeding behaviour can be excluded, as a higher δ^{15} N value would have resulted. A potential dietary contribution from bacteria and fungi on the decaying macroalgae cannot, however, be excluded as has been suggested by Currin et al. (1995), as this may be giving the depleted ¹⁵N values with those observed for the amphipod species and dipteran fly larvae. Supporting this theory, there has been evidence that high amounts of bacteria (ca. 98 %) can be found in the gut contents of talitrid amphipods (Fenchel 1970). The latter two reasons are the most likely explanations observed for the kelp fly larvae, which are very ¹⁵N depleted, and in the order of the strandline macroalgae itself.

7.5 Conclusions and Future Research

Carbon and nitrogen stable isotope analysis for the identification of the dominant food resources in the foodweb around the breakwaters at Elmer and Felpham, revealed the use of macroalgae derived detritus, from different stages of macroalgal decay. The consumers displayed a large variety of feeding modes being predominantly detritivorous (POM and decaying macroalgae) rather than herbivorous (microalgae and living macroalgae), and seem to consume all food sources available. Mann (1972) was the first to consider that detritus derived from seaweeds might be an important food resource in coastal systems. The contribution of decaying macroalgae deposits in the diets of the gastropods discussed above is more consistent at Elmer than Felpham, correlating with the abundance of deposits. The importance of macroalgae detritus has been observed (Smith & Foreman 1984) but its importance has not been precluded because of a lack of information regarding its formation and availability. The ISOSOURCE modelling allowed this quantification for the rocky shore fauna (on the CDSs), sedimentary fauna and the fauna associated with the macroalgae deposits at Elmer and Felpham beaches. My study showed that areas that receive large quantities of macroalgae-derived detritus (e.g. Elmer Beach) relied on detrital organic matter more than areas that do not (e.g. Felpham Beach). This

would suggest that the faunal species within the ecosystem at Elmer have either adapted to these additional inputs or they are being used opportunistically. The latter suggestion is more likely, as shown by the rapid increase in benthic faunal abundances of amphipods following large deposits of decaying macroalgae (see Chapter 4 for more detail).

Temporal resource partitioning in detritus-based food chains results from differences in the rate at which detritus becomes available (Tenore & Hansen 1980, Tenore et al. 1984). That is, the food available to benthic detritivores at any given time is derived not only from newly produced detritus, but also from the decomposition products of ageing organic detritus produced previously. This makes assumptions regarding the carbon isotope values of macroalgae detritus extremely difficult, as the detritus composition changes with time: definitely on a monthly basis, and perhaps even more frequently. Also carbon composition of the detritus will vary with the decay stage of the organic material of which it is comprised. Furthermore, assimilation of this nutrient source into the tissues of a consumer may take some time, and the isotope values of these tissues may not directly reflect the composition of the decaying macroalgae sampled at the same time (but instead decaying macroalgae compositions from e.g. two weeks to a month ago). This may explain the difficulty experienced when trying to determine the food sources of the fauna associated with the decaying macroalgae (e.g. Gammarus locusta, Orchestia gammarellus and *Idotea baltica*), when past studies have shown (from experimental and stomach analysis) that they consume macroalgae. This demonstrates that the use of SIA to infer detrital pathways in a multi-source system has to be used with care, especially where highly variable detrital compositions occur. Temporal SIA studies of the changes in detritus from daily to monthly are a prerequisite for future studies of this ecosystem, combined with a better understanding of the assimilation time of nutrients utilized by the consumers, being studied, and tighter controls on some of the assumptions made in the ISOSOURCE models such as diet-tissue fractionation for gastropods and other species in this ecosystem.

Chapter 8: Summary of Major Findings

This general discussion briefly summarises the major findings of the thesis, followed by discussion of the management role of the decaying macroalgae deposits around coastal defence structures. Comments are then made on the limitations of the thesis, with suggestions for further work.

8.1 Summary

The present study has investigated the influence of a low crested breakwater scheme in modifying the deposition of allochthonous macroalgae, the benthic macrofaunal communities surrounding them and rocky shore communities colonising them, as well as how the macroalgae deposits decay and consequently enter the foodwebs of the surrounding ecosystems. Two neighbouring beaches were also investigated, to contextualise the geographical location of the breakwater scheme, though they were not ideal sites as they were defended with groynes and cannot therefore be considered as controls. A composite scientific approach was used, in order to investigate and understand these processes. The approaches were: (i) complex spatio-temporal field surveys of the biological assemblages on and around the CDSs and the depositions of decaying macroalgae, (ii) field and laboratory experiments to investigate the macroalgae decay processes with the use of stable isotope analysis; and (iii) food web surveys of the biological assemblages on the CDSs, in the surrounding sediments and the fauna associated with the decaying macroalgae through stable isotope analysis and IsoSource modelling. Analysis of these results has led to a greater understanding of the CDS modified ecosystem at Elmer.

Low crested breakwater structures are widely perceived to be capable of providing beach protection, and from an engineering perspective, do not have the adverse impacts often associated with more conventional structures such as revetments and groynes (Ranasinghe & Turner 2006). However, they still alter coastlines and may lead to the direct loss or alteration of intertidal and shallow subtidal habitats (Glasby & Connell 1999), or the provision of new habitat that may be exploited by marine biota (Glasby 1999a, Chapman & Bulleri 2003, Bulleri & Chapman 2004). This is particularly relevant in areas where no natural hard substrata occur,

such as the coast of south east England (e.g. Moschella et al. 2005) and on the Adriatic coast (e.g. Bacchiocchi & Airoldi 2003). CDSs may be considered to have a positive effect on local biodiversity of an area, in that the species added to an area due to the presence of CDSs would not usually be found there due to the absence of such a suitable habitat type (Pinn et al. 2005). Bacchiocchi and Airoldi (2003) suggested that artificial structures may act by changing the patterns of distribution of locally abundant species rather than by increasing species diversity.

The traditional view is that the biodiversity of soft sediment assemblages is less than that found on rocky shores (Hayward 2004). The low diversity that has been found on CDSs situated solely in the intertidal in both this study and others (Davis et al. 2002, Lamberti et al. 2005, Moschella et al. 2005, Pinn et al. 2005, Burcharth et al. 2007), makes this view questionable especially with respect to the artificial shore created by CDSs. Not only will the soft sediment assemblages be destroyed by where the CDSs are put in place, but, in addition, their presence also affects the community zonation patterns of the adjacent soft substratum. Breakwaters situated in the intertidal, such as those at Elmer, may directly affect the surrounding sedimentary habitats, through the change in the hydrodynamics of the system (e.g. Plomaritis 2006).

From an ecological point of view, the complex interactions between physical and ecological processes on and around these artificial structures has only become of recent interest ((Smith et al. 2001, Bacchiocchi & Airoldi 2003, Airoldi et al. 2005, Martin et al. 2005, Moschella et al. 2005, Pinn et al. 2005, Burcharth et al. 2007). The DELOS project (Burcharth et al. 2007) addressed and developed a good understanding of the assemblages on and around these structures. As a result of this multi-disciplinary project it became apparent that there was a lack of understanding of how these low crested breakwaters retain and influence the decaying macroalgae deposits that have been observed both in the UK and Spain, particularly when these deposits were not seen to occur to the same extent elsewhere on the adjacent coastline. The findings from this study gave indication that the breakwaters at Elmer beach retained more decaying macroalgae than wooden (Climping beach) or granite groynes (Felpham beach). However, due to the small spatial replication at Felpham and Climping, further work is needed to make statistically validate these findings. In addition, it was found that the amount of macroalgae influenced the abundances of the benthic fauna, particularly deposit feeders such as *Bathyporeia* spp. and *Arenicola marina*.

Biological assemblages typical of exposed shores colonised the landward and westward ends of the breakwaters at Elmer, where exposure was high, and assemblages on the landward sides of the breakwaters were typical of more sheltered shores because they were protected by the structures. The eastward ends of the structures showed the highest diversity, motile species abundances and sessile cover; this may reflect their moderate exposure to wave action, exhibiting intermediate levels of disturbance (Sousa 1979). These areas were just in the lee from extreme wave and sun exposure, but not too sheltered to cut off food and larval supply (Chapter 5).

The low crested breakwater scheme at Elmer is a stable dynamic system, with interacting tide and wave processes and with resultant sediment transport processes (Plomaritis 2006). The localised tidal currents were shown to be an important driver influencing the deposition timings of decaying macroalgae (Chapter 3) and the benthic communities surrounding the structures (Chapter 4), whilst wave action was an important driver influencing the biological assemblages on the structures (Chapter 5),

What may have been a relatively uniform beach, prior to the establishment of these structures, with a typical concave shore profile similar to beaches along the rest of the coastline with simple vertical shore zonation patterns and benthic assemblages, is now a complex area with undulating tombolos and bays, resulting from complex tidally-driven currents. These variations in shore elevation mean that the beach has both vertical and horizontal shore zonation gradients and distributions patterns. The benthic assemblage structure at Elmer was similar to those beaches adjacent (Felpham and Climping), however, the vertical extent of these assemblages were different, with the bays exhibiting subtidal/intertidal species further up the shore than the tombolos, which is related to the beach morphology. The influence of macroalgae deposits further complicates this pattern, as it increases the abundances of detritivorous surface and subsurface deposit feeders, such as Arenicola marina, Spio filicornis and Cumopsis goodsiri. The deposits of decaying macroalgae did not appear to have a detrimental impact on the communities; there were reductions of certain delicate species (e.g. Bathyporeia spp.) after large (> 60% cover) deposits, but this species decline was followed by an increase in other opportunistic species in their place e.g. S. filicornis. Furthermore, at Elmer the sedimentary organic matter content was higher, and anoxic layers shallower, in comparison with Felpham and Climping, but these factors were still relatively insignificant despite the large allochthonous

inputs. The fact that the sediment environment was not made anoxic by large macroalgae deposits (> 60 % cover on 10 % of occasions) was probably due to the intricate hydrodynamic regime of the site. This constantly shifts the detritus within the system during every tidal cycle, but the detritus is retained in far greater proportions in comparison with the groynes at the adjacent beaches of Felpham and Climping.

8.1.1 Significance and Management of Decaying Macroalgae Deposits

This study has shown that subtidally derived detrital aggregates of macroalgae are important to intertidal coastal areas (Chapter 7), that trapped algae within the ecosystem at Elmer provides an central food resource to both fauna adjacent to the structures and those on the structures, as well as, the fauna directly associated with the decaying macroalgae deposits (Chapter 7). The LCSs appeared to enhance the retention of this allochthonous resource in comparison with other structures (e.g. groynes; Chapter 3) and the elevated abundances of some of the benthic fauna were undoubtedly due to the availability of this resource (Chapter 4). The detrital algae are mechanically broken down through the continual removal and deposition during the tidal cycle, and grazing by mobile species, such as *Gammarus locusta* and *Idotea baltica*, as well as being microbially broken down (Chapter 6). This detritus appears to be predominantly utilised by mobile faunal (e.g. *Gammarus locusta*), rocky shore fauna (e.g. *Littorina littorea*), benthic surface deposit feeders (e.g. *Arenicola marina*, *Bathyporeia* spp.), fauna associated with the macroalgae deposits (Chapter 7).

The temporality of these decaying macroalgae deposits has important implications for both the surrounding ecosystems and particularly amenity use. Many studies have found and stated without detailed investigation that deposits were greatest in the winter months when storms were greatest in frequency and size (Koop & Field 1980, Lenanton et al. 1982, Robertson & Hansen 1982, Griffiths et al. 1983, Marsden 1991a, 1991b, Crawley et al. 2006). At Elmer, maximum deposition was found in the late spring and summer months in the years of study. Deposition was largely driven by the differences in spring and neap tidal range and appeared to be influenced by rapid increases in coastal sea temperatures in the summer months. If these factors coincided with a storm, the size of the deposits was further amplified. The timing of these deposits results in the perception of a nuisance by the public, as this is the time of highest beach usage, and the summer temperatures, along with the dominance of ephemeral and

filamentous red algae mean it decomposes quickly and stagnates leaving undesirable smells (pers. comms. with local community members). The presence of the structures at Elmer ensures that the decaying macroalgae deposits are more liable to retention, with greater deposits documented at Elmer (600 - 2,300 kg/m²/yr) than on adjacent beaches with groynes (Felpham: 200 - 800 kg/m²/yr, Climping: 200 - 600 kg/m²/yr). The results appeared to demonstrate that the low crested breakwaters modified the energy flows and nutrient cycling, and ultimately could affect amenity use by the local people, particularly in the summer months.

The decaying macroalgae deposits did not appear to be detrimental to the infaunal community, as the sediments never showed extreme anoxic effects during the period of survey, even in the month following a large deposit of decaying macroalgae and in the following month. Instead of being harmful, these deposits are of great importance because of increase in the detrital food source in comparison to that expected to exist prior to the existence of the breakwater scheme. This increase in detrital food seems to have enhanced the abundance of detritivores with potential benefits higher up the food chain, though comparisons with control sites needs to be further investigated to validate these findings. This study has shown the direct assimilation of the decaying macroalgae by fauna within the ecosystem on and around the LCSs at Elmer groynes at Felpham. There were significant differences between the foodwebs at Elmer and Felpham. At Elmer, the large detrital input was being utilised, largely in the form of POM, and less so directly from the decaying macroalgae (although the POM will be derived from a large majority of the macroalgae, there remains difficulty in tracing decaying macroalgae with stable isotope analysis; see section 8.2) by gastropods on the CDSs, amphipods associated with the macroalgae and deposit feeding polychaetes (A. marina) at Elmer. At Felpham, the detrital input was not as large, and as it was a nitrogen-rich ecosystem because of the presence of a sewage outfall pipe within 100 m of the groynes studied, it was easy to determine whether the decaying macroalgae or POM were being utilised by the same species as at Elmer, which they were not. There were many other species that appeared to benefit from this allochthous resource that were not investigated, such as the oystercatchers were seen on a regular basis feeding off the amphipods when there were large deposits of decaying macroalgae. These birds were not seen at Felpham and only on very low tides at Climping Beach when the subtidal macroalgae chalk beds were exposed.

Understandably, the regular deposition of decaying macroalgae in the summer months is an aesthetic problem, and may continue to be objected to by the local community. Past studies have shown that regular beach cleaning of allochthonous inputs has detrimental impacts by decreasing the biodiversity of the communities over time (Llewellyn & Shackley 1996, Dugan et al. 2003). It is therefore recommended that the removal of the decaying macroalgae deposits on a regular basis is strongly discouraged as detrimental impacts may occur. The decaying macroalgae provides an important food resource for the infaunal community, and removal would have greater implications for the foodweb of the wider area. For example, removal may impact local juvenile fish species, by removing available prey items (e.g. amphipods and juvenile crabs) associated with the decaying macroalgae that are present in the surf zone during the moving tides, as well as removing a complex spatial matter that provides shelter from their prey, which may be effectively providing safe nursery areas, together with the CDSs. One suggestion that may potentially alleviate concerns of the macroalgae deposits from the local community, would be to display an interpretation board on the shingle bank between the beach and the houses; this is used a walk way and would gain much attention. This board would explain the importance of the algae to the beach ecosystem, showing the linkages between the sediment fauna, CDS biological assemblages, birds, fish, and mobile fauna associated with the decaying macroalgae.

There are some circumstances in which it would be possible to remove a percentage of the algae, such as when the deposits are obviously accumulating quicker than they are decaying or being removed by the tide. From this study, it would be recommended that the removal of algae so that anoxic conditions are not created and the local beach amenity do not become overly aesthetically unpleasing. Removal would be good following a bout of extreme and continual deposition of decaying macroalgae that has coincided with high temperatures and spring tides. For the two summer period studied (80 days in both 2005 and 2006), the occurrence of large deposits of over 60 % beach cover, and biomasses of over 25 kg/m² (maximum recorded biomass of 57 kg/m²) was 13% of the time in summer 2005 and 30 % in summer 2006; the latter was greater because of greater rapid fluctuations in temperature. It would be suggested that when cover is over 60 %, as well as with biomasses over 25 kg/ m² (as high coverage can occur with a low biomass and not be detrimental to either the benthic communities or humans) that a percentage is removed (e.g. 50 %). It is imperative however, that further research is carried out to determine the percentage of removal, as I have only stated a suggestive figure. Consideration

also needs to be given to the impact on the biological communities by the large vehicles that would be used for this type of algal removal work.

8.2 Methodological Limitations

The main limitation that has come to light, as a result of the findings of this thesis, is the use of stable isotope analysis (SIA) to infer detrital pathways in ecosystems that have a diverse composition of detrital material (e.g. allochthonous macroalgae). Temporal studies of the changes in detritus, from daily to monthly, are ideally required for further understanding of how the stable isotope values, particularly $\delta^{15}N$ isotopic values, change from living macroalgae to particulate organic matter, as well further understanding of the assimilation time of the consumers being studied, and the isotope values of the bacteria involved in this decay and assimilation process.

The extent of the studies in this thesis around the LCSs at Elmer, in comparison with the other two sites (Felpham and Climping) with groynes, was not proportional. Ideally, the same spatial replication should have been studied at the latter sites, but time was a limiting factor. Furthermore, this study could have incorporated deposition patterns on beaches without structures as a control, however, the stretch of coastline studied is heavily defended, and therefore it was not a possibility to have a control that experienced the same local environmental conditions in the same area. At the same time using an unprotected beach in a completely different geographical area would have introduced too many different environmental variables for it to be comparable (e.g. wave environment, currents and proximity to sources of drift macrophytes, such as rocky habitats and marine macrophyte beds).

8.3 Suggestions for Further Work

Further studies are required to directly understand the effects of different quantities of macroalgal deposits on the feeding modes of these organisms both after excessive deposits, and when there is very little deposition (during the winter months). The present study only correlated surveys between benthic assemblages and decaying macroalgae deposits and it would be advisable to carry out field experiments to determine the direct influence on these biological assemblages. These experiments need to done at different times of the year to gain an

understanding of temporal implications of small (< 20 % cover) to large (> 60 % cover) deposits. The problem with experiments of this kind are that because it is an exposed beach and used by the public and their dogs, it is difficult to set up experiments that are for a long enough period, without being destroyed naturally or unnaturally.

Further work is needed to determine what volume of macroalgae deposits is detrimental to the biological communities for this specific beach. Studies on the removal of algal deposits (percentages) would allow an understanding of the threshold of what would be a detrimental quantity to remove. There is a need to also study the effects of decaying macroalgae during high tide; this study only did so at low tide when it was deposited. There are several questions that remain to be addressed: How far does it move from the structures? Does it stay in the surf zone? What are the implications for juvenile fish species and other top predators? Are the bird species benefiting from this resource? It was noted that shore birds (e.g. dunlin and oystercatchers) were feeding on amphipods within the macroalgal deposits. There should be further studies on this aspect of the food chain, and whether there are any bird species of special conservation importance that are not present on adjacent beaches.

The assemblages colonising the LCSs at Elmer were not particularly diverse because of the location of the structures in the mid-intertidal, e.g. few red macroalgae are found except in the rock pools inside and at the foot of the structures. If the structures had been sited another 20 to 40 metres further down the shore, it would potentially have resulted in higher biodiversity, as the structures and communities would be subjected to less desiccation stress during low tide periods.

8.4 Concluding Comment

With rising sea levels and stormier seas, coastal defence structures such as low crested breakwaters, are likely to proliferate on vulnerable areas of British and European coastlines. There are complex interactions between hydrodynamic and ecological processes due to the placement of the structures in the coastal zone. My thesis has highlighted the importance of the modification of algal detrital flows by breakwaters, and has also shown the major contribution of macroalgal detritus to the foodwebs of coastal ecosystems, with the aid of stable isotope analysis.

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