ACADEMIC REGISTRY
Abstract of Thesis Form

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Title of Thesis: (complete in upper and lower case)	DETECTING RESPONSES OF ROCKY SHORE ORGANISMS TO ENVIRONMENTAL CHANGE FOLLOWING WAVE ENERGY EXTRACTION		
	Detecting responses of rocky shore organisms to environmental change following wave energy extraction		

Signature*:*	Andrew Want	Date:	6 April, 2017

Abstract

The highly energetic waters surrounding Orkney have recently attracted attention as a renewable resource to generate electricity. While the importance of wave exposure to littoral assemblages is well known, the ecological consequences of industrial-scale extraction of marine energy have not been directly studied on rocky shores. The aim of this study was to examine the potential consequences of wave energy extraction and other long-term forcing agents, such as climate change, to rocky shore assemblages. Baseline surveys were conducted in areas not previously described in scientific detail to serve as 'before' and 'control' sites in a BACI-style design. Composition and abundances of biological assemblages were compared with topographic measurement of coastal features expected to modify exposure through dissipation of incoming wave energy. Observed variation in assemblages between sites was explained by differences in exposure and topography, particularly substrate complexity. Rocky shore species were selected for monitoring long-term changes using a paired-species monitoring method, including key structuring organisms on high exposure shores. Monitoring and experimental manipulation identified species which respond to changes in wave energy extraction and temperature. This research will assist in elucidating ecological responses that might occur following removal of wave energy, amid warming seas.

Detecting responses of rocky shore organisms to environmental change following wave energy extraction

Andrew Want

Submitted for the degree of Doctor of Philosophy

Heriot-Watt University

Institute of Life and Earth Sciences

April 2017

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The highly energetic waters surrounding Orkney have recently attracted attention as a renewable resource to generate electricity. While the importance of wave exposure to littoral assemblages is well known, the ecological consequences of industrial-scale extraction of marine energy have not been directly studied on rocky shores. The aim of this study was to examine the potential consequences of wave energy extraction and other long-term forcing agents, such as climate change, to rocky shore assemblages. Baseline surveys were conducted in areas not previously described in scientific detail to serve as ‘before’ and ‘control’ sites in a BACI-style design. Composition and abundances of biological assemblages were compared with topographic measurement of coastal features expected to modify exposure through dissipation of incoming wave energy. Observed variation in assemblages between sites was explained by differences in exposure and topography, particularly substrate complexity. Rocky shore species were selected for monitoring long-term changes using a paired-species monitoring method, including key structuring organisms on high exposure shores. Monitoring and experimental manipulation identified species which respond to changes in wave energy extraction and temperature. This research will assist in elucidating ecological responses that might occur following removal of wave energy, amid warming seas.

To my Family…

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Table of contents:

List of abbreviations:

AMO	Atlantic Multidecadal Oscillation
ANOVA	Analysis of Variance
AT	Atmospheric Temperature
BACI	Before-After-Control-Impact experimental design
EMEC	European Marine Energy Centre
GIS	Geographic Information System
GLM	Generalised Linear Model
GPS	Global Positioning System
H_S	Significant Wave Height
kW	Kilowatt
MLW	Mean Low Water
MNCR	Marine Nature Conservation Review
MRE	Marine Renewable Energy
MRED	Marine Renewable Energy Device
MW	Megawatt
NAO	North Atlantic Oscillation
NEL	North-east Lewis
NWL	North-west Lewis
OSGB	Ordnance Survey – Great Britain
PC	Principal Component
PCA	Principal Component Analysis
P_W	Wave Power Density
RDA	Redundancy Analysis
RIB	Rigid Inflatable Boat
RSL	Relative Sea Level
SACFOR	Super Abundant/Abundant/Common/Frequent/Occasional/Rare

SLR	Single Lens Reflex camera
SST	Sea Surface Temperature
UAV	Unmanned Aerial Vehicle
WEC	Wave Energy Converter
WMO	West Mainland, Orkney
W_P	Wave Period

Chapter 1 - Introduction:

1.1 Orkney and marine renewable energy:

The aim of the current studies was to detect patterns in biological responses by the rocky shore community to changes in wave exposure, and to distinguish between the relative roles played by other environmental forcing agents. The understanding gained may help address ecological issues related to deployment of marine renewable energy devices (MREDs) and provide greater integration of knowledge between physical and biological processes on rocky shores. The ability to predict ecological effects of exposure on species distributions will become increasingly important in the face of expected changes in climate (Blanchette *et al*., 2008; Hawkins *et al*., 2008, 2009); accurate attribution of ecological change to a given forcing agent, requires the distinction of the relative role played by other factors. This presents some difficult challenges: wave exposure and its impacts on the biological community are notoriously hard to quantify, especially in the surf-zone (Jones and Demetropoulos, 1968; Denny, 1983); the relationship between chronic exposure versus acute storm events and the biological community is poorly understood (Thomas, 1986; Siddon and Whitman, 2003); and the role of co-occurring long-term changes such as increased sea temperature will not be easy to dissect out. This research has focussed on several key components of the littoral community including invertebrate and algal species with long pedigrees of ecological study, as well as species which have not previously been the focus of extensive study. The deployment of MREDs in Orkney waters provides a unique opportunity to study the ecological consequences of this emerging industry.

Orkney is an archipelago of around 70 islands separated from the mainland of NE Scotland by the fierce tidal currents of the 12 km wide Pentland Firth. While complex local weather systems bring powerful winds from all directions, at approximately 59° N latitude, the position of Orkney in the North Atlantic means that the islands are subject to a preponderance of westerlies across an expanse of ocean in excess of 3,000 km. In meteorology, ‘fetch’ refers to the linear unobstructed distance of water to a particular coastal location over which wind blows and, in doing so, transfers energy into the formation of waves (Wright *et al*., 1999). Off the west coast of Orkney, the combination of extreme fetch and dominant wind direction produces powerful waves (Figure 1.1), creating one of the world’s greatest near-shore wave resources (Neill *et al*., 2014). Exposure to wave energy plays a dominant role in both shaping this landscape and determining the biological community, in this case creating an assemblage of diverse organisms adapted to an extreme environment. The rocky shoreline of West Mainland, Orkney (WMO) is characterised by dramatic sandstone cliffs, complex geomorphologic features including sea stacks and caves, and a few embayments. The geomorphologic and hydrodynamic consequences of this wave environment have created interest in both conserving coastal features and harnessing this resource to generate electricity from renewable sources. Part of WMO is designated a National Scenic Area, and, at Skaill Bay, the World Heritage Site at Skara Brae is the best known of several important archaeological sites along this coast which are vulnerable to coastal erosion.

The UK government has set the objective of delivering at least 15% of electricity from renewable sources by 2020 (The Scottish Government, 2013). In Scotland ambitions are

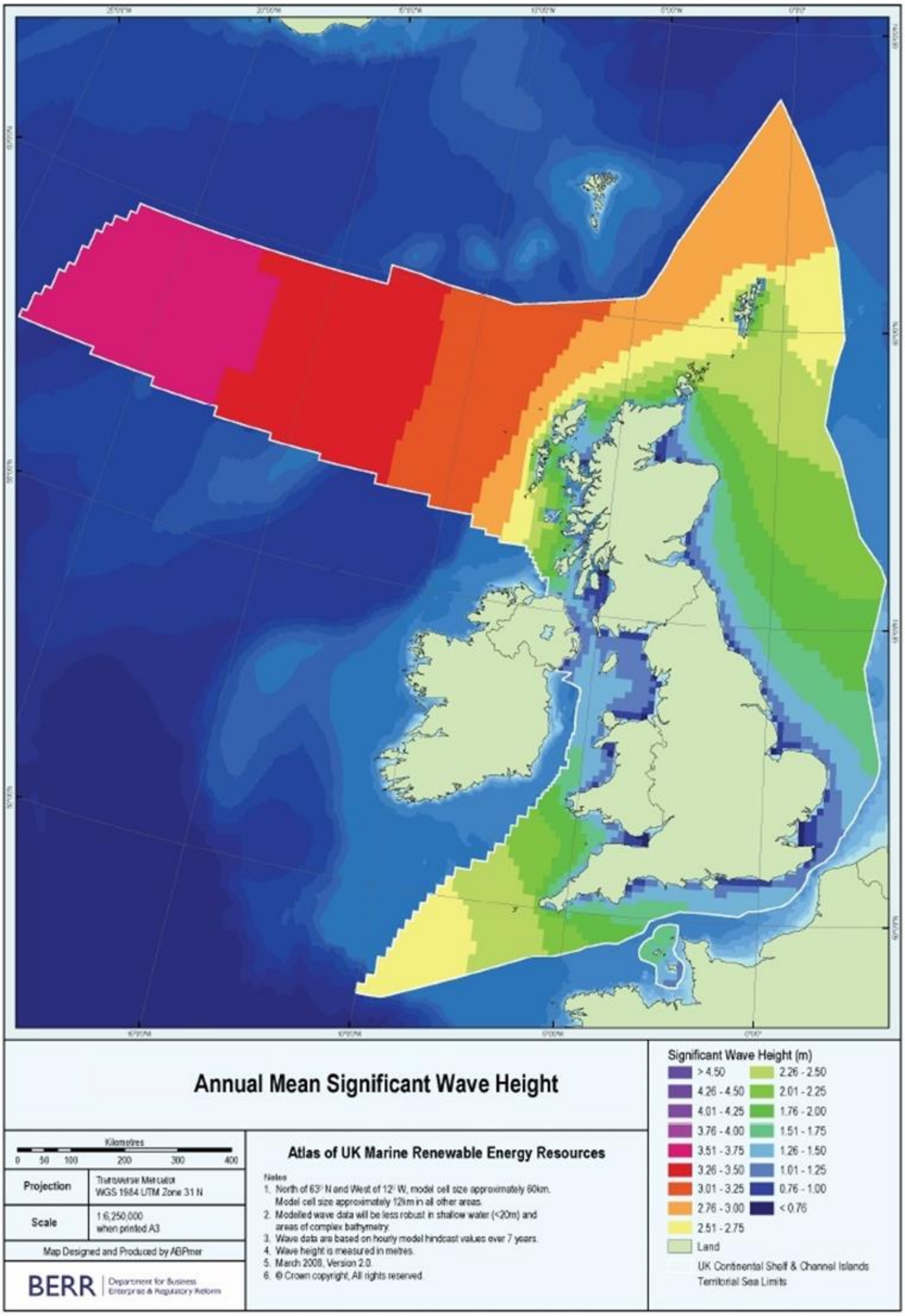


Figure 1.1: Annual mean significant wave height around the UK obtained from the UK Atlas of Marine Renewables (ABP Marine Environmental Research Ltd, 2008).

higher, with the objective of an equivalent of 100% electricity production to be sourced from renewable technologies by the same year (The Scottish Government, 2013). Energy capture can be achieved through many renewable options – a short list includes: wind, solar, hydroelectric, geothermal, biomass and marine energy. The utilisation of these different forms is varied and depends on many factors including the maturity of the technology, confidence in the economic deliverables, and political support (Twidell and Weir, 2015). To date, the greatest contribution to energy production from renewable sources in the UK has come from wind farms. In contrast to wind power generation, the medium of water carries a much higher density of energy and the potential for harnessing this is tremendous (Twidell and Weir, 2015).

The total wave energy resource in UK and Irish waters is estimated at 840 TWh/year, of which about 50 TWh/year could be harnessed using present technologies (RenewableUK, 2013). To place this in context, mean annual electricity demand in the UK is about 350 TWh/year (RenewableUK, 2013). As Figure 1.1 shows, off the west coast of Orkney near-shore wave resource is much higher than most of the UK. This resource, however, is highly seasonal: off the west of Orkney, mean wave power during the most energetic month (January) is above 30 kW/m, compared with the least energetic month (June) when mean wave power is below 4 kW/m (Neill *et al*., 2014) (Figure 1.2).

In 2003, the European Marine Energy Centre (EMEC) was established in Stromness to test wave and tidal energy extraction devices in the resource-rich waters around Orkney (EMEC, 2017). The wave energy test facility is located at Billia Croo off WMO. Subsequently, in March 2010, the Crown Estate announced leasing agreements with several developers and energy providers for deployment of marine energy devices,

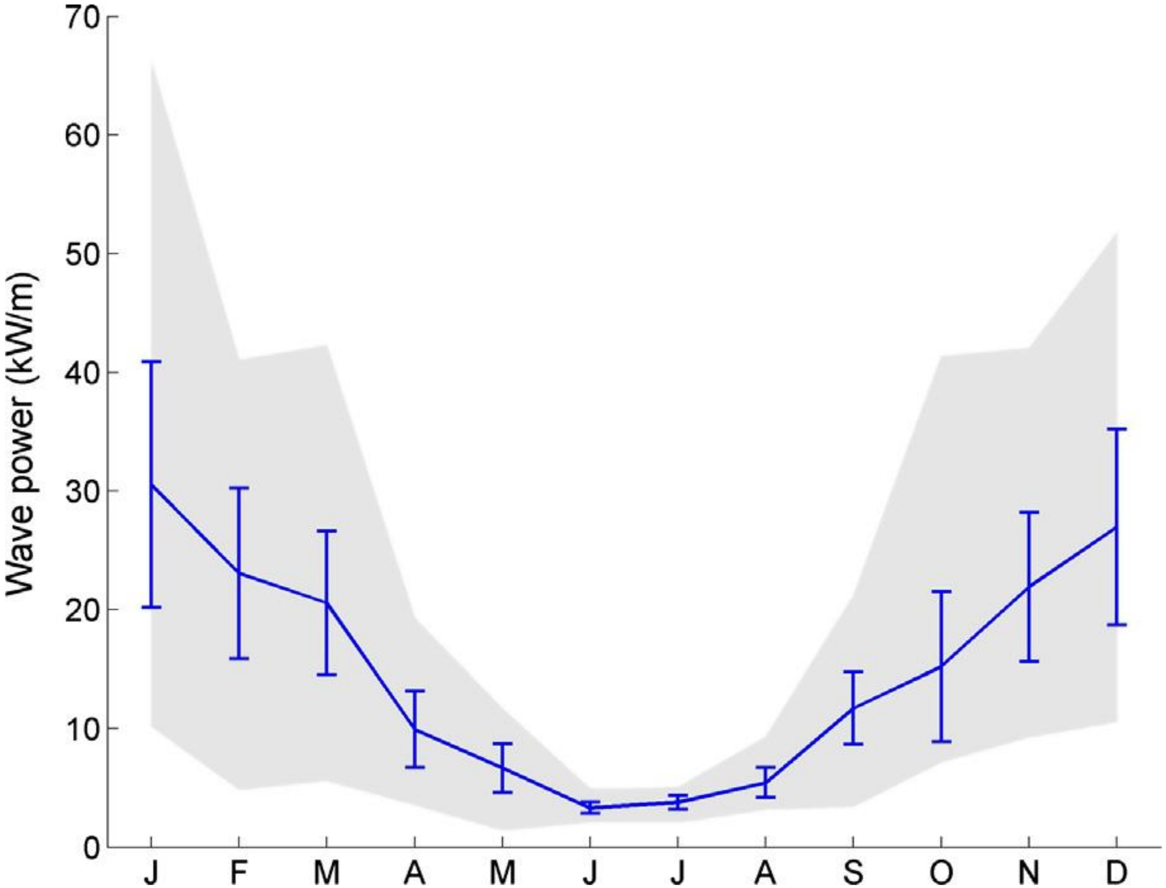
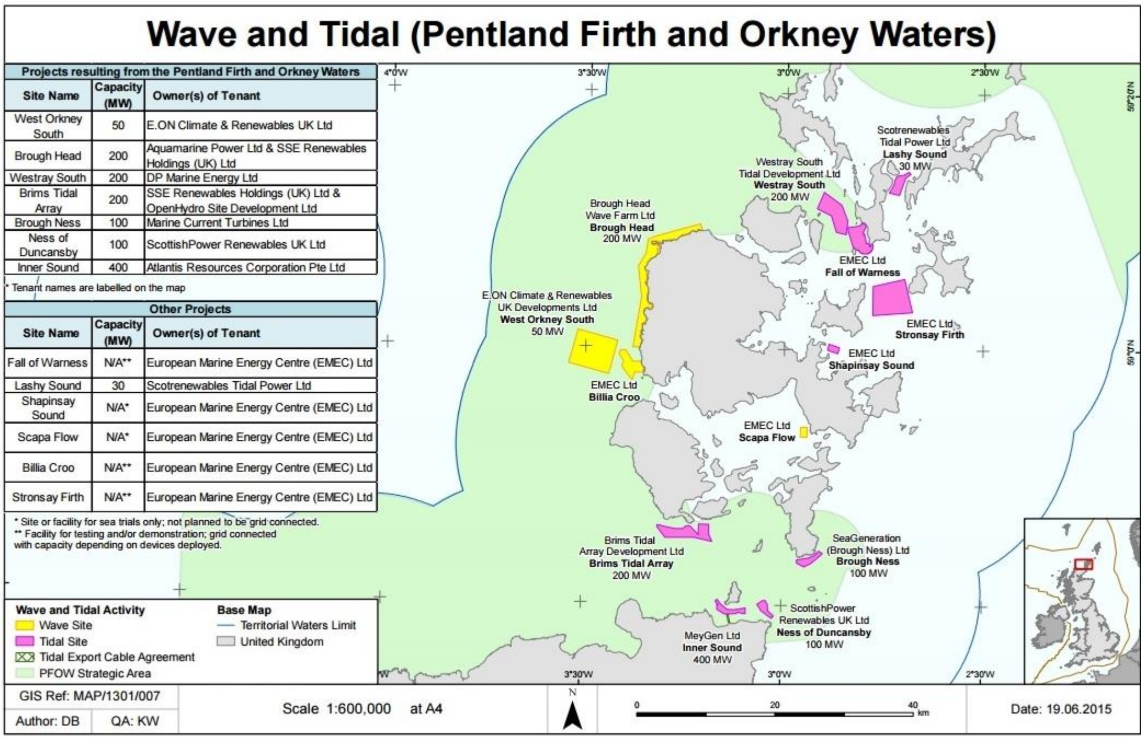


Figure 1.2: Annual cycle of monthly mean wave power (kW/m) for a 434 km^2 region to the west of Orkney. Error bars show 90% confidence intervals, and grey shading indicates range. From: Neill *et al*. (2014).

predominantly within Orkney waters and the Pentland Firth, including extensive lease sites along WMO (TCE, 2015) (Figure 1.3). Since its inception, EMEC has hosted 15 wave and tidal developers testing a variety of surface and subsea energy converting devices. Recently, wave and tidal-generated electricity from Orkney has contributed to powering the national grid for the first time in the UK (EMEC, 2017). To date, however, deployment in Orkney has been limited to individual devices with maximum generation capacities of 800 kW for wave converters, and 2 MW for tide converters. The world's first commercial-scale deployment of tidal stream devices is being developed in the Pentland Firth at Inner Sound, where a demonstration array of six 1 MW tidal turbines is planned for 2017, before expanding to a total capacity of 398 MW by the early 2020s (Meygen, 2016).



Projects resulting from the Pentland Firth and Orkney Waters

Site Name	Capacity (MW)	Owner(s) of Tenant
West Orkney South	50	E.ON Climate & Renewables UK Ltd
Brough Head	200	Aquamarine Power Ltd & SSE Renewables Holdings (UK) Ltd
Westray South	200	DP Marine Energy Ltd
Brims Tidal Array	200	SSE Renewables Holdings (UK) Ltd & OpenHydro Site Development Ltd
Brough Ness	100	Marine Current Turbines Ltd
Ness of Duncansby	100	ScottishPower Renewables UK Ltd
Inner Sound	400	Atlantis Resources Corporation Pte Ltd

* Tenant names are labelled on the map

Other Projects

Site Name	Capacity (MW)	Owner(s) of Tenant
Fall of Warness	N/A**	European Marine Energy Centre (EMEC) Ltd
Lashy Sound	30	Scotrenewables Tidal Power Ltd
Shapinsay Sound	N/A*	European Marine Energy Centre (EMEC) Ltd
Scapa Flow	N/A*	European Marine Energy Centre (EMEC) Ltd
Billia Croo	N/A**	European Marine Energy Centre (EMEC) Ltd
Stronsay Firth	N/A**	European Marine Energy Centre (EMEC) Ltd

* Site or facility for sea trials only; not planned to be grid connected.
** Facility for testing and/or demonstration; grid connected with capacity depending on devices deployed.

Figure 1.3: Locations of wave and tidal development sites in the Pentland Firth and Orkney waters, leased by the Crown Estate. From: TCE (2015).

Owing to a rich local tradition of working in the sea, Orkney has well-developed infrastructure supporting the marine energy industry, recently enhanced with the construction of additional piers and harbour structures designed to facilitate the growth of the renewable sector. Through the establishment of full-scale and nursery test sites for both wave and tidal energy, EMEC has helped develop local marine infrastructure to support device testing including subsea electrical cables, surface buoys, moorings, and a monitoring pod used for integrating environmental data collection. Despite growing interest in extracting energy from waves and tides, installations of marine energy converting devices beyond EMEC are also limited, especially on a commercial scale. Test centres for wave and tidal devices have been recently established in England (Wave Hub is located off the north coast of Cornwall), Portugal, Ireland (Galway Bay), Japan, USA (Pacific NW), and Canada (Nova Scotia), amongst others (Renewable UK, 2013). In addition to Orkney, other locations where devices have been grid-connected during power generation are in France (La Rance), Canada (Bay of Fundy), and Ireland (Strangford Lough) (Renewable UK, 2013).

1.2 Ecological impacts and the marine renewable energy industry:

It is assumed that the deployment and operation of MREDs will have consequences on the marine environment. With a general trend towards stricter statutory environmental controls, the onus will be on the marine renewable energy (MRE) industry to demonstrate minimal environmental disturbance. At present, there exists a paucity of studies addressing direct evidence of environmental and ecological consequences of wave and tidal energy developments (Frid, *et al.*, 2012; Langhamer, 2016); some relevant evidence regarding nearshore impacts of industrial development may be gathered from longitudinal studies conducted on pre-installation and control sites of offshore wind farms (Wilhemsson and Malm, 2008; Lindeboom *et al.*, 2011). Potential ecological consequences of marine MRED deployment can be broadly divided into impacts and interactions which might occur at the location of the device, resulting from its physical presence or operation, and effects occurring ‘downstream’ of the device as a result of removing energy from the ecosystem (Lohse *et al.*, 2008; Shields *et al.*, 2011).

Physical impacts might occur on the seabed during construction, maintenance and decommissioning (Shields *et al.*, 2011), and include risks of collision and behavioural disturbance to marine vertebrates during operation (Wilson *et al.*, 2006; Waggitt *et al.*, 2016). Additional impacts from device operations may result from electro-magnetic fields (Gill *et al.*, 2014), chemical pollution (Shields *et al.*, 2011), and noise (Farcas *et al.*, 2016). Deployment of marine infrastructure may provide suitable settlement habitats which can create ‘stepping stones’ across hydrographic barriers exploitable by range-expanding organisms (Miller *et al*., 2013; Adams *et al*., 2014). This may be especially true in high-energy environments (such as strong tidal currents) where an existing industrial ‘footprint’ is minimal (Nall *et al*., 2015). In areas already impacted by human development, the physical presence of MREDs may provide some potential benefits: the formation of artificial reefs and the creation of fisheries exclusion areas may function as refuges for local fish and crustacean populations with potential spill-over benefits for adjacent stocks and fisheries (Wilhelmsson and Langhamer, 2014); and rock armour laid to protect subsea cables may provide additional off-shore habitat for commercially valuable crustaceans (Linley *et al*., 2007). Downstream effects from deployment of MREDs, especially with large scale ‘farms’, would be expected to stem from changes in the wave climate or tidal flow, principally by reducing energy levels reaching the shoreline or interacting with the surrounding benthic community. In addition, hydrodynamic changes may affect sediment suspension and deposition (Langhamer, 2010; Kregting *et al*., 2016a; Van Der Molen *et al*., 2016), as well as nutrient exchange and larval transport along the coast (Roughgarden *et al*., 1985; Blanchette *et al*., 2000; Adams *et al*., 2014).

While the ecological consequences of extracting hydrokinetic energy by wave energy converting devices (WECs) has not been studied in detail, it is generally expected that observable impacts following reduced exposure to wave energy will occur in the intertidal zone (Shields *et al*., 2011). In marine ecological studies, the term ‘exposure’ is typically used to describe the magnitude of hydrodynamic forces impinging upon plants and animals (Ballantine, 1961). Exposure to wave action striking the shore is a major determinant of species composition, growth rates, reproductive success, and other aspects of life-histories (Lewis, 1964). It is relevant to ask whether or not reduction in wave energy breaking in the surf zone would be sufficient to produce observable changes in littoral communities. Even slight changes in exposure might result in shifts in species distribution (Blanchette *et al.*, 2008) and morphology (Ruuskanen *et al.*, 1999). Monitoring indices of these aspects can provide valuable data in assessing changes at individual, as well as community, level. Improved capacity to recognise these potential shifts may enhance our ability to predict environmental consequences following wave energy extraction. While the rocky shores of the British Isles have not experienced the major stressor of direct commercial fisheries exploitation seen in many other marine environments (Thompson *et al.*, 2002; Broitman *et al.*, 2008), this habitat is under increasing pressure from coastal developments, as well as impacts from adjacent land use (Frost *et al.*, 2016). The list of anthropogenic impacts on rocky shores now includes extraction of ocean energy and the necessary infrastructure associated with its development; on rocky shores the consequences of removing wave energy at an industrial scale are unknown. It is off the rocky coast of WMO that the testing and planning for commercial development of wave energy extraction is occurring and these shores are the setting for the current studies. Presently, on the WMO coast, north of Stromness, there is minimal coastal development; the EMEC substation at Billia Croo is connected to offshore test berths via five subsea cables, and a small slipway is located in Birsay Bay.

1.3 Rocky shore ecological studies:

In terms of monitoring and experimental studies, intertidal areas have several advantages over other marine habitats. These include the ease by which sites may be accessed and revisited from land, and the suitability of relatively inexpensive methods for direct observations. Some species are particularly amenable to quantitative sampling; the sessile nature of many of the key species on rocky shores provides convenient opportunities for study without causing dispersal or modified behaviour. Furthermore, with regards to studies involving exposure to wave energy, the littoral zone is where hydrodynamic forces are greatest and their effects are most manifest (Denny, 1995). This is not to suggest that dissipation of wave energy occurs only in the surf zone or that only intertidal organisms are likely to be affected. In fact, prior to breaking on the shore, waves begin inducing flows along the seabed, with possible consequences for sublittoral organisms at depths of up to 75 m (Denny, 1987). Wave interactions with the boundary layer and the sublittoral benthos will increase in the nearshore as depth decreases (Shields *et al*., 2011). When considering the consequences of energy extraction on the marine community, there are advantages in studying the sublittoral environment: there are a greater variety of habitats and species to study; scheduling is not necessarily limited by tide times; there is less variation from terrestrial and atmospheric influences; and research can be conducted in closer proximity to marine energy devices. In the present studies, the benefits of accessing the littoral environment and the choice of species available for research on rocky shores outweighed the advantages of studying sublittoral habitats.

The rocky shore has been the focus of peer-reviewed ecological studies for approaching a century with important work pioneered in British waters by Moore and Kitching (1939), Stephenson and Stephenson (1949), and Southward and Crisp (1954a), amongst many others, while across the English Channel contemporaries progressed the field on French shores (e.g. Fischer-Piette, 1936). Rocky shore studies have provided an important baseline for long-term, time-series research in marine ecology both in British waters

(Southward *et al.*, 1995; Thompson et al., 2002; Mieszkowska *et al*., 2007, 2014; Broitman *et al*., 2008; Hawkins *et al*., 2008, 2009) and further afield (Sagarin *et al*., 1999; Simkanin *et al*., 2005; Wethey *et al*., 2011; Jones *et al*., 2012). Littoral barnacles have proven to be particularly valuable in understanding population processes on rocky shores using time-series studies (Southward *et al.*, 1995; Poloczanska *et al*., 2008; Jones *et al*., 2012; Mieszkowska *et al*., 2014) (see Chapter 5). Several other groups of organisms have also emerged as the focus of many studies often owing to their dominant role in rocky shore communities, for example fucoid algae, patellid limpets, dog-whelks, topshells, and mussels. As studies have developed in sophistication, these organisms, as well as subsequent additions, have revealed greater details of processes affecting rocky shore species.

Community classification:

In addition to time-series studies or research directed towards individual species, another strategy utilised in rocky shore ecological studies is to look at broader-scale, community-based relationships using distribution and abundance data of key species (Moyse and Nelson-Smith, 1963; Burrows *et al*., 2008; Mieszkowska *et al*., 2013). Important early studies included the essential contributions of zonation characterisation (Stephenson and Stephenson, 1949) and the development of abundance scales used in mapping geographic distribution of rocky shore species (Crisp and Southward, 1958). Subsequent developments by Ballantine (1961) led to the assignment of key assemblages to an arbitrarily defined series of subjective energy levels. These concepts have been further refined and, more recently, the Marine Habitat Classification for Britain and Ireland (MHCBI), produced as part of the Marine Nature Conservation Review (MNCR), details biotopes found within the British Isles (Connor *et. al*., 2004), and provided the basis for the European Nature Information System (EUNIS) - part of the biodiversity data centre which contains additional biotopes found within European Union countries (EEA, 2008). The MNCR and the EUNIS habitat systems broadly group habitats within three qualitative categories of High, Medium and Low energy. These energy levels form a hierarchical base for eight sub-divisions of ‘exposure’ levels, decreasing in energy level from ‘extremely exposed’ to ‘ultra sheltered’.

1.4 Littoral zonation:

Littoral communities are constrained into a relatively narrow vertical range extending from the sublittoral, which is always underwater, up along a gradient of increasing emersion where terrestrial and atmospheric influences begin to dominate. Closer examination of the shore will typically reveal vertical subzones where certain species or assemblages of species can be seen to favour, or even dominate, a specific height on the shore (Figure 1.4). The overall height of the littoral zone is highly variable and depends, amongst other factors, on the tidal range of the shore and the level of exposure (Lewis, 1964). Tidal range is a manifestation of the bathymetric conditions surrounding the specific location; exposure is a manifestation of approaching wave energy modified by near-shore dissipative features. On littoral rocky shores, as with any given habitat, a broad variety of factors will influence the structuring of the biological community. As a general rule, the upper limits of littoral zones tend to be determined by abiotic factors, while lower limits of individual species are generally produced by biotic factors (Connell, 1961a; Schonbeck and Norton, 1978, 1980; Lubchenco, 1980). Exceptions to this rule include the setting of upper limits of fucoids on certain shores by periwinkle and limpet grazing and competition for space between algal species (Lubchenco, 1983; Hawkins and Hartnoll, 1985; Boaventura *et al*., 2002).

Figure 1.4: Littoral zonation on a vertical rocky shore visible at low spring tides at Marwick, WMO.

Abiotic, or physical, factors known to affect the vertical distribution of organisms on rocky shores include: exposure to hydrodynamic energy, temperature, ‘wetness’, salinity, substrate type, aspect relative to insolation, and timings of tides (Ballantine, 1961; Lewis, 1964; Schonbeck and Norton, 1978; Lubchenco, 1980; Wethey, 1983; Baxter *et al*., 1985; Benedetti-Cecchi *et al*., 2000). Many of these factors contribute to physiological desiccation stress on emerged organisms. For example, spray on high exposure shores, shading of surfaces orientated away from the sun, lower gradient slopes which drain more slowly, and the occurrence of low tides before or after the hottest time of the day, will all mitigate against desiccation stress. Biotic factors influencing littoral zonation include: competition between organisms for space or other resources, grazing, predation, and biogenic habitat provision (Connell, 1961a, 1961b; Lubchenco, 1980, 1983; Schonbeck and Norton, 1980; Hawkins and Hartnoll, 1985; Hawkins *et al*., 1992).

Complex interactions may occur between factors, and the impacts these factors have on rocky shore zonation may depend upon the stage in a given organism's life cycle (Underwood and Fairweather, 1989). In addition, the relative importance of factors causing zonation may fluctuate seasonally or over other time periods, and according to life history stages. For example: temperature may play a critical role during larval settlement owing to desiccation stress but may be less important for adult populations (Poloczanska *et al*., 2008); grazing activity may vary with temperature and target small members of an algal population, while leaving larger individuals unaffected (Jonsson *et al*, 2006).

In addition to vertical shore zonation (which is typically on a scale of centimetres), biotic and abiotic factors also create horizontal variability at different spatial scales. Local variation in the biological community may be apparent on a scale of metres, owing to any number of environmental variables but often mostly effected by exposure level. Depending on factors such as shore complexity, microhabitats of contrasting exposure can be found in close proximity (Raffaelli and Hawkins, 1996; Johnson *et al.*, 2003; Burrows *et al*., 2014). On a wider, latitudinal scale, community differences become increasingly apparent over tens or hundreds of kilometres, owing to climatic differences (Ballantine, 1961). Of importance in the current studies, high-exposure, high-latitude shores on the north of Scotland will typically see a significant up-lift of zones caused by increased wave activity, and reduced desiccation owing to sea spray, high frequency of fogs, moisture, and lower summer temperatures when compared with rocky shores farther south (Lewis, 1964; Raffaelli and Hawkins, 1996; Kendall *et al*., 1982; Baxter *et al*., 1985).

Fucoid-barnacle-patella complex:

On rocky shores of the NE Atlantic, among the more conspicuous members of the biological community are fucoid algae, barnacles, and patellid limpets. These organisms frequently dominate the mid shore along a hydrodynamic gradient, where sheltered shores tend to be associated with greater abundance of fucoids, and exposed conditions feature well-defined zones of abundant barnacles (Ballantine, 1961; Lewis, 1964). Sheltered shore assemblages, dominated by macroalgae, tend to be net producers; exposed shore assemblages tend to be more animal-dominated and net consumers (Hawkins *et al.*, 1992). On more moderately exposed shores, an intrinsically unstable relationship exists between fucoids, barnacles, and patellid limpets (Hawkins *et al.*, 1992). At these exposure levels, the key organisms form a patchy mosaic, prone to cyclical changes (Figure 1.5). Depending upon the stage in the cycle, fucoids tend to form canopy-providing clumps which favour aggregation of limpets (Baxter, 1982; Hartnoll and Hawkins, 1985; Moore *et al.*, 2007) but may limit barnacle settlement by sweeping action of the fronds (Hawkins, 1983) (Figure 1.6). When fucoids are lost, the remaining limpets will tend to prevent barnacle establishment by collateral removal of spat and juveniles while grazing algal films (Hawkins *et al.*, 1989), as well as targeting fucoid germlings (Jonsson *et al.*, 2006). After some time without the fucoid canopy, limpets will disaggregate, freeing barnacles to recruit onto empty patches of bare rock (Roughgarden *et al.*, 1985; Minchinton and Scheibling, 1993). Adult barnacles create complex surfaces which facilitate settlement of fucoid germlings, while reducing grazing pressure from limpets, leading to re-establishment of fucoid clumps, thus beginning the cycle anew (Hawkins *et al.*, 1992).

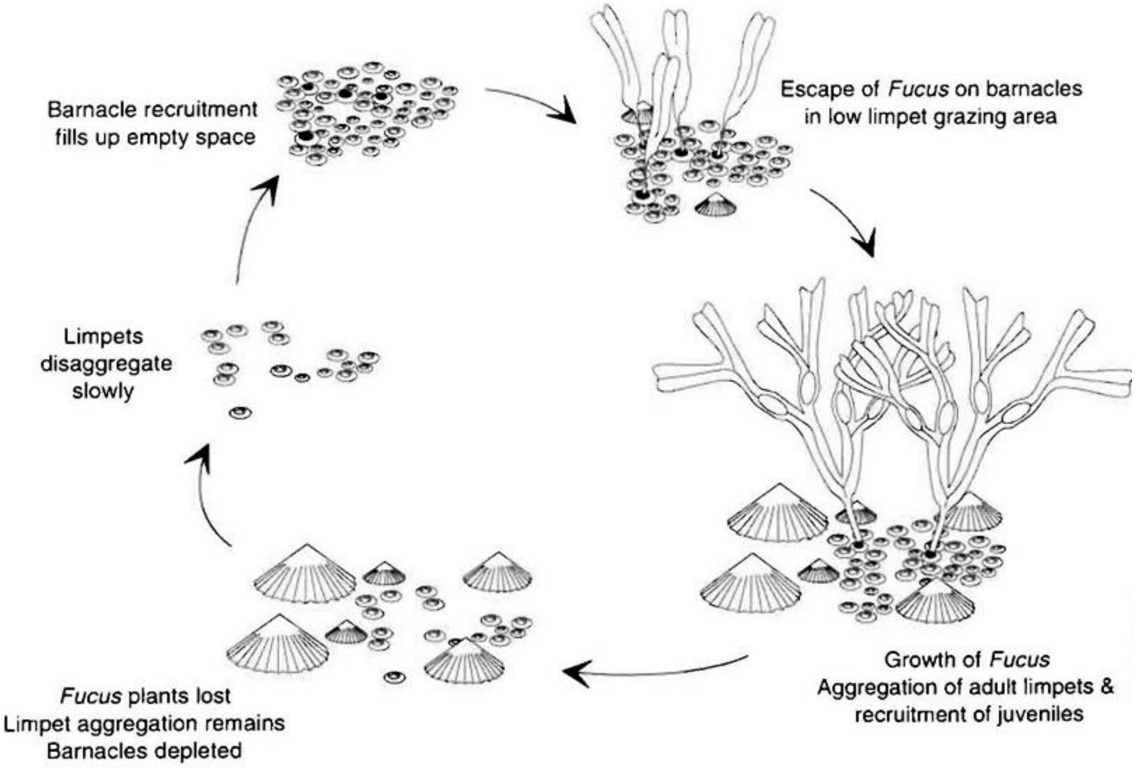


Figure 1.5: Pictorial representation of cycling of key organisms on moderately exposed rocky shores. From: Burrows and Hawkins (1998).

With increased exposure, this cycling appears to slow and shores become less patchy (Baxter *et al*., 1985); patellid grazing limits establishment of fucoids and, once established, wave action affects fucoid persistence (Jonsson *et al*., 2006). High exposure shores become increasingly stable and dominated by grazing and filter-feeding animals, i.e. barnacles and mussels (Hawkins *et al*., 1992), although subject to patch formation created by sediment impacts (Shanks and Wright, 1986). Menge (1976) has suggested that mussels will outcompete fucoids for space on higher exposure shores of New England. However, in studies conducted on rocky shores in SW England and Wales, the relationship between mussel and fucoid cover appears to be highly dependent on context (Crowe *et al*, 2011; Wangkulangkul *et al*., 2016). Experimental studies of mussels on the rocky shores of WMO has not been conducted. At higher latitudes, such as WMO, fucoids are less restricted to sheltered shores and survive under higher exposure conditions at the expense of barnacles and limpets (Southward *et al*., 1995). It has been suggested that latitudinal differences in grazing pressures may be explained in part by asynchrony between photoperiod-mediated plant growth and temperature-mediated foraging activity (Hawkins *et al*., 1992; Benedetti-Cecchi *et al*., 2000). The dynamic relationship between fucoids, barnacles and limpets has not been studied in detail on more extreme exposed coasts, such as those on westerly-orientated WMO. In addition, these shores feature species less represented in previous studies, e.g. *Fucus distichus anceps* and *Patella ulyssiponensis*, which may not respond to one another and their environment in the same manner as better known species such as *F. vesiculosus* and *P. vulgata*.

Figure 1.6: *Fucus vesiculosus* f. *linearis* clump with aggregated patellid limpets and exclusion of barnacles by sweeping action of the fronds, Billia Croo, WMO.

1.5 Rocky shore community and exposure:

While the importance of exposure in determining littoral zonation has been long recognised (Ballantine, 1961; Lewis, 1964), the precise manner by which this occurs is complicated and poorly understood (Thomas, 1986; Denny, 1999; Gaylord, 2000). Closer examination of exposure reveals a complex interaction between wave energy, the substrate, and the community. Hydrodynamic forces unleashed as waves break in the intertidal zone are considered amongst the greatest physical forces observed in nature and may result in removal of parts of organisms, i.e. algal fronds, or whole organism dislodgement (Denny, 1987; Gaylord, 2000). Exposure may further influence the biological community through a variety of means including: powering sediment movement and impacts, i.e. mechanical abrasion (Shanks and Wright, 1986); facilitating larval transport and settlement (Roughgarden *et al.*, 1985); increasing turbidity, gas exchange, and nutrient availability (Blanchette *et al.*, 2000); and, extending the intertidal zone far above high water (Lewis, 1964). In turn, exposure is modified by a complex array of elements including: fetch (Burrows *et al.*, 2008), local and distant meteorological conditions (Sundblad *et al.*, 2014), nearshore bathymetry (Folley and Whittaker, 2009), and shore topography (Thomas, 1986).

Two classic examples of rocky shore zonation along an exposure gradient are the distribution patterns of fucoids and barnacles on the shores of the northeast Atlantic. Fucoids typically form mid shore zones which, in certain conditions, e.g. greater shelter, may dominate cover. The presence of fucoid species will tend to follow a predictable pattern of relative tolerance to exposure (Figure 1.7), although other factors play important contributing roles (Lewis, 1964). Amongst the earliest studies of experimentally-verified space competition was made between rocky shore barnacles in Scotland (Connell, 1961a). In the UK, rocky mid shores are often dominated by a zone of barnacles which will broaden and extend higher up on more exposed shores, while narrowing and vertically lowering with more shelter (Lewis, 1964). As a general statement, the barnacle *Semibalanus balanoides*, occupies the lower parts of this zone, while upper barnacles belong to the genus *Chthamalus*. Within the chthamaloid zone, exposed shores tend to feature *Chthamalus stellatus*; less exposed shores tend to feature *C. montagui* (Crisp *et al*., 1981). Of the organisms on the rocky shores of WMO, fucoids and barnacles play the largest part in the present studies; the topics relating to these organisms introduced in this chapter will be addressed in further detail in Chapters 2-5.

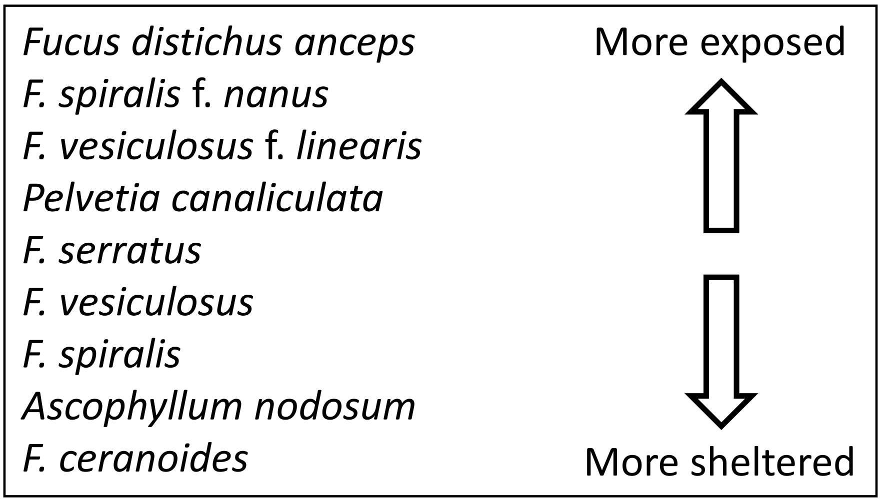


Figure 1.7 Fucoid tolerance to exposure: Modified from Lewis (1964).

Morphological adaptations to wave exposure:

Adaptive strategies used by organisms to survive exposure are highly varied. Mobile benthic species may mitigate the risk of detachment, and possible mortality, behaviourally by seeking sanctuaries such as rock pools, crevices, and empty barnacle shells, or to dwell high up in the spray zone (Blanchette *et al*., 2008). For sessile organisms, survival on exposed shores requires adaptations to either increase adherence capacity or to minimise hydrodynamic forces impinging on them through morphologic modification. On extreme exposure shores, macroalgae often exist as ‘dwarf’ forms with shortened and narrow thalli and feature robust holdfasts (Denny, 1999). On limestone reefs in Western Australia, mechanical force applied to the small kelp *Eklonia radiata* will usually break the substrate before the holdfast yields (Thomsen *et al*., 2004). Most algae minimise hydrodynamic forces through compliance. The fronds of large kelps (such as *Alaria esculenta* and *Egregia menziesii*) are passively carried by incoming waves; as long as oscillating water motion is shorter than the length of the plant, high forces are avoided (Friedland and Denny, 1995; Blanchette *et al*., 2008). Rigid animals feature hard shells shaped to mitigate hydrodynamic forces; while not sessile, limpets adhere with great strength using their muscular foot and significantly lower drag by orientating themselves parallel to flow (Gaylord, 2000). Animals with soft bodies may use flaccidity to assume streamline postures allowing hydrodynamic forces to pass with minimal interaction (Koehl, 1984).

Moving water imposes three kinds of forces on organisms: drag, lift, and acceleration reaction (Table 1.1). Drag and lift are proportional to the square of water velocity and to the area of the organism projected along the direction of force; acceleration reaction is proportional to the acceleration of the water and to the displacement volume created by the organism (Denny, 1987). Therefore, hydrodynamic forces imposed on an organism depend on its shape, e.g. stream-lined and compliant morphologies will minimise drag and acceleration reaction (Denny, 1987). As an organism grows, its volume typically increases faster than its area of attachment, resulting in greater hydrodynamic stress. In this manner, level of exposure appears to create a critical maximal limit to the size of littoral organisms (Gaylord, 2000). This appears to explain why, on the most exposed shores of WMO, mid shore macroalgae are limited to dwarf fucoids, *Mastocarpus stellatus* and a turf of small red algae; the largest resident animal is *P. ulyssiponensis*.

Table 1.1: The three major hydrodynamic forces acting on plants and animals in the wave-swept environment. From: Denny (1987).

Force	**Governing equation**	**Direction of action**
Drag	Density of water x Velocity^2 x Area x Coefficient of drag	Parallel to flow
Lift	Density of water x Velocity^2 x Area x Coefficient of lift	Perpendicular to flow
Acceleration reaction	Density of water x Acceleration x Volume of displaced fluid x Coefficient of inertia	Parallel to flow

Many species will display considerable plasticity in form across a hydrodynamic gradient. In the case of fucoid algae, distinct ecotypes may be associated with different levels of exposure and present at different shore heights (Powell, 1957a; Coyer *et al*., 2006). A partial list of rocky shore organisms that have been shown to respond to the level of exposure through morphologic adaptations includes: balanoid barnacles (Arsenault *et al*., 2001); fucoid algae (Back, 1993; Blanchette *et al*., 2000; Ruuskanen and Nappu, 2005; Wolcott, 2007); *Laminaria* spp. (Sjøtun *et al*., 1998; Kawanata, 2001; Pedersen *et al*., 2012; Kregting *et al*., 2016b); *Mytilus edulis* (Westerbom and Jattu, 2006); *Nucella lapillus* (Crothers, 1985); *Pollicipes pollicipes* (Borja *et al*., 2006); and *Strongylocentrotus purpuratus* (Gaylord, 2000). Without genetic data to compare between populations, these adaptations are presumed to be phenotypic in origin.

Consequences of energy extraction:

Given that exposure plays a major role in determining vertical and horizontal zonation on rocky shores, and affects the morphologic expression of community members, extraction of wave energy might be expected to produce measurable impacts in this habitat. Vertical zones would be expected to narrow and move further down the shore if exposure was reduced; this might be particularly pronounced in the spray zone which extends the upper limit of survival for marine organisms on high energy shores (Lewis, 1964). Depending on their relationship with exposure, different organisms and ecotypes would be more likely to increase or decrease abundance as shores became more sheltered; as high exposure transitions to more moderate exposure, populations of key rocky shore species might become less stable with greater frequency and magnitude of fluctuations in density and space occupancy (Roughgarden *et al.*, 1985; Hawkins *et al.*, 1992). As mentioned earlier, the role played by exposure on any organism's survival may be determined by many causative agents acting on different life stages. The response of rocky shore assemblages, species populations, and individual organisms to changes in exposure is the major theme throughout this project and will be discussed in greater detail in Chapters 3-5.

1.6 Climate change:

In addition to potential ecological consequences following deployment of WECs, changes to rocky shores resulting from global climatic change are becoming increasingly apparent. The biota of intertidal areas already experience considerable seasonal fluctuations (owing to cycles in temperature, light, nutrients, etc.) and longer-term trends linked to the local effects of large-scale climatic variables such as the Atlantic Multidecadal Oscillation (AMO) (Knight *et al.*, 2006; Delworth *et al.*, 2007), the North Atlantic Oscillation (NAO) (Hurrell, 1995; Pingree 2002), and the Russell Cycle (Russell, 1973; McManus *et al.*, 2015) may play some role in driving observed community changes (Hiscock *et al.*, 2001; Broitman *et al.*, 2008; Mieszkowska *et al.*, 2014). Of particular concern for designing long-term monitoring strategies are changes in the global marine climate. This is manifest most obviously in increased sea temperature, but includes other important considerations such as rising sea level (Rennie and Hansom, 2011; Church *et al*., 2013), increased atmospheric temperature (IPCC, 2013), increased winter storminess (Young *et al*., 2011; Collins *et al*., 2013; Woolf and Wolf, 2013), and ocean acidification (Ciais *et al*., 2013). In addition, global climatic change may alter other long term meteorological patterns such as the aforementioned AMO and NAO. A graph showing recent global increases in combined ocean and land surface temperature is presented in Figure 1.8; over the past three decades, sea surface temperatures in UK coastal waters have risen by an average of 0.3°C per decade (Dye *et al*., 2013). Recent predictions of global sea temperature changes suggest a 2°C increase by 2100 (Collins *et al*., 2013).

Shifts in species range are a predicted consequence of global climate change (IPCC, 2013). Species unable to respond rapidly may face the risk of extinction, reducing global biodiversity (Sala *et al*., 2000; Frost *et al*., 2016). Patterns of climate change are highly variable; different rates of warming, as well as cooling, are occurring in different regions (Burrows *et al*., 2011). As a general statement, temperatures over land have risen faster than sea temperature, but the rate of shift in both species range and timing of the onset of seasonal events is occurring faster in marine systems, especially in more northern latitudes (Parmesan and Yohe, 2003; Cheung *et al*., 2009). The rate differences between marine and terrestrial ecosystems may be owing to smaller scale seasonal temperature variations normally seen in the oceans relative to land, i.e. moderate changes in sea temperature may have greater impacts on marine organisms than similar changes in atmospheric temperature will have on terrestrial organisms (Burrows *et al*., 2011). For terrestrial organisms, moving to different altitudes may allow survival during changing climate (Parmesan and Yohe, 2003; Heegaard and Vandvik, 2004); a similar option may

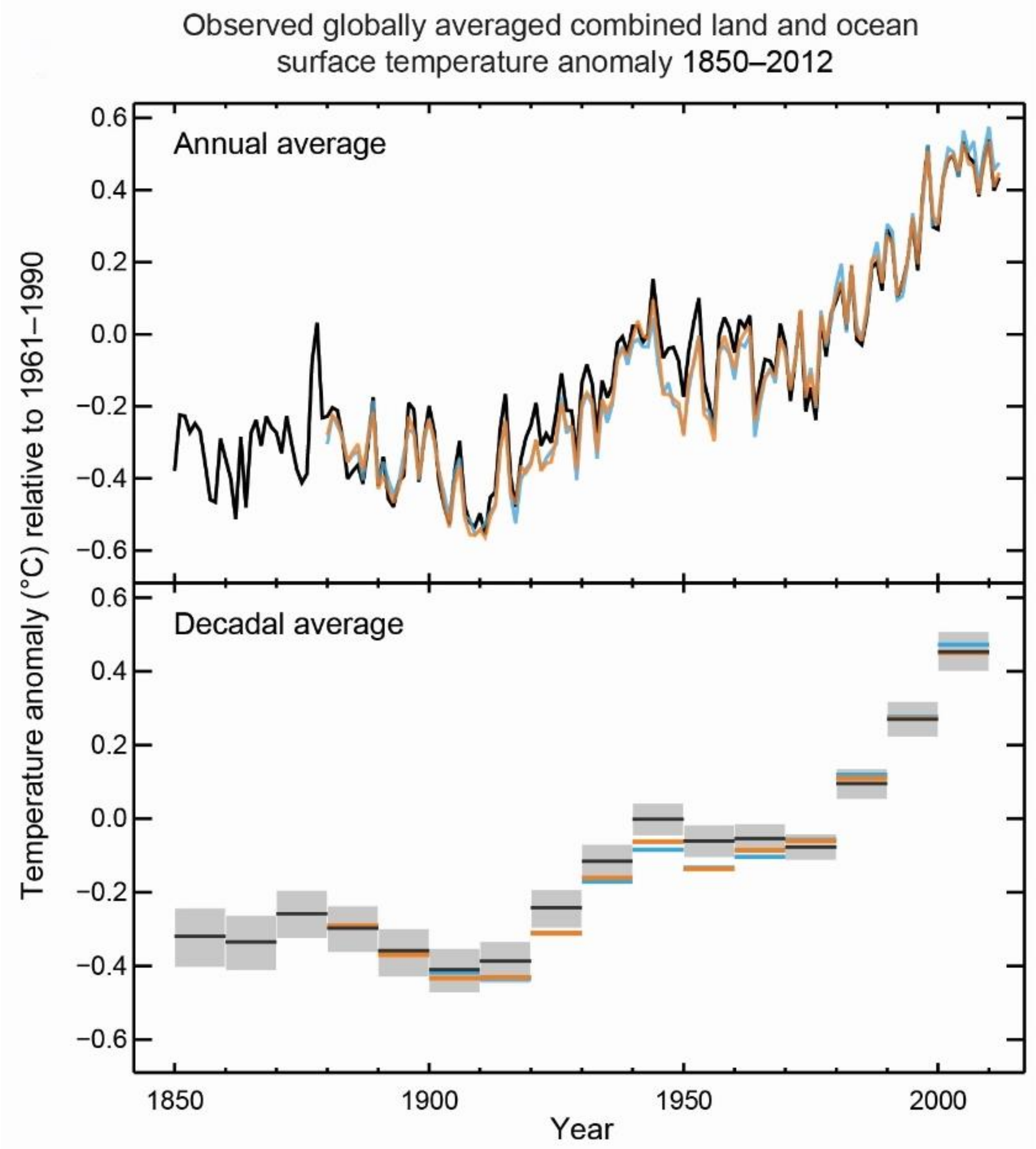


Figure 1.8: Observed global mean combined land and ocean surface temperature anomalies from 1850 – 2012. Anomalies are relative to the mean of 1961 - 1990. From: IPCC (2013).

be available to marine species capable of adjusting their depth, such as certain species of fish (Perry *et al*., 2005; Nye *et al*., 2009). For marine species that cannot adjust their depth, e.g. littoral species, coping with climatic change may be limited to latitudinal range shifts into suitable habitats (Burrows *et al*., 2011). In addition to range changes at population scale, individual organisms have been shown to respond to climate change in a number of ways including phenologically and physiologically, often resulting in increased or decreased growth/fecundity depending on whether conditions become more or less optimal (Kendall *et al*., 1987; Herbert *et al*., 2003; Mieszkowska *et al*., 2006). For example: *Fucus gardneri*, collected from the US state of Washington, responds to increased SST through increased net photosynthesis, peaking at 18°C (Colvard *et al*., 2014); and, increased summer temperatures may prolong release of larvae and lead to additional broods in *Chthamalus* spp. (Burrows *et al*., 1992). In the half century following 1960, spring phenology in the oceans advanced by 4.4 days (Poloczanska *et al*., 2013).

In pelagic studies, the first records of fish species appearing in regions or habitats where they have previously been absent may provide early evidence of distributional changes associated with climatic change (Arvedlund, 2009). Records and abundance of warmer-water fish species are increasing in the North Sea due to regional temperature increases and a recent positive NAO (Edwards *et al*., 2010). In addition, records of organisms occupying the base of the food web include planktonic studies dating back over a century (Russell, 1935; Hays *et al*., 2005). In the North Atlantic, the distribution of warm-water calanoid copepods has been expanding northwards, while the ranges of cold-water species have been contracting (Beaugrand *et al.*, 2002). Studies of calcifying plankton in the North Sea have shown long-term trends in abundance shifts consistent with global climatic change, although the relationship between these observations and ocean acidification remains unclear (Beare *et al*., 2013).

Climate change on rocky shores:

The rich history of rocky shore studies in British waters provides an extensive background by which to compare recent and current species' range and abundance. These studies, and individual species time-series data have formed much of the foundation of the MarClim project which produced a broad-scale characterisation of British rocky shore assemblages and long-term change (Hawkins *et al.*, 2008, 2009; Mieszkowska, 2009; Burrows *et al.*, 2014). Many recent studies have provided evidence of responses to climatic change in littoral organisms, several of which are important in, or near, British waters. As a general statement, in the Northern Hemisphere, the northern distribution limit of warm water species is extending poleward, while the southern distribution limit of colder water species is tending to contract poleward (Southward *et al.*, 1995; Hiscock *et al.*, 2001; Wethey *et al.*, 2011).

One of the fastest range expansions observed in any global system has been a 240 km expansion eastwards along the English Channel over about half a century by the topshell *Gibbula umbilicalis* (Mieszkowska *et al.*, 2006). Similarly, other recent observations along the English Channel have shown that the range of the warm water barnacle *Balanus perforatus* has extended eastward by upwards of 100 km in the past 25 years and is now found in areas along the Kent coast formerly considered too cold for survival through the winter (Herbert *et al.*, 2003); the range of the topshell *Phorcus lineatus* has extended eastwards along the Dorset coast by 55 km over a two decade period (Mieszkowska *et al.*, 2007) (see Figure 1.9). Cold water fucoids *F. spiralis* and *F. vesiculosus* are becoming increasingly restricted to sheltered locations at their southernmost limits (Ladah *et al.*, 2003), while the range of the latter has contracted northwards from West Africa to

Portugal by over 1200 km in the past 30 years (Nicastro *et al*., 2013). Isolated individuals of the warm-water seaweed *Bifurcaria bifurcata* were found at Portland Bill in 2002, and have since become abundant at this location, establishing a new range boundary (Mieszkowska *et al.*, 2006). Meanwhile, towards its southern limit on the north coast of Spain, growth rate and biomass of *B. bifurcata* has decreased from 1977-2007, while *Cystoseira baccata* has responded in an opposite manner (Méndez-Sandín and Fernández, 2016). Relative abundance of the limpet *Patella depressa* was significantly higher during warmer episodes in the latter half of the 20th century (Southward *et al*., 1995; Leaper *et al*., 2002). The kelp, *Laminaria hyperborea*, which forms dense, biodiverse sublittoral forests extending into the littoral zone on higher exposure shores, has been shifting poleward from northern Norway to southern Spitzbergen (Müller *et al*., 2009).

In addition to examples provided above, studies have identified potential rocky shore indicator species which may provide evidence of long-term changes in climate, including species found at or near their distribution limit in Orkney (Hiscock *et al*., 2001; Burrows *et al*., 2014). Brodie *et al*. (2009) have suggested that the boreal fucoid *F. distichus* may be vulnerable to extinction in British waters in the near future. Monitoring studies of the high-exposure, northern kelp, *Alaria esculenta*, have been recommended (Mieszkowska *et al*., 2006). It is well established that gains or losses between the competitive barnacle species *Semibalanus balanoides* and *Chthamalus* spp. in the North Atlantic is strongly related to temperature (Southward *et al*., 1995; Wethey *et al*., 2011; Jones *et al*., 2012). Chthamaloid barnacles reach their cold-water distributional limit in British waters around the Northern Isles of Scotland (Crisp *et al*., 1981), and may be particularly useful in examining responses to climatic change in Orkney. Similarly, Orkney forms part of the northern edge of the rapidly expanding range of the marine snail *Gibbula umbilicalis*.

Potential rocky shore indicator species sensitive to changes in either temperature or exposure located in Orkney waters are discussed in greater detail in Section 2.2.2.

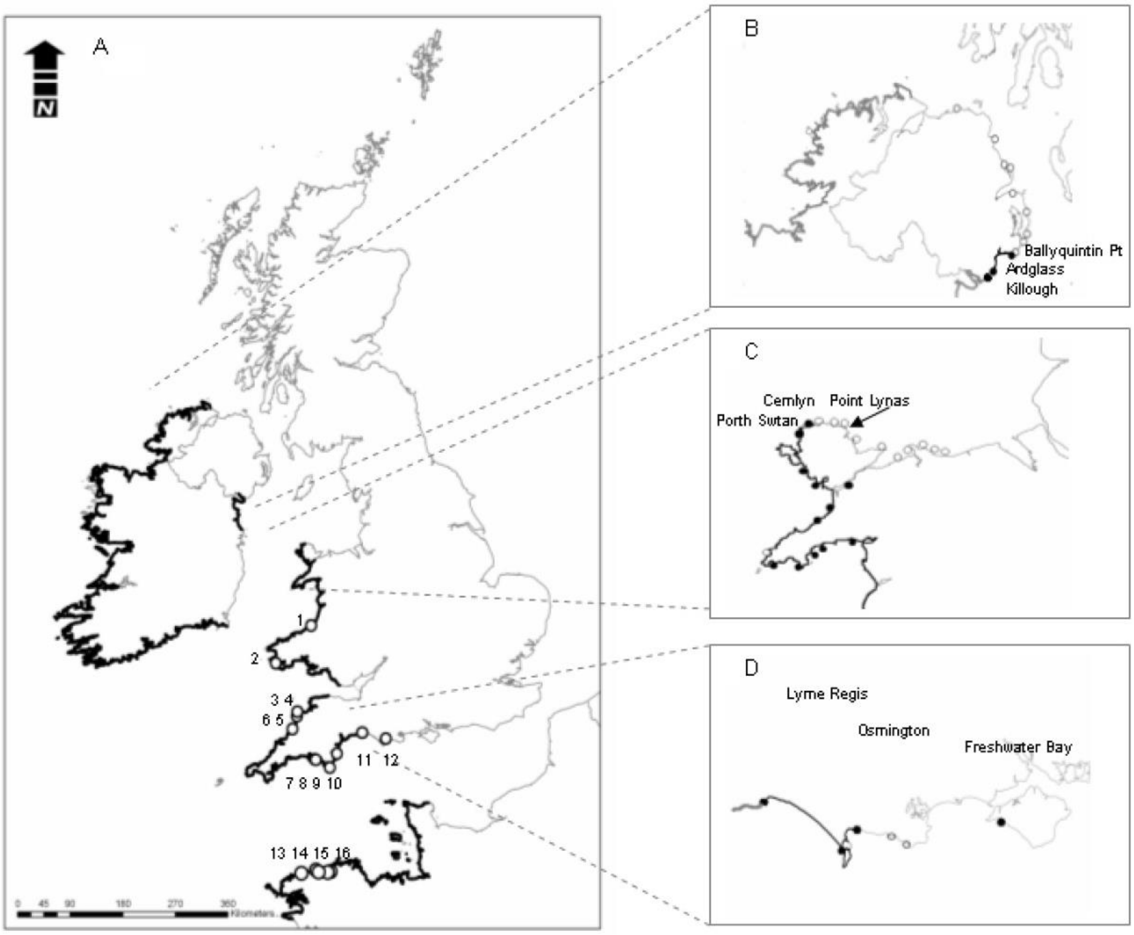


Figure 1.9 Recent distribution range extension of the topshell *Phorcus lineatus*: A) Previous records of distribution and numbered sites reported in the 1950-60s (Southward and Crisp, 1954b; Crisp and Southward, 1958; Lewis, 1964); B), C), and D) recent range extensions in Northern Ireland, Wales, and the English Channel. From: Mieszkowska *et al.* (2007).

Recent cooling periods:

While British waters have generally warmed over recent decades, episodes of marked cooling have periodically interrupted this trend. Short-term cooling periods, possibly linked to cyclical events such as the NAO and the AMO, may arrest, or even reverse, changes in population distributions observed during warming trends. The extreme cold winter of 1962/1963 saw reduction in the eastward limits on the English Channel of some warmer water rocky shore species, including the aforementioned examples of recent expansion, *Balanus perforatus* and *Phorcus lineatus*; extensive mortality was also noted of some key species, such as *Patella vulgata* and *Mytilus edulis* (Crisp, 1964). A major portion of recent expansions observed in the English Channel appear to be reclamation of habitats lost during these more acute cooling episodes (Herbert *et al*., 2003; Mieszkowska *et al*., 2007).

More recently, following a return to a cooling NAO, three consecutive winters from late 2008 until early 2011 were particularly cold in Europe, and included the coldest conditions since 1962/1963 (Wethey *et al*., 2011; Burrows *et al*., 2014). During this recent period, the distribution of the cold-water barnacle *Semibalanus balanoides* extended southwards in Europe at a rate of 20-25 km/year (Wethey *et al*., 2011). This same study found that, following high recruitment correlated with these recent cold winters, the southern limit of the northerly polychaete *Arenicola marina* extended southernwards on the Portuguese coast (Wethey *et al*., 2011). In a review of the distribution in southern England of the peacock-tail alga *Padina pavonica*, an unusual sequence dating back to 1680 has identified several localised extinction events coinciding with periods of cold and stormy weather (Herbert *et al*., 2016). A strong correlation was found between the relative success of the competitive barnacles *Semibalanus balanoides* and *Chthamalus* spp. and the AMO, rather than the NAO (Mieszkowska *et al*., 2014). It is worth noting that this recent acute cold period coincided with the start of preliminary data collection used to inform the current studies. The complexity of interactions between environmental forcing agents also emphasises the importance of caution when assigning causation in time-series studies.

1.7 SuperGen Marine Energy Consortium:

In December 2008, staff at the Orkney Campus of Heriot-Watt University began a 3-year project within Workstream 10 of the SuperGen Marine Energy Consortium to examine the ecological consequences of marine energy extraction (UKCMER, 2017). During this time, I was employed part-time to develop monitoring protocols which might be of value in quantifying the response of rocky shore organisms to energy extraction. This involved selection of rocky shore species and sites, and led to experimentation with several approaches to monitoring long-term change in patellid limpets, fucoids, barnacles, and topshells. This work was completed in December 2011 and a review published shortly thereafter (Want *et al.*, 2014). This studentship represents a continuation and progression of this project; some of the methodological approaches established in this earlier research were subsequently utilised and further developed in the current studies.

1.8 Road map to the current studies:

Rocky shore habitats have been the focus of ecological studies for several decades; broadly-speaking, the relationship between wave exposure and the biological community has been long recognised (Ballantine, 1961; Lewis, 1964). Quantification of wave energy at the shoreline, however, has remained challenging (Peregrine, 1983; Gaylord, 2000). Furthermore, ecological consequences following large scale energy extraction from the marine environment remain unknown (Shields *et al.*, 2011). The research presented here describes the approach taken to studying ecological responses in the intertidal zone which may be indicative of wider environmental changes. This research was chiefly conducted on Orkney, an area where large scale deployment of WECs is anticipated in the near future. Exposure is the most obvious physical gradient along WMO and is of the greatest interest to WEC developers. The location of Heriot-Watt University's campus in Stromness allowed all year access to this important coast, with the nearby rocky shores serving as a 'living laboratory'.

In Chapter 2 ("Setting the scene: methodological development of long-term littoral studies on West Mainland, Orkney"), preliminary studies are described where potential indicator species used to detect changes in exposure and climate on rocky shores are considered, and suitable study sites on Orkney are identified. A strategy of using paired-species monitoring to study responses along environmental gradients is introduced. In some cases, selected species are not well represented in the scientific literature; gaps exist in what is known about how certain species respond to change, especially at the limit of their distributional range. Chapter 2 concludes with an assessment of local wave and temperature data which are used in subsequent chapters to compare biological responses to environmental variables. In addition to using species-based studies, the ecological consequences following deployment of WECs into leased sites along large portions of WMO lends itself well to a Before-After-Control-Impact (BACI) study design (Underwood, 1994). In Chapter 3 ("Before impact and control assessment of WMO: the relationship between topography, wave exposure, and the littoral community"), an extensive survey of the littoral community along WMO is described including areas where wave energy extraction impacts are most expected and control sites of similar exposure but distant from planned WEC deployments. These data provide a detailed 'before-impact' description of the rocky shore biological community available to inform comparisons after wave energy extraction has occurred. In addition, these also provide baseline data for monitoring impacts of other long-term forcing agents, such as climatic change. Many of the sites surveyed have never previously been described in scientific detail owing to difficulties of access. Chapter 3 also considers the relationship between topography and dissipation of wave energy impacting the biological community using data collected during these surveys; several established exposure indices are compared with and without topographic modification. Comparing assemblages from locations of differing topography provides a spatial proxy for responses in littoral organisms following removal of wave energy.

Studies of potential indicator species, identified in Chapter 2, followed established methods using previous work as guidelines (e.g. Southward *et al.*, 1995; Wolcott, 2007) and, when necessary, novel approaches were explored and developed. In Chapter 4 ("Assessment of *Fucus distichus anceps* as an indicator species of wave exposure and climatic change"), studies of the high-energy variant fucoids, *F. distichus anceps* and *F. vesiculosus* f. *linearis* are assessed in terms of their suitability as indicator species for changes in wave exposure and climate. Fucoid responses to seasonal variation in wave exposure and temperature was examined by comparing growth and abundance data with various meteorological indices. Similarly, in Chapter 5 ("Long-term monitoring of littoral barnacle recruitment at the northern distribution limit of *Chthamalus* spp."), the competitive relationship between two important littoral barnacle species, *Chthamalus stellatus* and *Semibalanus balanoides*, is examined in greater detail. Acute temperature changes during the study period allowed the opportunity to examine the response in barnacles, and consequences to the barnacle zone following alteration in wave energy exposure were examined. Experimental manipulation of free space allowed study of resource competition and behaviour-mediated recruitment. Finally, in Chapter 6 ("Conclusions and suggestions for further work"), an overall appraisal of the strategies utilised in the current studies is conducted, including a critical review of methods, and recommendations for improvement. The key findings at both species and assemblage level are reviewed, and unresolved or new questions are discussed. Additional species identified as potentially valuable indicators of long-term ecological changes for future studies in Orkney are recapped.

Chapter 2 - Setting the scene: methodological development of long-term littoral studies on West Mainland, Orkney:

2.1 Introduction:

The rocky shores of West Mainland, Orkney are characterised by westward-dipping platforms beneath spectacular, sheer cliffs. The tide is semidiurnal with maximum amplitude of 4.5 m. The coast is extremely exposed; significant wave height recorded offshore is frequently >5 m and maximum wave periods frequently above 20 seconds. Within these areas of extreme wave energy are less extensive habitats created by caves and small rocky inlets (known locally as 'geos'), as well as a few larger embayments which allow significant sediment deposition. Differences in wave exposure created by these geological features may play a major role in determining community composition. Low light levels will be an important factor in sea caves, frequent along parts of this coast; small streams draining higher coastal areas create localised littoral areas of reduced salinity but no significant rivers empty onto this coast. Development of the WMO coastline is minimal.

Littoral studies in Orkney:

North of the EMEC wave test centre at Billia Croo, the cliff-dominated coast of WMO extends 23 km from Black Craig to Birsay Bay (Figure 2.4.2) of which only about 7 km of shore is accessible by foot. Owing to these difficulties in access, there has been limited scientific evaluation of the existing biological community along most of this coast. A number of important studies have occurred at some sites along WMO: some examining individual species such as *Fucus distichus* (Powell, 1963) and *Patella vulgata* (Baxter, 1983); and others looking at broader groups of organisms (Wilkinson, 1975; Wells *et al*., 2003). In the 1970s and 1980s, monitoring associated with the development of an oil terminal in Scapa Flow resulted in some published work on rocky shore ecology, particularly involving patellid limpets (Baxter, 1982, 1983; Baxter *et al*., 1985). In the 1990s, a characterisation of marine biotopes in Orkney was made as part of the MNCR programme (Murray *et al*., 1999). This included a large portion of south-west Mainland, specifically the high-energy coastline from south of Billia Croo (prior to its development as the EMEC wave test site) north to the Bay of Skaill. In total, the MNCR surveyed seven littoral sites north of Billia Croo, along the coast where commercial-scale WEC deployment is proposed. More recently, the MarClim project has featured data collected on Orkney shores (see Burrows *et al*., 2014 for review of publications). Additionally, littoral knowledge of the local biological community has been complemented by sublittoral work conducted by Marine Scotland Science in 2009 to establish base-line conditions before marine renewable energy device deployment (Moore, 2010; Baxter *et al*., 2011). Furthermore, with specific regards to the developing marine renewable energy sector, there are a number of environmental reports produced by consultancies for developers. These reports however, are not peer-reviewed and are protected by confidentiality.

The rocky shores of WMO provide an important opportunity to study intertidal community structure before and after large-scale extraction of wave energy. The extensive coastline also provides potential study sites close to proposed deployments, where consequences of energy extraction would be most expected to occur, as well as more distant sites which may serve as controls where consequences of wave extraction would not be expected. Orkney features a high diversity of rocky shore organisms (Burrows *et al*., 2008) including many species which have been identified as potential valuable indicators of long-term environmental change in Scotland (Hiscock *et al.*, 2004). Year-round residence in Orkney by the author has provided the opportunity to study extensive areas not previously surveyed in scientific detail and during seasons less frequently used for field sampling.

Wave exposure on WMO:

Wave energy is one of the most important factors determining marine species distributions and community structure along rocky shorelines (Lewis, 1964). This is typically manifest as differences in vertical distribution of organisms correlated with energy exposure with upper littoral zones more strongly linked to wave energy than lower zones (Thomas, 1986). Since the entirety of WMO is encompassed within a modest extent of approximately 25 km, it is assumed that climatic and oceanographic regimes are relatively similar along the entire coastline. Predominant wind and wave direction is from the west (Figure 2.3.5) meaning that the westerly-orientated cliffs are directly facing the dominant fetch. In addition to the few embayments, the presence of the high island of Hoy, and Cape Wrath further afield, might be expected to modify waves towards the southern parts of WMO (especially during episodes of more southerly winds).

Additional variables that might create differences in the biological community along WMO were discussed in Chapter 1 and include nutrient concentration, light and salinity (Lewis, 1964). While seawater nutrient concentrations can differ between geographically-close sites (Blanchette *et al*., 2000), in highly energetic waters, such as those off WMO, nutrients are well-mixed and concentration would not be expected to vary substantially (Burrows *et al*., 2008). Rocky shores generally have high water clarity due to low levels of suspended particulate matter in the water column or fine sediment close to shore; this allows light to reach kelps and red algae enabling them to survive at greater depths than near shores dominated by sediment outflows. In certain areas, such as the Solway Firth and the Clyde Sea, higher levels of suspended sediment or phytoplankton can reduce clarity (Burrows *et al*., 2014). The break-up of organic matter and the subsequent undercurrents created by wave action can favour benthic filter feeders including sponges and molluscs, such as mussels (Westerbom and Jattu, 2006).

Biological responses to environmental changes:

Changes in the abundance of a species in relation to a gradient of environmental conditions are often visualised as taking the form of a bell-shaped curve (e.g. Gauch and Whittaker, 1972). According to this simple model, there is a peak of abundance that occurs at an optimum on the environmental gradient representing conditions that are most suitable for the species. The whole ecological niche of a species is defined in terms of responses to many such environmental gradients. In reality, these multiple gradients may be complex and interactive in their effects, but the simple idea that environmental optima exist has important implications for the design of monitoring programmes. It means that, depending on starting conditions, responses may be either to increase or decrease in abundance with any given direction of change in environmental conditions. If conditions are close to the optimum for a species at a given location, any change in environment will likely lead to an eventual decline in its abundance at that location. Using wave energy as an example, even slight shifts in an organism's survivability on exposed shores may have substantial consequences for the overall population (Blanchette *et al*., 2008). However, unless the environmental preferences of a given species are known rather precisely, and unless also the baseline environmental conditions can be measured with equal precision, it may be unwise to base monitoring programmes on the responses of individual species.

Measuring changes in the composition of assemblages of multiple species is often used in benthic impact studies (e.g. Benedetti-Cecchi *et al.*, 2000; Pranovi *et al.*, 2000). This approach was taken in an extensive survey of high energy rocky shores described in Chapter 3. However, the first approach to measuring biological responses to changes in wave energy acting on rocky shores was instead to consider carefully chosen pairs of species, where each indicator or sentinel species was matched with a second similar species with known differences in environmental preferences. Knowing that one species differs from a second species in terms of its occurrence in relation to wave exposure (or other environmental variables) is a much less challenging requirement than having to identify how conditions at a given site match up with the precise preferences of a single species.

The use of species pairs, and of 'indicator species' more generally, to index changes in marine environments has a long pedigree. Russell (1935), for example, demonstrated that changes in the proportions of two chaetognath species in plankton samples from the western English Channel were related to large scale patterns of movement of oceanic and shelf water bodies. More recently, long-term changes in the proportion of warm water *Chthamalus* species in intertidal barnacle populations ('Barnacle Index') have been related to changes in water temperature at a site near Plymouth (Southward, 1967, 1991; Southward *et al.*, 1995). When designing effective monitoring programmes, species pairs may be of greater utility than single species: while the abundances of individual species are likely to show unimodal patterns of variation in relation to a given gradient of environmental change such as exposure to wave energy, i.e. over different ranges of the environmental variable they show increases as well as decreases for any given direction of change, the proportion of each species in a pair is much more likely to change in one direction only (Figure 2.1a). All that is necessary to interpret a change in species proportion is to know that one species differs from the other in its preference (or tolerance) for a given environmental variable.

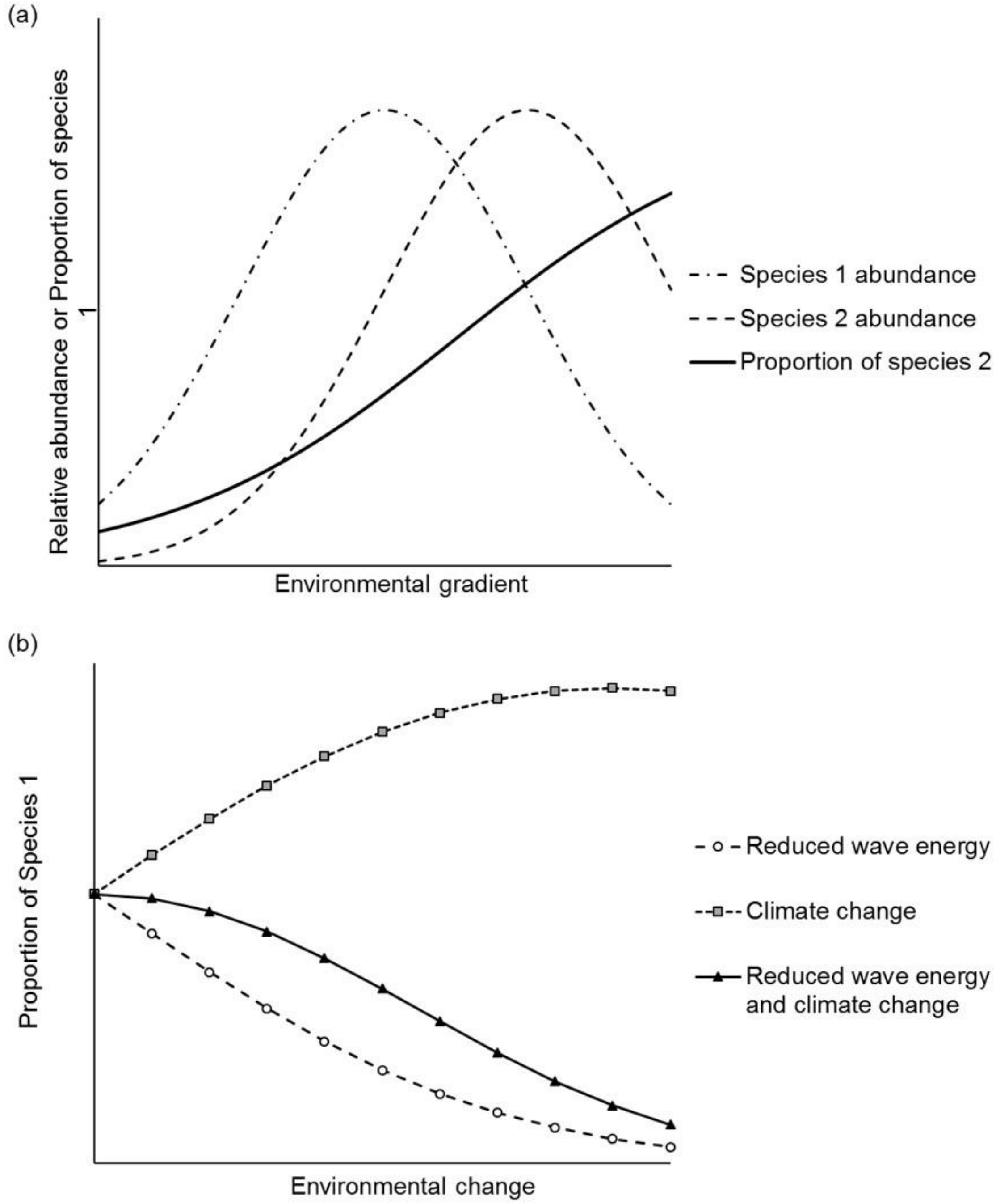


Figure 2.1: Use of paired species monitoring to detect biological responses to environmental change: (a) abundance of individual species and proportion of one species in relation to an environmental gradient; (b) modelled response of species proportions to environmental changes, when species 1 is disadvantaged by reduced wave energy and favoured by climate change. From: Want *et al*. (2014).

The use of paired species also offers at least two other advantages over single species monitoring protocols. Firstly, measuring species proportions does not depend on determining absolute densities, i.e. numbers per unit of habitat area. Quantifying habitat areas is a notoriously difficult task in structurally complex rocky shore environments. All that is required for estimating meaningful proportions is that the sampling efficiencies are comparable between the two species, or are at least stable in relation to changes in the environmental variable of interest. This is a reasonable assumption for pairs of species that are similar in conspicuousness (e.g. limpet species). Secondly, the statistical power to detect changes and correctly identify their direction has been shown to be consistently higher across the range of environmental conditions for species proportions than for single species abundance (Want *et al.*, 2014). If, as is likely for closely related species, there are features of the environment (other than the variable of interest) that favour both species rather than one at the expense of the other, the statistical power of the proportional variable to detect change will increase still further.

Detecting responses against a background of other environmental changes:

In designing a monitoring programme to detect biological responses to wave energy extraction, it is important to recognise that reduced exposure is probably only one among many ongoing environmental changes that influence life on rocky shores. Climate change has already been highlighted as an important driver of change for marine organisms; depending on the species, this has the potential either to augment the expected direction of response to energy extraction, making it more difficult to assign causality, or else to dampen, cancel out or even reverse the expected response. Without accounting for concurrent climate change, there is a strong risk of drawing wrong conclusions from monitoring outcomes – either concluding that energy extraction has had no effects, when climate change has obscured or compensated the response, or wrongly ascribing changes to the effects of energy extraction when climate change has been the real forcing agent.

The potential for multiple and confounding influences on response variables does not in itself invalidate the use of indicator species and the paired species protocol to monitor the biological consequences of energy extraction. However, it does mean that care must be taken in the selection of species for monitoring to ensure that the contributions of different forcing agents are clearly separable. In the present study, several pairs of species were considered, differing in their expected magnitude and directions of response to reduced exposure and climate change. Figure 2.1b illustrates notional responses for a species pair in which species 1 is expected to be disadvantaged by reduced wave energy and favoured by climate change. In this example, concurrent climate change would make it more difficult to detect responses to reduced wave energy. Other examples could have been constructed showing very different response patterns, depending on the location of optimum environmental conditions for each species in relation to baseline conditions. By careful selection of a suite of indicator species, the capability to detect biological responses to wave energy extraction may be possible by the differential patterns of response expected under any given scenario of environmental change.

2.2 Rationale and preliminary surveys:

This research has focused on exposure and the relationship with the rocky shore community; wave energy is the most obvious physical process affecting WMO and is of the greatest interest to WEC developers. Research developed here has also been cognisant of other long-term forcing agents, most notably climatic change manifest as increasing temperatures. This chapter details steps taken as groundwork in establishing more focussed studies, described in Chapters 3-5. Provided here are criteria used to identify which rocky shore species may be of value as indicator species of long-term environmental change. For each potential indicator species, a suitable congener or closely related species has been selected to allow paired-species monitoring methods to be utilised. Locations of study sites and options for monitoring strategies appropriate for selected species are considered. Studies of ecological response to change in exposure or temperature require comparison between biological and environmental data. Characterisation of the WMO environment in the present study includes analysis of meteorological data, specifically wave and temperature indices.

The coastline of WMO from Billia Croo to Birsay runs on a generally straight north to south axis orientated to the west (Figure 2.4.2). The rocky shores forming the bases of the cliffs along WMO are composed of Devonian sandstone dipping offshore in a generally westerly orientation. On average, these platforms dip at approximately 12° (ranging from 3° to 20°). Rocky shore communities along large areas of WMO shores are characterised by organisms generally adapted to extreme wave energy exposure - the most common littoral assemblages feature *Alaria esculenta*, *Chthamalus stellatus*, *Corallina officinalis*, *Mastocarpus stellatus*, *Mytilus edulis* and high-energy variant fucoids with the shallowest edge of an extensive *Laminaria hyperborea* forest exposed at low tide.

The assemblages do, however, vary somewhat between rocky platforms of different slope. On lower gradient platforms, canopy-forming *Fucus vesiculosus* f. *linearis* is common; beneath the canopy and on open surfaces are the ubiquitous microphagous grazing limpets, usually *Patella vulgata*; and *Laminaria digitata* forms a zone at the boundary leading to the sublittoral forest of *L. hyperborea*. On higher gradient platforms, fucoid cover thins and is frequently represented in the mid shore by the small *Fucus distichus anceps*; there are typically fewer limpets on these shores with an increasing proportion of *Patella ulyssiponensis*; and the dominant kelp on the lowest littoral and shallow sublittoral is *A. esculenta*. Barnacle zones are well developed along most of WMO. Lower gradient platforms tend to feature more *Semibalanus balanoides* relative to *Chthamalus stellatus*, and upper shore barnacles include *Chthamalus montagui*. Higher gradient shores tend to feature more *C. stellatus* relative to *S. balanoides*, and less *C. montagui*. On the exposed lower and mid littoral rocky shores of WMO, non-limpet grazers are limited to *Calliostoma zizyphinum* and abundant *Melarhaphe neritoides*, the latter typically found in empty barnacle shells and crevices. Mobile sublittoral organisms, such as *Echinus esculentus*, may follow the rising tide to graze this area during periods of immersion but generally avoid shallow water on more energetic shores (Bekkby *et al*., 2014).

2.2.1 Selection of indicator species:

Selection of species which might serve as valuable indicators of long-term environmental change was considered using an approach modified from Hiscock *et al*. (2004). In the present study, selection was weighted towards species with preference towards higher levels of exposure, and whose geographic distribution limits are found in, or near, Orkney waters. Selection was based on two premises, that: species favouring more sheltered conditions will benefit from wave extraction, while species adapted to higher energy environments will be adversely affected; and, with increased sea temperature, northern species may vacate this area; while, southern species will move north providing there are no biogeographical or hydrographical barriers preventing movement (Crisp and Southward, 1953; Lima *et al*., 2007). Presumably the strong tidal currents and width of the Pentland Firth may act as a barrier to some organisms extending their range from northern Scotland to Orkney. Several life history factors can be examined to determine whether or not an organism is suitable for consideration as an indicator of environmental change. The following criteria, adapted from Hiscock *et al*. (2001), have been used to select species for consideration in this long-term monitoring programme:

(a) Association with shores ‘downstream’ from exploitable wave energy; can they be studied in areas of potential WEC deployment?

(b) Populations at or near their range limits in local waters may be more responsive to environmental factors affecting their distribution.

(c) Mobility of existing populations, i.e. are they dependent on larval dispersal to increase distribution or can individuals propel themselves?

(d) Longevity of the individual: populations of short-lived species will respond faster than those with increased longevity.

(e) Type of reproductive and/or dispersal mechanisms which favour extending distribution, i.e. motility of larvae or length of larval stage, i.e. populations with greater dispersal capability may be able to respond to changing environments more easily.

(f) Contribution of viable larvae from individuals – non-gamete producing ‘outliers’ will not contribute.

(g) Larval and adult temperature tolerance – less tolerant species should experience more rapid distribution changes following temperature changes.

(h) Suitable habitats for extension of range during dispersive stages.

(i) Geographical barriers preventing spread – near Orkney, the hydrodynamic characteristics of the Pentland Firth may retard the movement of certain species.

Ideally, candidate species should include a broad range of short-lived, high-energy adapted, temperature- sensitive organisms living at the extremes of their range distributions. This would enable detection of responses to energy extraction while accounting for long-term responses to changes in temperature. Based on these criteria, a list of candidate species was produced including an appropriate congener or closely related organisms to allow for paired species studies.

2.2.2 Candidate species:

Based on the selection criteria described above, several species were identified as potential indicators of long-term change in Orkney (Table 2.2.2). Evidence suggests these species are good candidate indicators for changes on WMO following energy extraction, climate change, or a combination of these two forcing agents. Following field observations, four species were short-listed owing to overall suitability based on certain selection criteria or practicalities of study in Orkney waters: *Chthamalus stellatus, Fucus distichus anceps*, *Gibbula umbilicalis* and *Patella ulyssiponensis*. Detailed studies of *Anemonia viridis* and *Tectura testudinalis* were not progressed at this time owing to their preferences for more sheltered habitats, and low incidence and abundance of these species in Orkney. Opportunistic data collection continued however, and future consideration of these species is recommended.

The short-listed organisms have all been previously identified as potentially valuable indicators of long-term global climatic change, specifically increased sea temperatures (Southward, 1967, 1991; Southward *et al*., 1995; Hiscock *et al*., 2001; Mieszkowska *et al*., 2006; Wethey *et al*., 2011). *Chthamalus stellatus* has been shown to be particularly

Table 2.2.2: short-list of selected species for long-term monitoring on WMO. All of these species are found at or near their distribution limit in Orkney waters; N/S refers to whether the species are typically ‘Northern’ (‘Boreal’) or ‘Southern’ (‘Lusitanian’); WE refers to species most associated with high wave exposure; and Temp. refers to species identified as sensitive to changes in temperature. Status refers to degree of study presented in this document: a) major focus of study; b) preliminary focus of study; c) not taken forward for further study.

Species	**N/S**	**WE**	**Temp.**	**Status**
Anemonia viridis	S		✓	c
Chthamalus stellatus	S	✓	✓	a
Fucus distichus anceps	N	✓	✓	a
Gibbula umbilicalis	S		✓	b
Patella ulyssiponensis	S	✓	✓	b
Tectura testudinalis	N		✓	c

sensitive to short-term changes in sea and air temperature (Southward *et al*., 1995); range extension or contraction through success or failure of planktonic larvae have been observed within two years of acute temperature events (Poloczanska *et al*., 2008). *Gibbula umbilicalis* is a conspicuous gastropod, which matures at two years of age. Dramatic range extensions have been recorded in the English Channel (Mieszkowska *et al*., 2006) and suitable habitats for continuing expansion exist in Orkney. *Fucus distichus anceps* is a high-energy variant, boreal seaweed found only on the most extreme exposed shores. Reproductive maturity is reached in two years; gamete distribution is highly localised (Pearson and Brawley, 1996). *Patella ulyssiponensis* is found on exposed rocky coasts where their planktonic larvae settle into midshore rock-pools after about four days in the water column. These pools serve as nurseries before, as adults, they migrate to open and lower shore rock surfaces (Delany *et al*., 1998).

In each case, the selected organisms are located at or near their distribution limit in local waters (Figure 2.2.2). It is anticipated that this will increase their sensitivity to a wide range of environmental stressors manifest in observable population changes. In each of the selected organisms, a congener or similar species has been assigned which has overlapping habitat requirements, including the high-energy rocky shoreline. The exact nature of the interaction between these species is not always known: between chthamaloid and balanoid barnacles, the competitive relationship is well established (Connell, 1961a) (See Section 5.1); in other pairings, the degree of direct competition may not be certain. Recommended monitoring consists of both the selected organisms and their pairs as follows: *Chthamalus stellatus* and *Semibalanus balanoides*; *Fucus distichus anceps* and *Fucus vesiculosus* f. *linearis*; *Gibbula umbilicalis* and *Gibbula cineraria*; and *Patella ulyssiponensis* and *Patella vulgata*. In most pairings, one of the species appears to be better adapted to high exposure coastlines where removal of wave energy may be expected to have a detrimental effect (e.g. *Chthamalus stellatus*, *Fucus distichus anceps*, and *Patella ulyssiponensis*). In all cases, the species paired with the potential climatic indicators are more ubiquitous in British waters and have ranges extending far beyond Orkney waters. Widely distributed species located within the middle of their range may be less responsive to local environmental changes than species found at their range limit (Kendall and Bedford, 1987; Poloczanska *et al*., 2008; Wethey *et al*., 2011).

Following preliminary data collection and method development, and owing to available time under the studentship, the decision was made to further focus studies on to fucoids and barnacles. On WMO, *Gibbula* spp. are only located in boulder fields formed in the relative shelter of several large embayments, i.e. Marwick and Birsay bays. The abundance of *G. umbilicalis* was found to be insufficient at these locations for detailed study with limited available resources of time and labour. Data of *Gibbula* spp. were

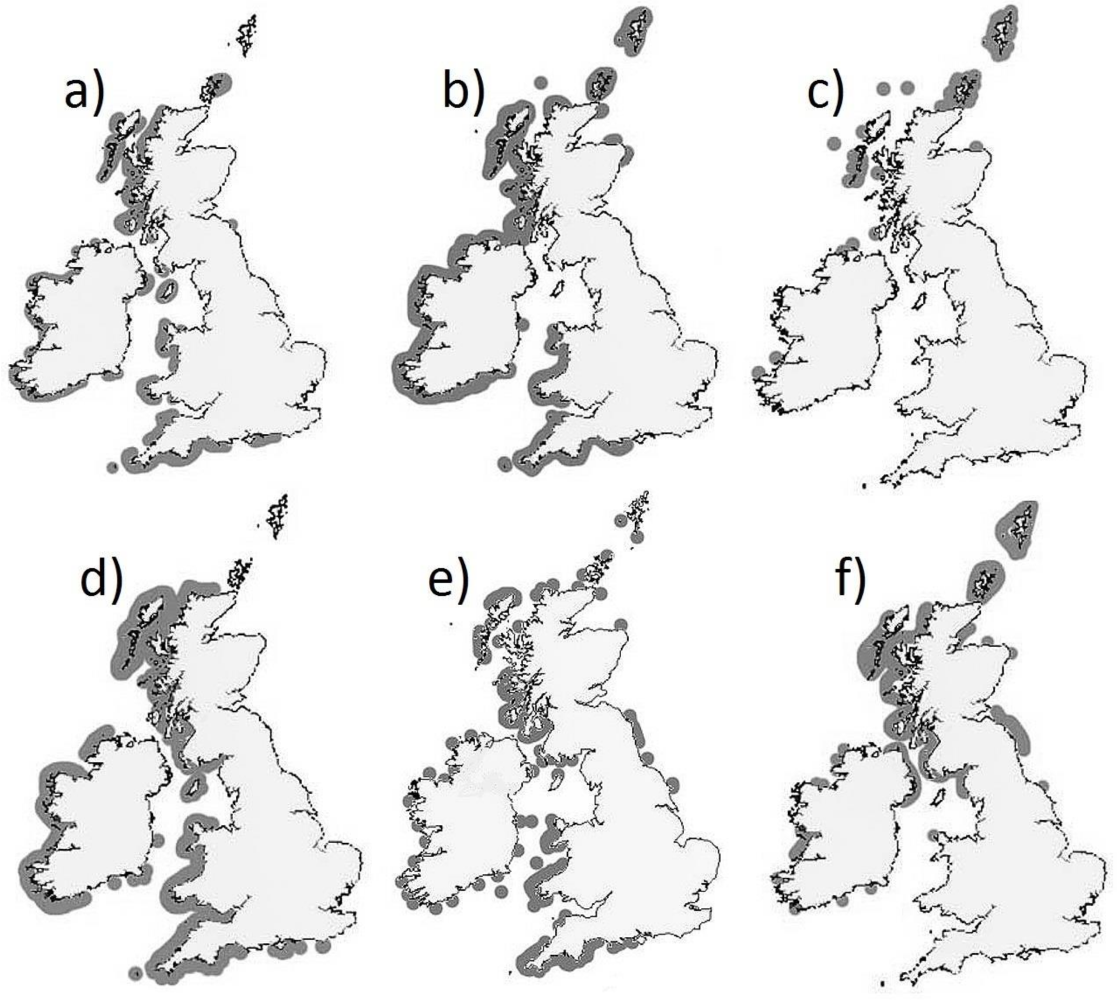


Figure 2.2.2: current distribution in the British Isles of: a) *Anemonia viridis*; b) *Chthamalus stellatus*; c) *Fucus distichus anceps*; d) *Gibbula umbilicalis*; e) *Patella ulyssiponensis*; and f) *Tectura testudinalis*. Modified from MarLIN (2016).

collected opportunistically, and several previously unreported locations for *G. umbilicalis* have been identified (not presented here). *Gibbula* spp. also featured in rocky shore characterisations described in Chapter 3. Patellid limpet studies focussed on abundance and species proportional data, and correlations with various environmental variables collected at 41 sites on WMO and 8 sites on Lewis (see Chapter 3). The present studies recognise that with additional time and resources beyond this studentship, further scope exists for progressing limpet research including conducting manipulative experiments (see Section 6.4: Grazer studies).

2.2.3 Littoral site selection:

In this study of the consequences of wave extraction on WMO, littoral survey sites were selected to conform to a 'beyond Before-After-Control-Impact' (BACI) design (Underwood, 1994). Using this strategy, surveys were conducted in areas where likely effects following environmental change are expected ('impact sites') and areas distant from expected impacts ('control sites'). Surveys were conducted prior to deployment of WECs ('before sites'), and are planned to be repeated following future deployment ('after sites'). Therefore, this study provides data representing 'before' and 'control' states; 'after' and 'impact' states remain to be characterised.

Several sites along the wave-exposed WMO coast were examined and evaluated at low spring tide for the following criteria:

- High-energy environment
- Presence of appropriate organisms
- Stable substrate*
- Accessibility for observation (including health and safety issues)
- Potential for deployment of WECs

*Because these studies focussed on rocky shores and the relationship of the biological community with high exposure, surveys were not conducted in areas with mobile substrates such as boulder fields.

2.2.4 Selected sites:

Three main sites were chosen to establish long-term studies of high-energy variant fucoids and barnacles. These sites best fitted all of the selection criteria described in above. These sites were: Billia Croo (Ordnance Survey Grid Reference [OSGB36]: 101040 N; 322273 E); Marwick (102448 N; 322510 E); and Northside in Birsay (102885 N; 325418 E) (Figure 2.4.2). Based on the Ballantine scale (Ballantine, 1961), Marwick and Birsay are classified as ‘extremely exposed’; the modest embayment at Billia Croo is best described as ‘very exposed’. The seas to 45 m depth off Billia Croo are currently in use as the wave test centre for WECs at EMEC; Marwick is located within the leasing site where the largest WEC array (in 13 m depth) has been proposed; and, Birsay, in contrast, faces the NW rather than due west and is located about 8 km north-east of Marwick. A detailed characterisation of each site is provided in Appendix 1.

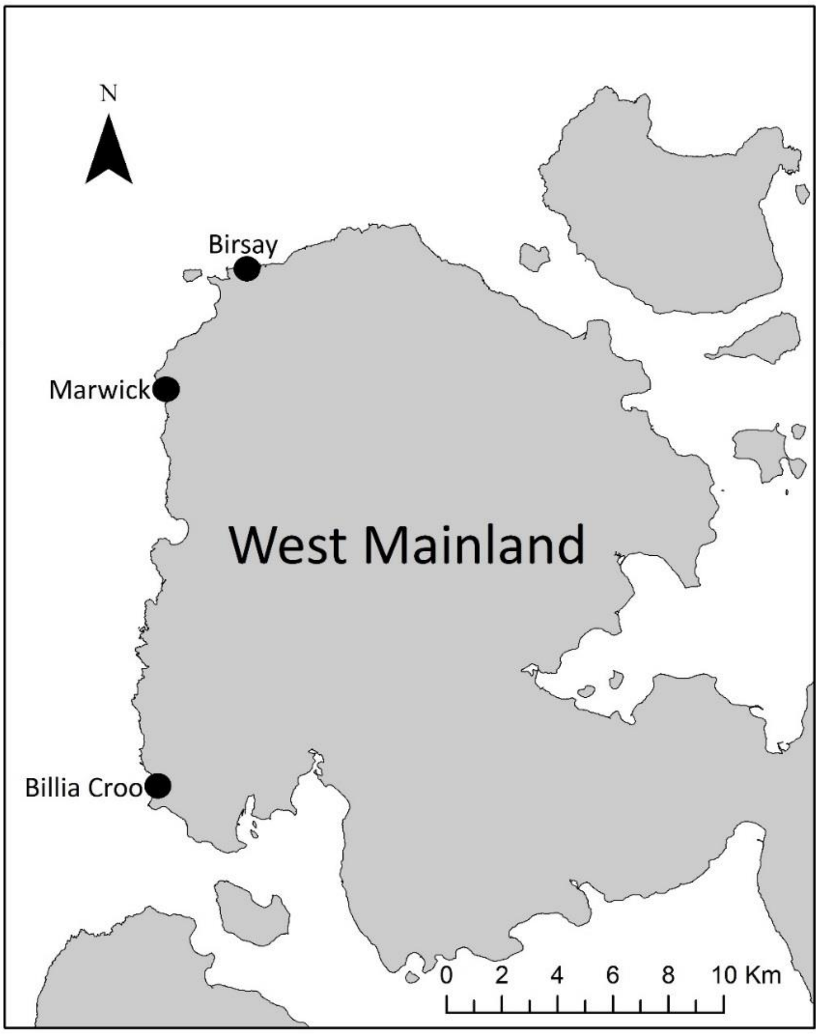


Figure 2.4.2: main research sites - following field assessment, these sites were identified as most suitable for high exposure rocky shore studies using the criteria described in 2.4.1.

2.3 Meteorological data:

Wave, wind, and temperature data were kindly provided by the European Marine Energy Centre. Significant wave height (H_S), wave period (W_P), and sea surface temperature (SST) were collected at 30 second intervals from a Waverider buoy (Datawell, 2016) located off Billia Croo (101024 N; 321155 E) from 2009-2015, covering the years immediately before and during this study. Daily mean atmospheric temperature (AT), and wind direction and speed data (recorded at 5 minute intervals), were collected from the EMEC substation located onshore at Billia Croo (101020 N: 322495 E). Graphs of SST, AT, significant wave height, wave period and wind rose data for Billia Croo are presented in Figures 2.3.1-5. Temperature graphs feature linear interpolation during short periods of missing data. When included in calculation of averages, interpolated data were not found to create any bias. Raw wind data from Billia Croo was converted into mean daily direction and was assigned to 16 directional sectors of 22.5° each. Mean wind speed was determined for each sector and converted from m/s into knots (Figure 2.3.5).

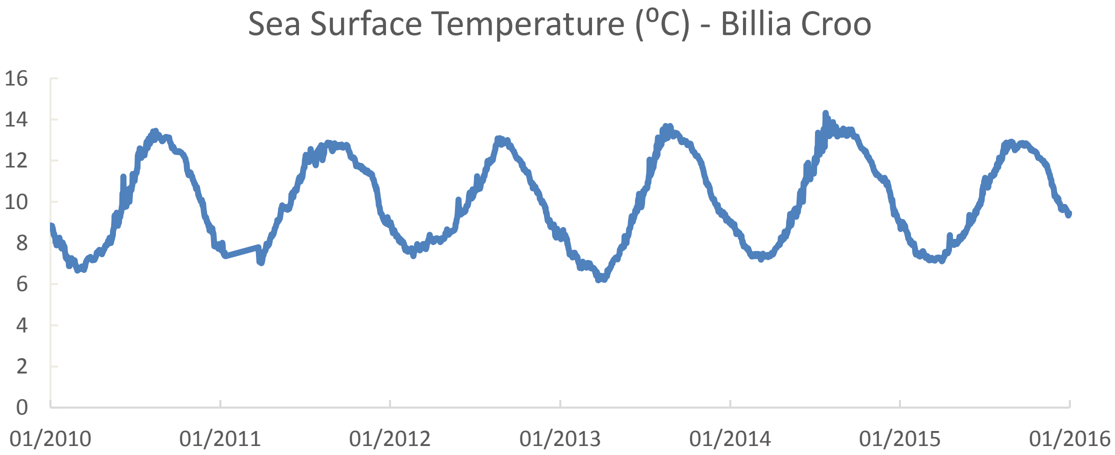


Figure 2.3.1: Mean daily sea surface temperature (°C) recorded by Waverider buoy deployed off Billia Croo.

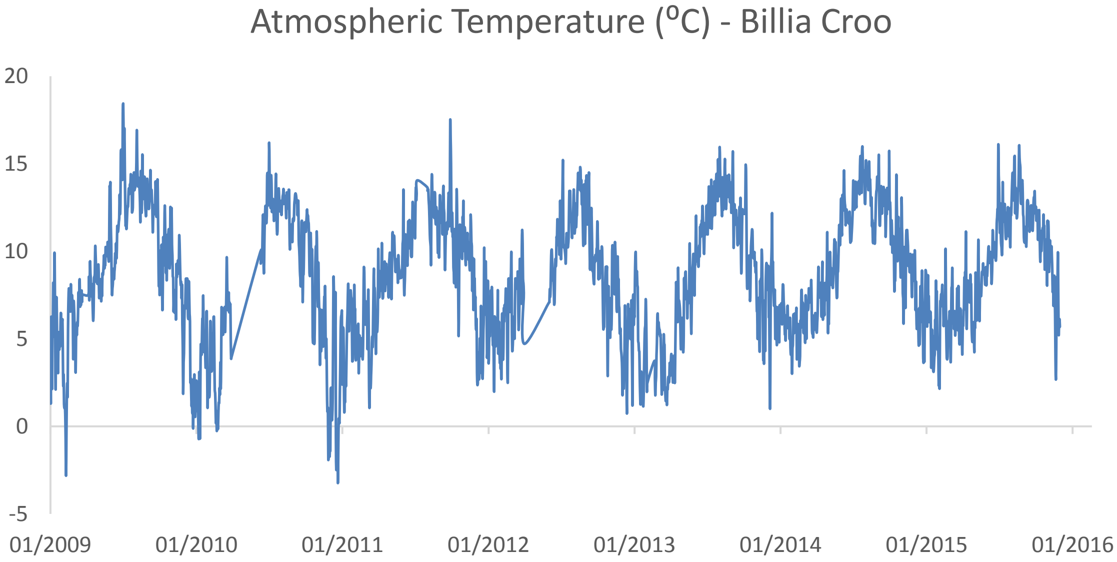


Figure 2.3.2: Mean daily atmospheric temperature (°C) recorded at Billia Croo weather station.

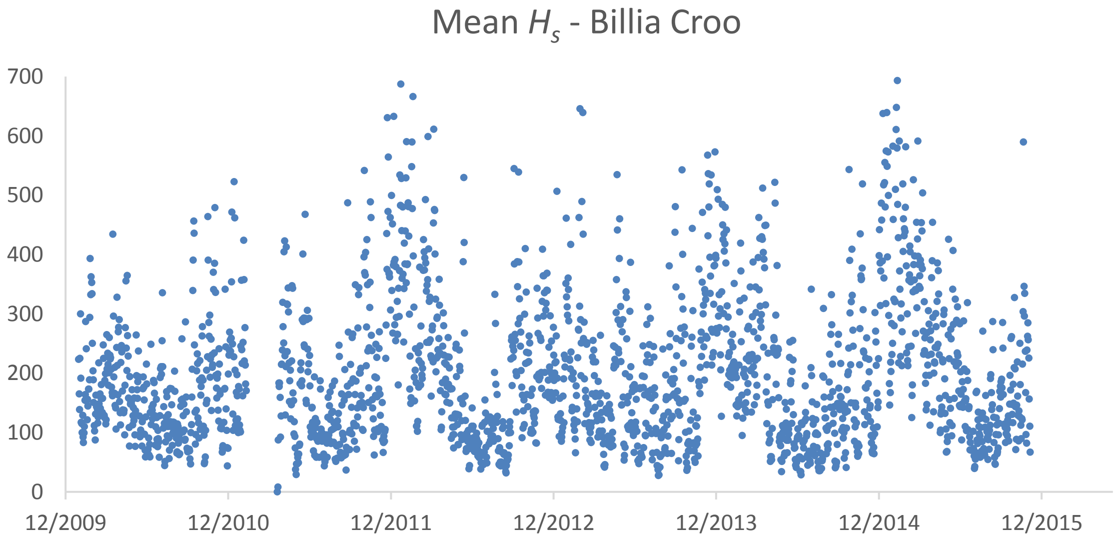


Figure 2.3.3: Mean Significant Wave Height (H_S) in cm calculated daily from Waverider buoy deployed off Billia Croo.

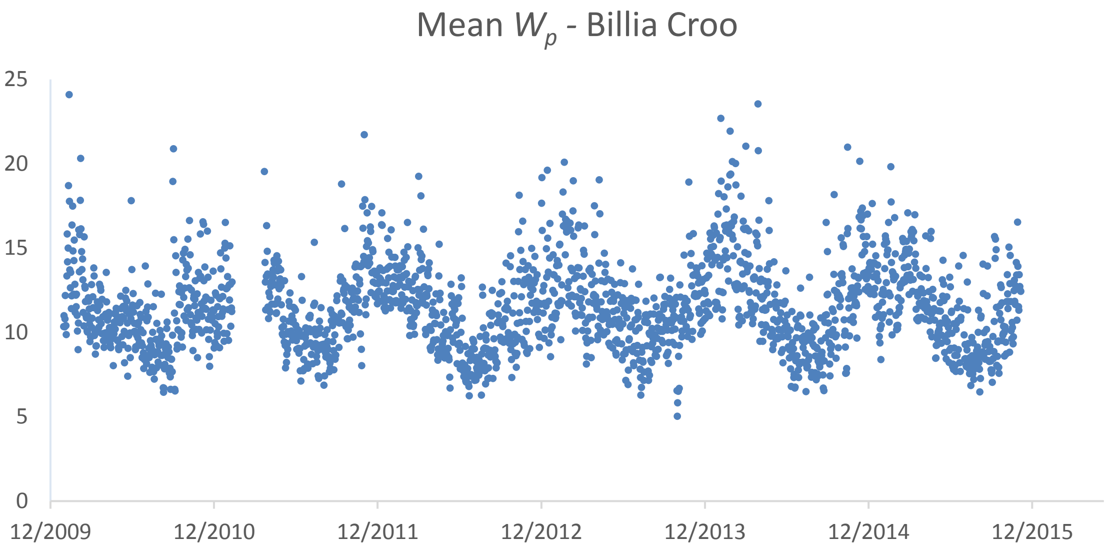


Figure 2.3.4: Mean Wave Period (W_P) in seconds calculated daily from Waverider buoy deployed off Billia Croo.

Subsets of environmental data were applied to biological data, described in greater detail in Chapters 3-5. Wind speed and directional data were combined with fetch data to inform indices of exposure for sites on WMO (Chapter 3); SST, AT, H_S, and W_P were used to examine seasonal changes in fucoid abundance and growth rate (Chapter 4); and, SST and AT were used to examine responses in barnacle recruitment following acute temperature changes (Chapter 5).

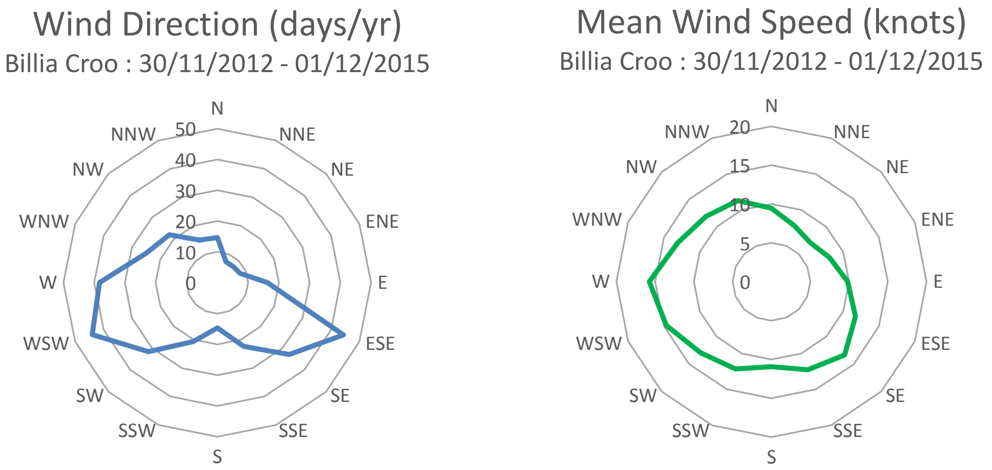


Figure 2.3.5. Wind data (30 Nov. 2012 – 01 Dec. 2015) from Billia Croo assigned to 22.5° sectors: left) wind direction count per sector (mean daily direction/year); right) means wind speed per sector (knots).

2.4 Discussion:

The western shores of Mainland, Orkney provide an ideal ‘field laboratory’ to develop methods and conduct long-term monitoring of rocky shores organisms, specifically in relation to alterations in wave energy profile. The early stage of MRE technologies, and remoteness of Orkney, has meant that the local rocky shore community, and the relationship to exposure, has not been described in great detail by previous studies. There is a richness of candidate indicator species, inclusive of ‘southern’ and ‘northern’ distribution ranges, and, as the major focus of WEC deployment in the foreseeable future, biological studies here are excellently placed to help inform these developments. While deployment of industrial-scale WEC arrays has not yet occurred, other agents of long-term change are apparent: during the years immediately preceding and continuing into the early period of the current studies witnessed some of the coldest winters in almost half a century (Crisp, 1964; Wethey et al., 2011). Reproductive or recruitment failure is important in determining the distribution limits of species (Kendall *et al.*, 1987) and species sensitive to temperature, might be expected to suffer repeated failures and eventual local extinction in response to continuing adverse trends (Southward *et al*., 1995). During such circumstances, reduced fecundity may result in inadequate dispersion of propagules necessary to maintain connectivity at population distribution limits (Gaines *et al*., 2007). In contrast, during periods of favourable temperatures, reproductive successes will tend to promote range extension (Mieszkowska *et al*., 2006; Wethey *et al*. 2011).

The two greatest challenges for this programme are to: (a) identify observable long-term changes; and (b) distinguish between the relative roles that different environmental variables play in these changes. Development of paired-species monitoring and the use of multiple indicators may provide greater ability to dissect out the relative roles of energy extraction from climatic change or other environmental fluctuations. Monitoring a suite of indicator organisms differentially responsive to energy extraction and climatic change may provide greater confidence in determining the relative roles of each environmental variable. The rate of response to environmental changes may vary greatly between species, depending on factors such as mortality, mobility, and reproductive strategy. Observable changes are expected to be first apparent in species most capable of dispersal; amongst benthic species, the greatest response may be in those with a planktonic stage in their life history (Hiscock *et al*., 2001).

The preliminary studies described in this chapter have identified organisms at or near their geographical distribution limits which may serve as indicators of long-term change, as well as additional organisms necessary to conduct paired-species monitoring. Rocky shore locations pertinent to the developing WEC sector have been assessed and selected. These include: a) Billia Croo – the shore facing the EMEC wave test site - where wave energy extraction is limited to individual devices during sea trials; b) Marwick – onshore from the proposed site of the largest WEC array to date – where industrial scale extraction may occur; and c) Birsay – distant from the first phase of planned deployment – where the impacts of wave energy extraction are not expected and may serve as a control. Species and site selection, and the proposed use of paired-species monitoring described in this chapter has formed the base of subsequent studies detailed in Chapters 3-5.

Chapter 3 - Before impact and control assessment of WMO: the relationship between topography, wave exposure, and the littoral community:

3.1 Introduction:

This chapter describes research conducted on WMO to examine the responses in the littoral community to exposure and the relationship with topographical variables which may modify wave energy. In addition to studying selected individual species (Chapters 4 and 5), it was decided to extensively survey the overall biological assemblage along the rocky shores of WMO. The geographic scope of the survey was informed by discussions with the wave energy industry and was designed to provide a BACI-style monitoring programme with multiple control and impact sites (Underwood, 1994). The survey area included rocky shores located within leasing sites for deployment of large-scale WEC farms, thus providing a baseline record to compare with future surveys following device installation. In addition, the survey extended to include areas geographically distant from the leasing sites, thereby producing control shores which may function to contrast with potentially impacted shores. The methods and approaches developed in the present studies may be applied to measurements of biological responses following changes in exposure to wave energy.

Measuring exposure at ecologically meaningful scales:

The descriptive term ‘wave exposure’ has long been used to describe the forcing hydrodynamic stress mechanism that can have a modifying effect on the form and abundance of species within littoral zones. As previously mentioned (Section 1.3: Community classification), early attempts to define energy impacts on the shoreline were based on assigning assemblages within the biological community to an arbitrarily-defined scale of perceived exposure (Ballantine, 1961). This approach is limited in that it is subject to circular thinking, i.e. shores are assigned as 'exposed' because they are inhabited by organisms associated with exposure. Researchers began including physical data in an attempt to quantify exposure and allow more objective comparisons between shores. The earliest approaches to developing indices of shore exposure to wave action derived from physical data were based simply on measuring fetch from charts and maps (Baardseth, 1970). Cartographic methods alone, however, may be insufficient to describe shoreline wave forces because they fail to take into account additional geomorphic variables which modify wave energy (Ruuskanen and Nappu, 2005). Later improvements involved using wind data to weight the fetch in different directions from a site (Thomas, 1986; Sjøtun *et al.*, 1998; Burrows *et al.*, 2008; Sundblad *et al.*, 2014). Such methods remain the basis for habitat classification systems (Connor *et. al*., 2004; EEA, 2008), and have been shown to be useful in characterising exposure and predicting habitat for some species in fetch-limited locations where local wind conditions and aspect are important determinants of wave action (Ruuskanen *et al*., 1999; Bekkby *et al*., 2009). In studies of the west coast of Scotland, wave fetch indices have been shown to explain approximately 50% of variation in rocky shore community abundances (Burrows *et al*., 2008).

Fetch-based modelling has been improved by the inclusion of cartographically-derived topographic features such as slope determined by measuring shore extent (Thomas, 1986; Isæus, 2004; Burrows *et al*., 2008). These models do not, however, describe the slope in the surf-zone where waves break and the hydrodynamic forces are greatest (Denny, 1987; Gaylord, 2000). Simple cartographic measurements may not accurately represent complex modification of wave patterns on shores with relatively complicated geomorphology (Ruuskanen and Nappu, 2005). Furthermore, these models do not account for oceanic swell dominating the wave regime at locations open to a wider range of incoming wind directions (Westerbom and Jattu, 2006; Hill *et al.,* 2010), the typical location where commercial scale WEC arrays are designed to operate. Coastal areas bordering large bodies of deep water are subject to prevailing long frequency swell waves that propagate high energy over great distances. While swell waves possess greater stability in terms of mean energy levels, their direction often bears little correlation with the local and intermittent wind climate (EMEC, 2006).

Direct measurements can be made of offshore wave climate using modern remote technology such as satellite altimeter data together with weather hindcasts. These data have been used to produce a detailed worldwide average wave climate atlas but lack the resolution needed for specific shoreline site assessments (Gulev *et al.,* 2003; Gallagher *et al*., 2014) (see review of satellite missions and validation studies in Ramos *et al*., 2012). More accurately, spherical wave buoys and acoustic Doppler current profilers (ADCP) are often used to measure offshore and nearshore wave fields, allowing direct measurement at renewable energy sites and providing data for wave propagation models (Hoitink *et al*., 2007; Folley and Whittaker, 2009). Both these technologies, however, have serious problems when used in the littoral to sublittoral fringe, mainly owing to breaking waves either creating excessive buoy mooring line forces or entrained bubbles which result in acoustic opacity for ADCPs (Castelle *et al*., 2009). These problems can lead to erroneous or missing data during high energy events. Furthermore, both these *in situ* devices are expensive to purchase and install, making large-scale deployment impractical. The high probability of total loss or severe damage by debris impacts in the littoral zone can quickly make implementing continuous data acquisition uneconomical over prolonged periods.

Inexpensive devices for the measurement of littoral hydrodynamics were created for intertidal studies in 1960s providing a method for measuring maximum wave forces (Jones and Demetropoulos, 1968). These are based upon spring extensional force (Denny, 1983; Fuji, 1988; Bell and Denny, 1994; Castilla *et al*., 1998) designed to record maximum water velocity (the intensity of wave force) to determine the link between hydrodynamics and survivorship, mechanical strength and distribution of particular species. One study using these maximum flow meters showed that it was possible to correlate wave action measurements with offshore significant wave height (Denny, 1995). Other researchers have used the dissolution of plaster blocks to estimate average water flow (Lindegarth and Gamfeldt, 2005; Jonsson *et al*., 2006), although these suffer from limitations of time consuming methodologies and water temperature/flow regimes affecting the rates of dissolution. The key drawback to all these devices is their susceptibility to impact damage and erroneous data induced by coarse sediment and flotsam. The problems described above led directly to the development of the Terobuoy device which uses a sacrificial polymer block to record wave action and direction. Terobuoys have been successfully used to quantify wave exposure at two sites on the rocky shores of WMO (Want *et al*., 2014). Measuring hydrodynamic forces at the spatial scale and locations of the receptor organism of interest, may allow more ecologically meaningful determination of exposure.

Topography and exposure:

Our understanding of wave exposure is made more difficult by the complex interaction of forces as waves break on the shore. In the intertidal zone, where waves break most violently, the biological community is subject to the greatest hydrodynamic forces experienced in nature (Denny, 1987; Gaylord, 2000). The relationship between energy and the rocky shore community, is modified by, amongst other factors, the topography of the coast (Ballantine, 1961; Lewis, 1964) including depth, slope and substrate complexity (Smith, 2003; Folley and Whittaker, 2009; Sundblad *et al*., 2014). While other important factors in determining rocky shore communities have been described (Chapter 1), the present study has primarily focused on the effects of wave exposure, since this is the most obvious physical gradient affecting WMO and is of greatest commercial interest in this area. Since the entirety of the westerly-facing coast of WMO is located within a modest geographic distance and along a generally linear orientation, the overall climatic and oceanic regimes are assumed to be relatively similar along the entire region; assemblage differences between littoral sites along WMO are expected to be most associated with small-scale variation in exposure created by ‘openness’ to fetch and other topographic variables.

Topographic variables:

The steepness of the intertidal zone and nearshore seabed plays an essential role in determining the form of waves as they approach the shore, and affects energy dissipation, from wave to substrate, before the wave breaks in the surf-zone. As a general statement, with increasing substrate steepness, wave form at breaking will tend to transition from: spilling waves (on gentler slopes); to plunging waves; and to surging and collapsing waves (on steeper slopes) (Peregrine, 1983; Smith, 2003). On steeper slopes, wave forms break more violently (Janssen and Battjes, 2007) subjecting littoral organisms to greater forces. On more gradual slopes, energy dissipation begins farther offshore, which may result from shoaling, leading to reduced hydrodynamic forces in the surf zone (Denny, 1995; Smith, 2003). This is graphically illustrated in Figure 3.1.1 which uses four seabed slopes to demonstrate increased wave energy dissipation on lower angled slopes (Folley and Whittaker, 2009). As such, gentler slopes are associated with less exposed assemblages (Ballantine, 1961). Similar to studies by Thomas (1986), Burrows *et al*. (2008) found that fetch-based models relating rocky shore assemblages to wave exposure were improved by including cartographically-defined slope. This was achieved by measuring horizontal shore extent and explained about 10% of variance in assemblage composition.

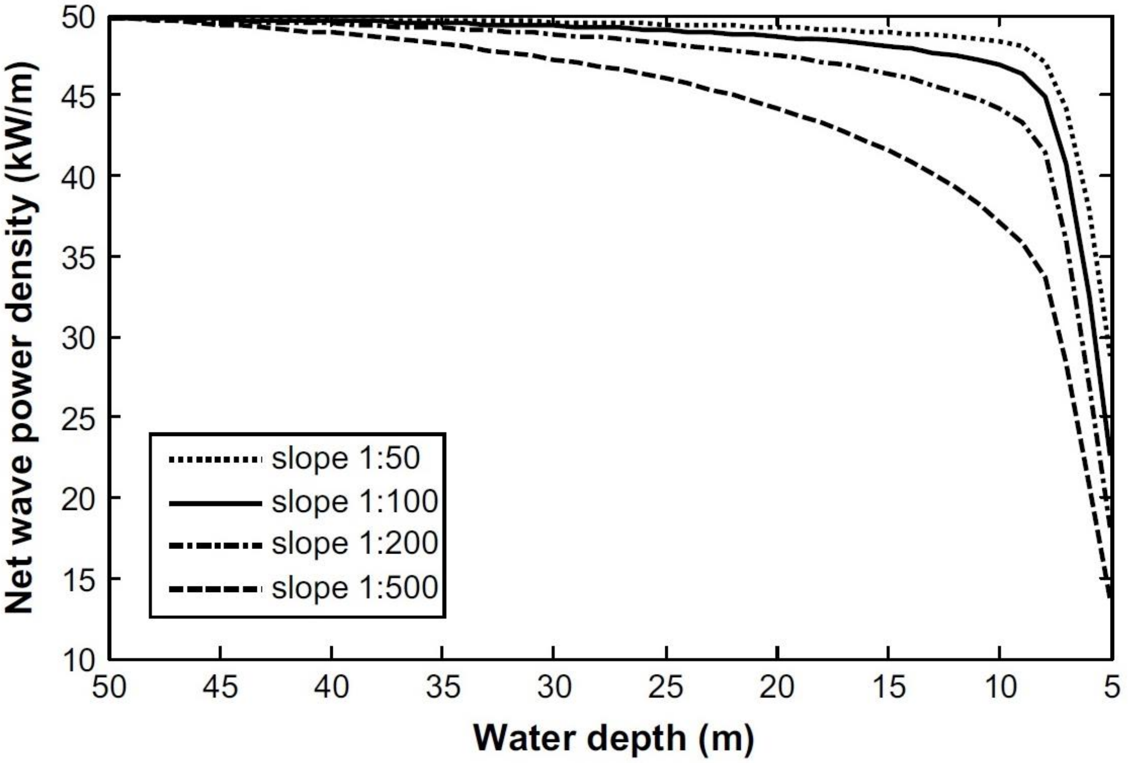


Figure 3.1.1: Shoaling of a 10 second energy period wave propagating orthogonal to depth contours over four different seabed slopes. From: Folley and Whittaker (2009).

Wave dissipation is further increased by seabed heterogeneity, including the presence of offshore reefs where shoaling occurs (Smith, 2003; Lowe *et al*., 2007). The presence of geomorphic features which add complexity to the shoreline would be expected to contribute to further dissipation of wave energy while also creating greater variation in exposure at small scales (including micro-habitats of relative shelter, and increased hydrodynamic forces) (Folley *et al*., 2010). Increased bottom friction, e.g. with extensive kelp forests in the North Atlantic or coral reefs in tropical waters, plays an important role in wave dampening (Mork, 1996; Ferrario *et al*., 2014); this process increases with shallowness and shortening waves (Lowe *et al*., 2007). The direction that rocky shores face may have a pronounced effect on exposure owing to the related but distinct influences of orientation to fetch and wave refraction. Shores facing the dominant direction of fetch will be subject to greater focussing of exposure than those orientated towards an increasingly deviating bearing. Refraction occurs when the incoming wave direction is oblique to the shoreline or nearshore depth contours (Smith, 2003). As illustrated in Figure 3.1.2, increasing the angle of deviation between wave direction and depth contour in effect ‘stretches’ the wave laterally, resulting in reduction in gross wave power density, i.e. energy is spread over a wider area, while net wave power is largely unaffected by refraction (Folley and Whittaker, 2009). On shores that face the dominant wave direction, non-refracted waves will have a greater effect on the littoral assemblages (Thomas, 1986). Modelling of approaching waves suggests that by the 10 metre depth contour approximately 32% of the offshore wave resource has been reduced by dissipative processes (Folley *et al*., 2010).

In addition to modifying hydrodynamic forces impinging on organisms in the littoral zone, shoreline topographic variation may affect other important ecological processes. Plunging waves, generated on steeper slopes, will break closer to shore and tend to aid forward transport of larvae; surging waves, generated on gentler sloped seabeds, usually break further offshore and tend not to favour larval deposition owing to oscillating movement (Peregrine, 1983; Raimondi and Keough, 1990; Tucker and Pitt, 2001). Similarly, mechanical abrasion from mobile sediment is affected by gradient with steeper slopes tending to be subject to more frequent and larger impacts (Denny, 1995). In studies of *Chthamalus fragilis* on Cape Cod, Wethey (1983) found that slope and orientation of the substrate play important roles in mitigating competition with *Semibalanus balanoides*. Under these conditions described in this study, desiccation appears to be the underlying causative agent favouring chthamaloid survival. Aspect of rocky shores will vary stress

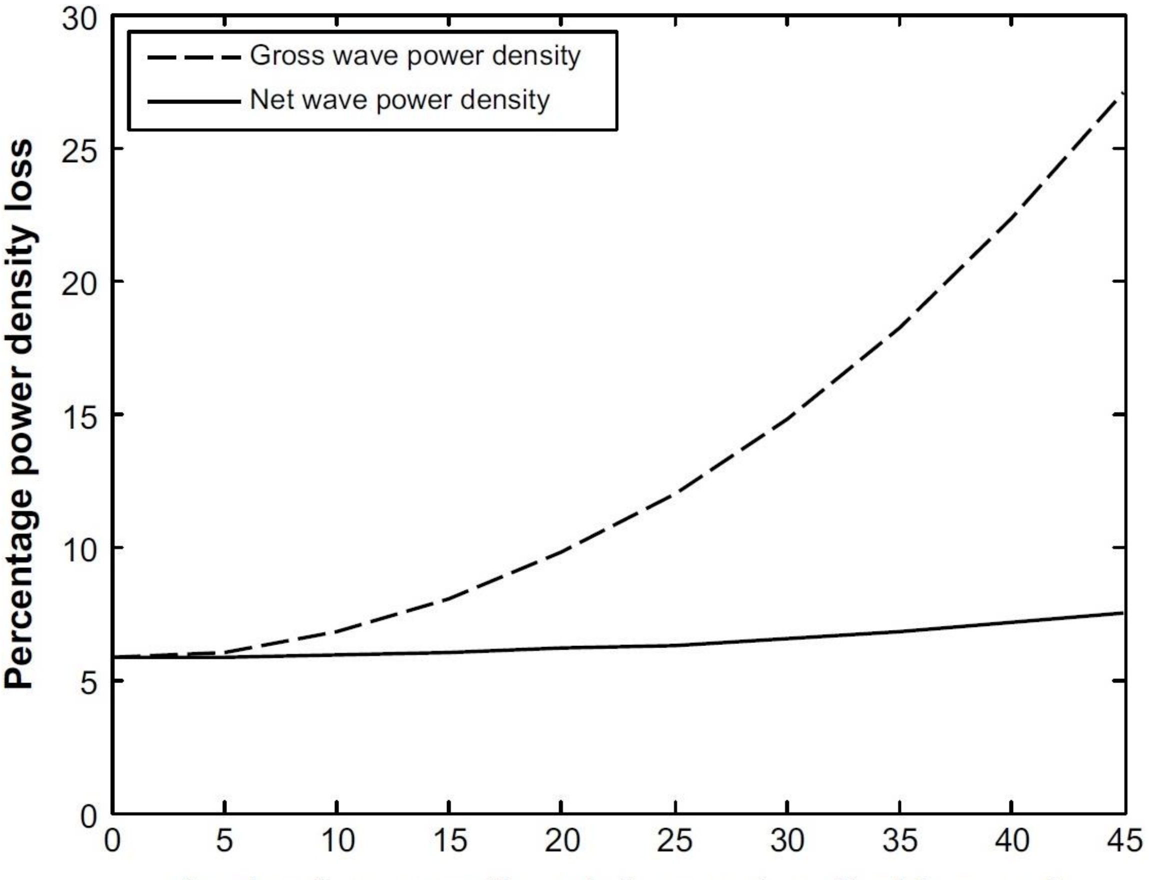


Figure 3.1.2: Variation in percentage power loss from offshore (50 m depth) to nearshore (10 m depth) for the uni-directional sea state: T_P = 10 sec; P_W = 50 kW/m (terms defined in 4.2.5 – Analysis of wave and climate data). From: Folley and Whittaker (2009).

from insolation, especially on vertical surfaces (Glasby and Connell, 2001). Shore slope is an important modifier of desiccation by varying drainage patterns; Benedetti-Cecchi *et al*. (2000) found that macroalgae persisted better on more horizontal surfaces which retained more moisture. Physical features, like slope, may also mediate foraging activities of important grazers, such as limpets (Benedetti-Cecchi, 2000). In addition to affecting wave energy dissipation and producing greater heterogeneity in small-scale exposure habitats on rocky shores, increased substrate complexity may create micro-habitats of contact with and escape from several important ecological stressors including desiccation, predation, and changes in temperature and salinity, as well as creating additional surface area for organisms to exploit (Johnson *et al*., 2003; Pirtle *et al*., 2012).

Areas with complicated coastlines, such as the west coast of Scotland with its sea lochs and numerous islands, will have great differences between shores in both fetch distances and direction (Burrows *et al*., 2008). In contrast, owing to the open and mostly straight coastline of westerly-facing WMO (from Billia Croo to the Brough of Birsay) with few embayments, modelling wave resource based on fetch will show little variation along this coast. Fetch should be very similar between sites with only the ‘shadow’ from the high island of Hoy, and Cape Wrath further distant, influencing the southern-most areas when winds turn southerly or south-westerly. Fetch is also reduced in limited local areas formed by geos and other large rock features. Observable difference in high wave-energy platform communities including those on WMO, may be correlated to small variations in topography, such as slope, complexity and aspect, which are not detected through fetch-based modelling alone (Sundblad *et al*., 2014).

Although the role of certain topographic features in modifying wave energy is well established, if littoral exposure is a direct alternative for wave action then exposure varies both spatially and temporally. Exposure is not characterised simply by the quantifiable ‘openness’ of a site to a fixed level of wave action or to any other combination of essentially ‘fixed’ topographic features. Instead, hydrodynamic forces will vary seasonally as wave height and period typically increase in winter under the direct influence of changing wind directions and speed (see Figures 2.3.3-4, Chapter 2). The correlation between cartographically-based models of rocky shore communities with wave energy will remain coarse if exposure is derived from only averaged wave or wind data (Ruuskanen and Nappu, 2005; Hill *et al*., 2010). In addition, long-term changes in world climate are becoming increasingly apparent: meteorological data from 1985-2008, have shown a global trend towards greater wind speeds, and to a lesser degree greater wave heights. These trends are seen most significantly in extreme events and at more northerly latitudes (Young *et al*., 2011). More recently, major beach damage on the southwest of England which occurred over an unprecedented period of extreme wave conditions in the winter of 2013/2014 may be indicative of a multi-decadal trend towards increasing southerly-dominated storm climate (Scott *et al*., 2016).

3.1.1 Objectives:

There were two main objectives of extensively surveying WMO shores: 1) to gather background biological data of an understudied area where large-scale extraction of the wave resource is planned; and 2) to examine how littoral communities are determined by exposure and its topographical modifiers. For the first major objective, surveying included the entire region within the WMO leasing sites defined by the Crown Estate (Figure 1.2), as well as extending to more sheltered shores, terminating in the south and east at Pulse Skerry and Clay Geo, respectively (Figure 3.2.1.1). For a large proportion of this coast, this represents the first comprehensive scientific characterisation of intertidal assemblages. These studies form a ‘beyond BACI’-style data set (including multiple potential impact and control sites) by which potential changes to the WMO rocky shore community owing to energy extraction or changes in other long-term forcing agents may be measured, as well as identifying areas which may be of particular interest or concern. For the second major objective, a semi-quantitative littoral exposure index was developed for use in the field and several topographic factors, recorded at each survey site, were applied to wind and wave energy data in the preliminary development of a novel quantifiable exposure index. These factors are expected to influence the dissipation of wave energy along these shores and thus influence assemblage composition. Topographic differences between sites may serve as predictors of ecological consequences following alteration in hydrodynamic conditions. The semi-quantitative exposure index was compared with previous indices using biological data recorded during the current study and quantification of topographic modifiers was explored.

In addition to survey work on WMO, during late spring - early summer of 2013 and 2014 the opportunity arose to collect similar biological and topographical data along the rocky shores near the Butt of Lewis in the Western Isles. Like WMO, the north-west facing shores of Lewis are orientated towards an enormous fetch and thus potentially subjected to tremendous wave exposure. As with WMO, this wave resource has attracted commercial interests with a portion of this coast leased for future development of an extensive WEC array (TCE, 2016). These surveys may provide important predevelopment baseline data and included sites within and distant from the areas where impacts from WEC deployment might be expected. Comparison between rocky shore communities on Orkney and Lewis, two locations with extreme wave resources but different shoreline topography, may provide the opportunity to better understand how topographic variables determine exposure. Furthermore, revisiting the same sites on Lewis at a roughly one year interval allowed the study of potential annual effects on species abundance and assemblages – an opportunity that was not possible on WMO owing to access difficulties and available resources.

3.1.2 Hypotheses:

The following hypotheses were tested which examine littoral assemblages on high wave-energy rocky shores and the role played by topographic variables in modifying the exposure of these assemblages to wave energy:

-The horizontal distribution of littoral organisms along the rocky shores of WMO varies owing to topographic heterogeneity in an area exposed to, broadly-speaking, the same wave climate. In particular, variation in slope, openness, complexity and orientation of the shore will produce differences in species assemblages evident along WMO. In this model, the following scenarios of community response to topographic variation are examined (note: topographic variables are explicitly defined below in Methods: Littoral site survey):

1. Slope: lower shore gradients will increase dissipation of approaching wave energy resulting in more sheltered littoral assemblages; greater shore gradients will have less of an impact on wave dissipation resulting in more exposed littoral assemblages.
2. Openness: coasts more open to a wider arc of fetch will capture more wave energy resulting in more exposed littoral assemblages; coasts with reduced

openness will capture less wave energy resulting in more sheltered littoral assemblages. Openness is dependent on bearing relative to dominant wave direction (see below).

3. Mean bearing: shores with mean bearing parallel to dominant wave energy direction will minimise dissipation of approaching wave energy resulting in more exposed littoral assemblages; shores with mean bearing increasingly deviating from dominant wave energy direction will increase dissipation of approaching wave energy resulting in more sheltered littoral assemblages.
4. Aspect: shores with substrate orientation parallel to dominant wave energy direction will minimise dissipation of approaching wave energy resulting in more exposed littoral assemblages; shores with substrate orientation increasingly deviating from being parallel to dominant wave energy direction will increase dissipation of approaching wave energy resulting in more sheltered littoral assemblages.
5. Complexity: more structural variation in the substrate will increase dissipation of approaching wave energy resulting in more sheltered littoral assemblages; substrates featuring reduced structural variation will dissipate less wave energy resulting in more exposed littoral assemblages.

-The consequences of differing topography on wave energy dissipation is evident through comparison of rocky shore assemblage abundance data from WMO and Lewis in relation to the variables described above. While both coasts are similarly characterised by extreme, offshore wave climates, when compared in general: the topography of Lewis is more complicated and shore slope is more gentle producing greater dissipation of approaching wave energy resulting in more sheltered littoral assemblages; the topography of WMO is steeper and less complicated producing less dissipation of approaching wave energy resulting in more exposed littoral assemblages. The individual role of topographic variables on Lewis is the same as that described above for WMO.

-Using data sampled on consecutive years (2013 and 2014), differences between sites in rocky shore assemblages on Lewis are explained by differences in topographic variables rather than annual variation in species abundance or presence.

-The abundances of certain species, high-lighted in Section 2.2.2 as potential indicators of wave exposure, are associated with specific topographic variables affecting littoral exposure.

3.2 Methods:

3.2.1 Littoral site survey:

Rocky shores at 41 sites along WMO were accessed at low spring tides from 2013 to 2015 (Figure 3.2.1.1) (coordinates of sites provided in Appendix 2a). Scheduling of littoral surveys was planned to minimise seasonal or annual differences by completing site visits within a relatively short time window each year and over as few years as possible; constraints in boat availability, spring low tide timings, and sea conditions, meant that the full survey could not be completed in one season. Owing to the predominance of sheer cliffs, fractured platforms, and offshore reefs and skerries along this coast, 19 of these sites required the use of a rigid-inflatable boat (RIB) capable of navigating shallow waters and safely deploying and retrieving survey personnel. These practical issues of accessibility, have focussed this research onto cliff-base platforms and skerries rather than sheer, vertical cliff faces (see Section 4.4: Exposure limits and vertical surfaces). Sites were defined as discrete rock units of approximately 10-20 metres length, i.e. a section or platform at the cliff base or an emerged skerry, allowing data collection within approximately 45 minutes while applying equal effort to each survey site. Sites were selected to provide as comprehensive an assessment of the rocky shores of this coastline as feasible and to ensure that variations in topographic features and biological communities were sampled.

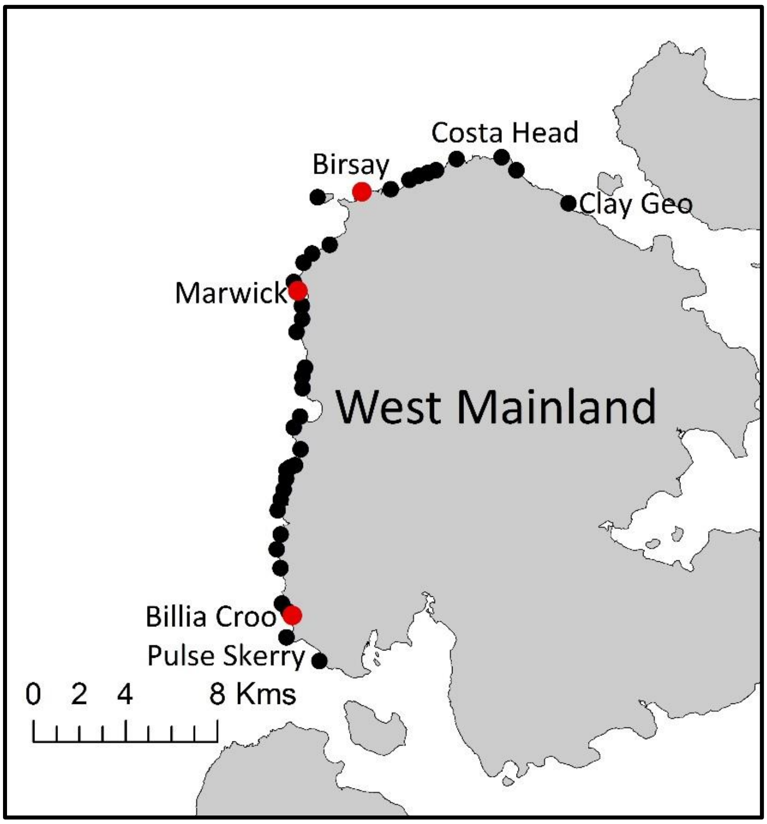


Figure 3.2.1.1 Survey sites on West Mainland, Orkney: three main research sites are shown in red; southernmost and easternmost limits of the survey are the more sheltered sites at Pulse Skerry and Clay Geo.

Topographic assessment included determination of slope, openness, median site bearing, aspect, and complexity. In this study: slope was recorded using a digital protractor at three positions most characteristic of each site; ‘openness’ is the maximum angle of exposed coast to open ocean, i.e. when compared with headlands, embayments have reduced ‘openness’; ‘bearing’ refers to the mean direction of ‘openness’; ‘aspect’ refers to the orientation of the substrate with respect to direction; and ‘complexity’ is based on a semi-quantitative 10-point scale to assess the presence or absence of rock features which would be expected to complicate the interaction between waves and substrate (Table 3.2.1.1;

Figure 3.3.1.1). This scale was developed as an alternative to established field methods of quantifying topographic complexity such as chain links, dividers, and distance wheels (Frost *et al*., 2005; Wilding *et al*., 2010), which were considered impractical given the limited time available for the single observer to conduct data collection. Regarding 'openness', on the shores used in the current studies, the absence of offshore islands and relatively linear coastlines, allows a simple measurement of maximal angle to be assigned at each site; in other locations, such as the west coast of Scotland with numerous islands, convoluted shores, and sea lochs, 'openness' would need to be qualified at different spatial scales. Directional variables, i.e. bearing and aspect, were refactored as deviation from mean wave energy direction (defined as mean wind energy direction described in Chapter 2.5; in this study, mean wind direction for WMO was determined to be 259°). Mean wave energy direction for Lewis was based on Waverider buoy data from Oct. 2011 – Sept. 2012 and determined to be 281° (Vogler *et al*., 2013).

Table 3.2.1.1: Semi-quantitative 10-point scale of complexity applied to rocky shore surveys on WMO and Lewis, based on the presence and absence of rock features which might be expected to complicate the interaction between wave energy and the substrate, including: broken shores, rock pools, steps, and off shore rocks or skerries. Within score ranges described below, e.g. 2-4, sites are scored dependent on how much features are shared within the category and with categories above and below. Photographic examples are provided in Figure 3.3.1.1.

Score	Description of features
1	Uncomplicated platform featuring minimal deviation from 'planar' surface
2-4	Minimal presence of low, stepped features, small and shallow rock pools, and little or no offshore rock features
5-6	Increasingly broken shores with larger steps, deeper and more numerous rock pools, and presence of small off shore rock features
7-9	Broken shores with combinations of gullies, varied rock pools, substrates providing distinct seaward and leeward surfaces, and large offshore rocks or skerries
10	Unusually contorted shore with all features present in maximal level of complexity, and presence of several offshore rock features

In addition, ‘exposure’ was initially scored with a semi-quantitative value, from 1 to 5, concisely encapsulating a great deal of the variation in these sites which might affect exposure. This exposure scale was informed by regular visits to research areas of Billia Croo, Marwick and Birsay which serve as well-studied references; quantitative measurement of wave energy breaking on the rocky shores at Billia Croo and Marwick has been assessed using the Terobuoy littoral hydrodynamic monitoring device and validated against wave data collected by EMEC (Want *et al*., 2014). Similarly, corroborative exposure data have been collected at Birsay (Beharie, unpublished data). Semi-quantitate evaluations of sites on Orkney were made in comparison to these main study sites and an overall appraisal of the physical features which might be expected to modify exposure (Table 3.2.1.2). Evaluation of complexity and exposure were completed immediately upon arrival at each site, prior to any biological measurements, to avoid biasing which might occur owing to preconceived associations between certain organisms and levels of exposure.

Table 3.2.1.2: Semi-quantitative 5-point scale of exposure applied to open rocky shore sites on WMO and Lewis prior to biological surveying and detailed recording of topographic variables, based on overall visual appraisal of physical features which would be expected to affect exposure and comparison with three reference sites on WMO with quantified littoral exposure (Want *et al*., 2014). Physical features considered included the degree of embayment, shore gradient, orientation to known wind direction, presence of offshore reefs, proximity of islands, and substrate heterogeneity. Quantified reference sites and scores: Billia Croo = 2; Marwick = 3; Northside in Birsay = 4 (see Appendix 1).

Score	Description of features/quantified reference site
1	Open rocky shore with maximal contribution of exposure reducing features, i.e. tending towards embayment, low gradient, orientated away from prevailing winds, presence of offshore reefs, fetch-reduction from neighbouring islands, and broken shores.
2	Open rocky shore with contribution of many of exposure reducing features. Similar to the slight embayment studied at Billia Croo.
3	Open rocky shore with a general middle level of features affecting exposure. Similar to the study site at Marwick.
4	Open rocky shore with few features associated with reduced exposure. Similar to Northside in Birsay.
5	Open rocky shore with minimal contribution of exposure reducing features, i.e. headlands, steep gradients, orientated towards prevailing winds, absence of offshore reefs or neighbouring islands, and planar platforms.

Species abundance was assessed at each site using the SACFOR scale as described by Crisp and Southward (1958) modified by Hiscock (1981) (Appendix 3). In keeping with well-established methods, evaluation of highest abundance was conducted on each site in the habitat/zone most typical of each species. SACFOR scores were enumerated to a 0-6 point scale, with 0 assigned to species not observed and 6 assigned to 'super-abundant' species. The procedure was applied to 45 littoral species ranging across trophic levels, including primary producers, and primary and secondary consumers (Appendix 4). The procedure allowed sufficient time to characterise a site within the necessarily short periods of access – owing to boat-based deployment necessary for many of the sites. For the purpose of these analysis, all species were evaluated on open rock surfaces where they are fully subject to exposure rather than in the lee of rock features or in crevices, where abundance of certain organisms may be higher, e.g. *Mytilus edulis*. An important advantage in this study was that all the sampling of biological and topographic data was performed by the same observer, thus prevented inconsistencies which might be created using multiple personnel. When necessary, samples were collected for identification in the laboratory and quadrat images were analysed to quantify percentage cover. Image analysis was performed using the same method as described for quadrat analysis of *F. distichus anceps* (see Section 4.2.1.2). In addition, at each rocky shore site, quadrats were photographed for later determination of abundance of barnacles, and limpet abundance was recorded using a 1m x 1m quadrat placed in the most representative location per site. In the mid-shore on exposed shores, patellid limpet species distribution can vary substantially between open surfaces and rock pools (Delany *et al*., 1998). Representative quadrats for limpet assessment were placed on open rock surfaces where the effects of wave exposure are expected to be most evident, and complicating effects of rock pools are minimised. In addition to abundance determination, a subset of 20 individual limpets was randomly selected within quadrats for species verification based on foot colouration (Fish and Fish, 1989). On shores with limpet density below 20/m^2, additional individuals were randomly selected for species identification from the quadrat periphery. In addition to abundance determination of barnacles used in the current study, images were recorded of a 50cm x 50cm quadrat at upper, mid and lower shore heights at each site. Barnacles were not quantified to species level but stored images may be used for identification and further studies in future. Abundance of small rhodophytes (predominantly *Ceramium rubrum* and C. *shuttleworthianum*, *Polysiphonia broidiei*, and *Callithamnion* spp.) which typically form a turf on the mid to low shores, were collectively described as ‘red turf’.

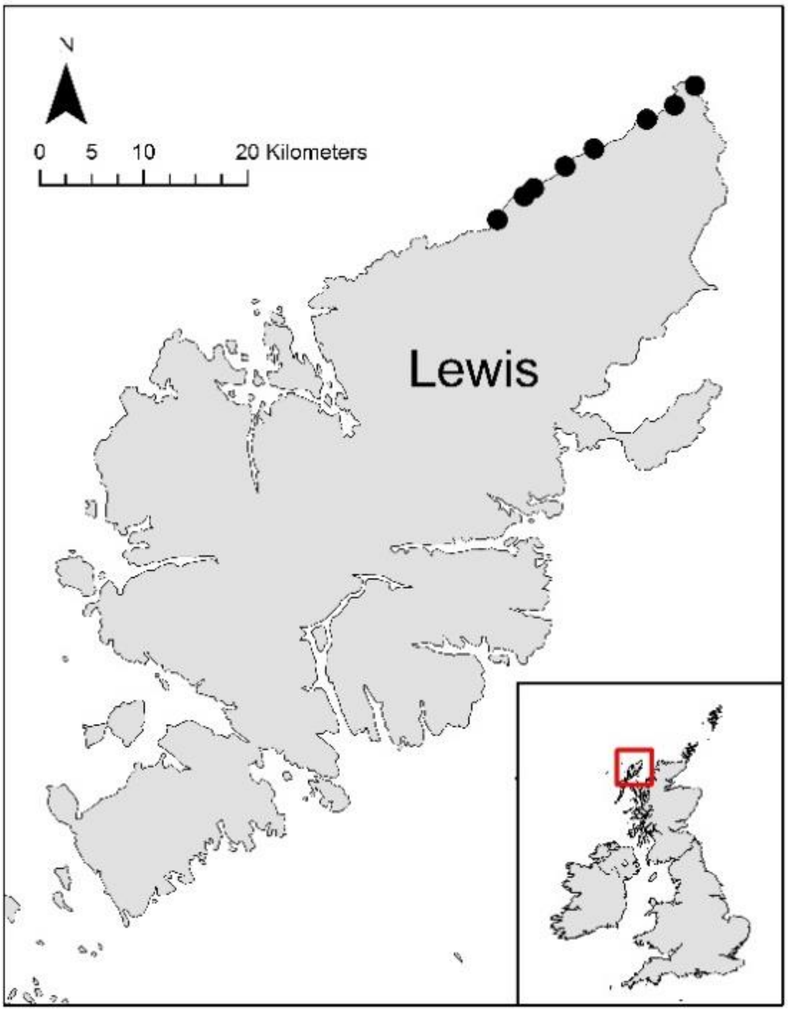


Figure 3.2.1.2: Eight sites on Lewis were surveyed in June 2013, and again in May 2014.

In June 2013, seven sites on the north-west coast of Lewis (NWL) and one site on the north-east coast (NEL) (Figure 3.2.1.2) were studied (coordinates provided in Appendix 2b) using the same survey protocol for biological abundance and topographic data as described for WMO. All Lewis sites were resurveyed in May 2014.

3.2.2 Calculating exposure indices:

In addition to semi-quantitative evaluation of exposure conducted upon arrival at each site, exposure was subsequently calculated using the methods described by Ballantine (1961), Thomas (1986), and Burrows *et al.* (2008), hereafter known as 'Ballantine', 'Thomas', and 'Burrows' Indices. The 'Ballantine Index' was originally developed based on observations of rocky shore communities around the Dale peninsula, Pembrokeshire, Wales. Assemblage and abundance data of key species were applied to a descriptive exposure scale ranging from 'extremely exposed' to 'extremely sheltered', scored as 1 and 8, respectively. Biological data collected in the present study were applied to the same system and each survey site assigned a value on the 'Ballantine Index'. The 'Thomas Index' was empirically derived using fetch and wind data (from 22.5° directional sectors) modified by an estimate of slope using the following formula (Thomas, 1986):

$$\sum \log W \text{ x} \log \left[1 + \frac{F}{CS + 0.1\,DS}\right] \text{x } S$$

Where: W is wind energy determined by summation of percent time that wind blows in each sector/100 multiplied by wind speed^2; F is fetch in nautical miles (nm) (to a 100 nm maximum); CS is extent in nm of water <6 m deep adjoining the shore; DS is extent in nm of water <6 m deep but not adjoining the shore, i.e. accounting for offshore islands, reefs, etc.; and S is a proportional representation of slope determined from intertidal survey of shore height from the top of the supralittoral zone to mean low water. Wind data (2012 –2015), and admiralty charts for WMO, were used to determine 'Thomas

Index' for each survey site in the present study without slope, as well as a modified index using slope data recorded during the present study. On parts of WMO, Admiralty charts lack sufficient resolution of depths shallower than 20 m; *CS* and *DS* used in the 'Thomas Index' were extended to 20 m depth contours. The 'Burrows Index' is a further development of the 'Thomas Index' where wave exposure is calculated using a GIS-based, digital coastline database to determine maximal fetch (to 200 km) in 22.5° directional sectors, which may be further informed by including wind speed and incidence. For convenience, the model code and wave fetch data for the UK used in the 'Burrows Index' are available as an appendix to Burrows *et al.* (2008), allowing relatively easy automation of fetch calculation. Similarly to the 'Thomas Index', the 'Burrows Index' was modified with inclusion of cartographically-derived estimates of gradient, in this case using horizontal shoreline extent determined by measuring linear distance, perpendicular to the shoreline, from mean high water springs to mean low water springs. Each survey site on WMO was characterised using the model code provided by Burrows *et al.*, (2008) to summate fetch values for each directional sector, averaged between closest GIS-based 'cell' and its immediate neighbours. 'Burrows Index' was used with and without modification using admiralty chart data of shoreline extent; wind data were not applied to this index. After applying each of these indices to site data from the current study, wave indices were compared to one another using the non-parametric Spearman's rank correlation (Sokal and Rohlf, 1995). This included the semi-quantitative exposure measurement determined in the present study, hereafter known as 'Want SQ Index'. In the present studies, application of exposure indices was restricted to WMO sites; in future, these applications may be extended to data from Lewis.

3.2.3 Multivariate analysis:

Multivariate analyses were used to examine the relationship between species composition and topographic variables conducted in three ways using a combination of Minitab 17 (Minitab, 2010) and the R software package (R Core Team, 2013) with the aim of comparing different methodological approaches in identifying the main sources of variability in assemblage composition. Firstly, principal component analysis (PCA) was performed on faunal and floral abundance data (both separately and combined) from WMO and Lewis survey sites (also, both separately and combined) for about 20 littoral rocky shore species. While many more species were recorded during cliff surveys, the shortened list resulted from the elimination of organisms that were considered to be either: a) too infrequent (e.g. *Calliostoma zizyphinum* was located at only 5 of the 41 WMO sites during standardised searches); or b) strongly associated with small scale micro-habitats of much reduced wave energy, i.e. their abundance was not a true representation of the overall hydrodynamic conditions of the site, (e.g. *Halidrys siliquosa* can be found in mid-shore pools on otherwise extremely exposed shores). Secondly, stepwise regression (backward elimination, $\alpha=0.1$) was performed on the first three principal components to determine the relationship between assemblage composition and topographic modifiers of exposure. Additional models were considered incorporating the following exposure indices: ‘Ballantine’, ‘Thomas’, ‘Burrows’, and ‘Want SQ’. To prevent aliasing, owing to the inclusion of slope as a topographic variable, ‘Thomas’ and ‘Burrows’ indices modified by slope were not tested. While ‘Want SQ Index’ may be informed by these topographic variables, evaluation occurs prior to any actual numbers been recorded, therefore testing of this index against these variables was considered valid. Exposure indices were included as fixed model offsets in the stepwise regressions, thereby allowing the contribution of topographic variables to be assessed after the effects of these indices had been accounted for. Stepwise regression identified variables which made the greatest contribution to explaining variance in rocky shore assemblages. Lastly, as an alternative approach to PCA, species abundance and survey site data site, constrained to a limited number of environmental variables, were compared and plotted using redundancy analysis (RDA). It is recommended when performing RDA to select fewer constraining variables when possible (Oksanen, 2014); RDA of WMO data were constrained to three environmental variables (complexity, slope, and exposure) selected following modelling using stepwise regressions.

3.2.4 Comparison of annual variation on Lewis:

To examine rocky shore assemblage variation between years, separate PCA was performed on data collected on Lewis in 2013 and 2014. Assemblage composition and species abundance was compared between years by plotting site scores on the first two principal component axes. Site by site species abundances were compared between years to further characterise any differences.

3.2.5 Generalised linear modelling of rocky shore species and topography:

Generalised linear modelling was used to investigate the relationship between the abundance of certain organisms and environmental variables from 41 survey sites on WMO. Patellid limpets and fucoids are key species in many rocky shore assemblages; in 2.2.2, *Patella ulyssiponensis* and *Fucus distichus anceps* were identified as potential indicator species of long-term change in exposure and temperature. Using Minitab 17 (Minitab, 2010) parsimonious models were generated for limpet and fucoid data against topographic variables using backward elimination ($\alpha = 0.1$). Limpet abundance data were analysed using least-squares linear regression; proportional data of *P. ulyssiponensis* were analysed using logistic regression. Abundance data of *F. distichus anceps* were compared with topographic variables using linear regression. Exposure indices were also tested by stepwise regression (backward elimination, α = 0.1) using proportional data for *P. ulyssiponensis* (logistic regression), and abundance data for *F. distichus anceps* (linear regression) to create models with all topographic variables. As before, exposure indices were treated as fixed model offsets, not included in backward elimination. To prevent aliasing, owing to the inclusion of slope as a topographic variable, 'Thomas' and 'Burrows' indices modified by slope were not tested.

3.3 Results:

3.3.1 Littoral site surveys:

The following description is based upon observations made during littoral site surveys on WMO. At a broad scale, the littoral assemblages on the open rocky platforms of WMO are characteristic of high wave energy shores. The upper shore assemblage extends far above mean high water and features less biomass and biodiversity than lower shore zones. On WMO, upper shores are chiefly characterised by the lichens *Verrucaria maura* and *V. mucosa*, the littorinid grazers *Littorina saxatilis* and *Melarhaphe neritoides*, and a film of cyanobacteria. An abundant band of *Porphyra umbilicalis* is typically found in the upper mid shore, although this is ephemeral and less conspicuous at certain times of the year. The upper mid shore is usually the top of a prominent barnacle zone which may extend through the lower shore. Other animals often found in association with the barnacle zone are *Melarhaphe neritoides* and *Nucella lapillus*. Further down the mid shore, there is typically a major zone of fucoid macroalgae, often with patellid limpets, amphipods and isopods beneath the canopy. Below the fucoid zone, in the lower shore, it is common to find additional macroalgae species. On WMO, these include *Mastocarpus stellatus*, *Himanthalia elongata*, a turf of small rhodophytes, and the calcareous *Corallina officinalis*. In addition to lower shore barnacles, this zone typically features the animals *Mytilus edulis* and *Actinia equina*, the latter in clefts which remain moist when the tide withdraws. Other, less abundant, animals include *Halichondria panicea* and mobile species such as *Calliostoma zizyphinum*, *Eulalia viridis*, and *Idotea* spp. The vertical extension of zones on highly exposed shores also applies to the uppermost sublittoral zone (Lewis, 1964) and means that, on WMO, lowest tides reveal an emerged and abundant kelp forest. The fringe of the sublittoral zone on WMO is usually populated by *Alaria esculenta* or *Laminaria digitata*; immediately below the fringe, with the former tending to be found on more exposed shores; most nearshore benthic communities are dominated by *Laminaria hyperborea*.

While many of these species are found along much of WMO, the distributions and abundances of these organisms are not homogenous. Localised differences exist where certain species are more or less likely to be found: *Palmaria palmata* can form broad, abundant zones in what appear to be recently disturbed shores (Hawkins and Harkin, 1985; Jenkins *et al*., 2005); *Ulva intestinalis* may dominate areas where freshwater runs down the shore; and *Halidrys siliquosa*, and fucoids found on more typically sheltered shores, may thrive in deep rock pools amid assemblages associated with high exposure conditions. One of the most conspicuous horizontal changes on WMO is in the fucoid species contributing to the main macroalgal mid shore zone and the magnitude of canopy provided: on the most extreme-exposed shores on WMO, fucoid cover is sparse and typically created by *F. distichus anceps*, sometimes with a higher shore zone of *F. spiralis* f. *nanus*, both high-energy dwarf forms; on less extreme but still very exposed shores, the high-energy variant *F. vesiculosus* f. *linearis* grows larger than dwarf fucoids providing greater substrate cover; and, on more moderately exposed rocky shores, *F. vesiculosus* develops its characteristic bladders and grows larger still with higher shore zones of lower energy fucoids, such as *F. spiralis*, forming. On the more extreme-exposed shores, a barnacle zone is typically apparent consisting chiefly of *Chthamalus stellatus* in the upper zone and *Semibalanus balanoides* in the lower zone; on less exposed shores with greater fucoid cover, the barnacle zone is typically patchier and dominated by *S. balanoides*.

The rock substrate at all survey sites on WMO is comprised of Devonian sandstone with the singular exception being at Inga Ness where original sedimentary rock has been metamorphosed by adjacent Permian igneous intrusions (McKirdy, 2010). An important geomorphic difference in the highest energy areas on WMO is found between essentially vertical cliff faces and more horizontal wave-swept platforms found at many cliff bases. While the relatively uncomplicated planar rock platforms of WMO generally dip offshore at about 12°, there exists a range of slopes from approximately 3° to 20°. All of westerly-facing WMO is potentially subject to a similar wave resource owing to the westerly orientation of the substrate towards essentially an open sea where wave and wind energy arrive from a typically westerly direction. Exceptions may be created in the south of WMO where fetch from more southerly directions is reduced by the ‘shadow’ of the high island of Hoy (see Pulse Skerry: Figures 3.2.1.1 and 3.3.1.1). Other exceptions would be expected in the limited number of embayments located along this coast. Examples of assemblage differences found on sloping platforms of varying gradients on WMO are represented schematically in Figure 3.3.1.2. On lower gradient shores on WMO, fucoids tend to be represented by *F. vesiculosus* f. *linearis*, the barnacle zone is dominated by *S. balanoides*, limpets are usually *P. vulgata*, *N. lapillus* is frequently found, especially away from open rock surfaces, and, at the sublittoral fringe, *L. digitata* emerges at lowest waters. In contrast, on higher gradient shores on WMO, the fucoid population transitions to *F. distichus anceps*, barnacle zones feature greater cover from *C. stellatus*, limpets are increasingly represented by *P. ulyssiponensis*, *N. lapillus* is typically rarer or absent, and emergent *A. esculenta* is abundant in the sublittoral fringe.

Figure 3.3.1.1: Shoreline complexity: top left) Skrowa Skerry, WMO: a near planar, steeply-sloped (~19°) site with abundant *F. distichus anceps* (complexity score = 1); top right) Hole o'Row, WMO: a stepped platform shore with offshore reef, with some *F. distichus anceps* and *F. vesiculosus* f. *linearis* (complexity score = 4); bottom left: Pulse Skerry, WMO: a moderate-gradient (~8°) shore featuring substantial substrate variability with abundant *F. spiralis* and non-variant *F. vesiculosus* (complexity score = 7); and, bottom right) Tada Ghabhsainn, Lewis: a broken shore featuring heterogeneous rock features and pools with common *F. vesiculosus* and *Ascophyllum nodosum* (complexity score = 9).

In addition to varying slopes, on westerly-facing shores of WMO, survey site complexity ranged from near perfect planar surfaces to broken shores with offshore reefs and plentiful rock pools (Figure 3.3.1.1). Angle of openness to incoming waves ranged from a minimum of 98°, at the relative embayment at Borwick, to a maximum on 224°, at the promontory of Breckness. The mean angle of openness, i.e. the directional bearing, varied from 220°-303°, i.e. in a generally westerly direction. Unsurprisingly, aspect, which relates to bedrock orientation, was similar at most sites, predominantly facing in a westerly direction (mean, 279°). There were, however, a few sites whose aspect deviated considerably with extremes found at: 214° at Alga Bar; and 331° at Cut Taing.

When compared with the westerly-facing coast from Billia Croo to Birsay, the northwest-facing coastline (Birsay to Costa Head) provides contrasting shoreline topography as the rock platforms and features continue to dip to the west while waves approaching the shore tend to do so obliquely and therefore must refract. The rocky shores of northwest-facing WMO are typically simple, low-gradient, platforms and feature less variation in openness, the latter metric clustering at approximately 165° among the 8 survey sites on this coastal section. It is not uncommon for platforms on northwest-facing WMO to be divided by broad ‘steps’ of up to a metre, with the vertical face more or less orientated towards the sea. This produces an interesting phenomenon where the gradient of the emergent shore, in totality, may be moderate, but at a finer-scale is defined by low-gradient platforms punctuated by these vertical steps. The possible importance of this topographical arrangement is discussed in Section 4.4: Exposure limits and vertical surfaces. Mean site bearing is predominantly in a NNW direction, ranging from 338° to 2°. Further contrasts are provided from studying the rocky shore beyond Costa Head to Clay Geo on Eynhallow Sound. The sites studied on this shore provide additional background information of lower energy locations and are sufficiently far removed from potential deployment sites to serve as further controls. The rocky shores of Eynhallow Sound are generally low gradient, relatively uncomplicated, and open to much reduced fetch owing to the proximity of the neighbouring island of Rousay (the effects of an enhanced tidal flow on littoral assemblage of this coast are not known).

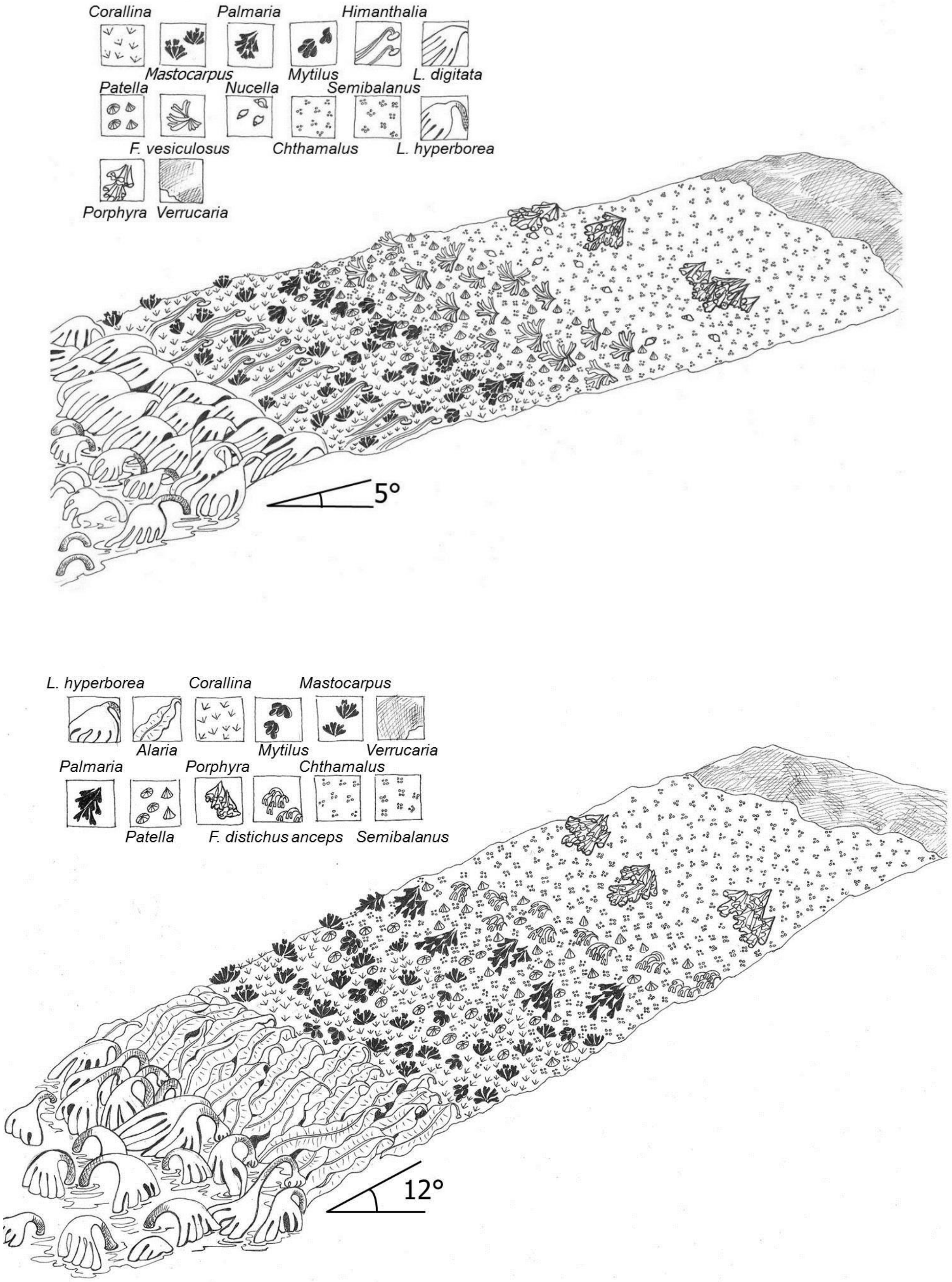


Figure 3.3.1.2: a) above, assemblage members on typical, moderate-gradient (5°), wave-swept rocky platform on WMO; b) below, assemblage members on typical, steep-gradient (12°), wave-swept rocky platform on WMO.

Lewis surveys:

In contrast to WMO, metamorphic rocks found on much of the northwest-orientated coast of Lewis (NWL) create more complicated and varied topographic features. Most sites feature broken rocky shores extended over a low gradient with frequently large mobile sediment (i.e. boulders) located on the upper shore. To the east of Ness Point, northeast-orientated Lewis (NEL) is typified by steeply sloped, planar shores much more reminiscent of WMO except lacking the broad uniformity seen on Orkney's sedimentary-based rocky platforms. The biological community on NWL is more varied than on WMO including many species associated with lower wave exposure such as *Ascophyllum nodosum*, *Saccharina latissima* and lower shore littorinids. In contrast, NEL is not only topographically more similar to WMO but also features a similar assemblage of littoral organisms including the high-energy variant fucoids *F. distichus anceps* and *F. spiralis* f. *nanus*.

3.3.2 Exposure indices:

Six exposure indices were applied to rocky shore survey sites on WMO (Appendix 5). These indices were: Ballantine, based on identification of key members of the community; Thomas, based on fetch, wind energy, and cartographic measurement of distance from MLW to 20 m depth contour; Thomas-modified, including a slope factor determined during the present study; Burrows, based on fetch; Burrows-modified, including an additional factor based on cartographically-derived shoreline extension; and Want SQ, semi-quantitative evaluation conducted at each site prior to topographic or biological data collection.

Table 3.3.2: Spearman's rank correlation of wave exposure indices describing 41 rocky shore survey sites on WMO. Thomas-mod is the Thomas Index modified by slope recorded during shore surveys as part of the current study; Burrows-mod is the fetch-based Burrows Index modified using shore extensive; and Want SQ is the semi-quantitative exposure measurement used in the current study. Confidence symbols: *<0.05; **<0.01; ***<0.001.

	Ballantine	Thomas	Thomas–mod	Burrows	Burrows-mod
Thomas	-0.077				
Thomas-mod	-0.109	0.815***			
Burrows	-0.086	0.202	0.233		
Burrows-mod	-0.578***	0.322*	0.413**	0.443**	
Want SQ	-0.612***	0.132	0.205	0.417**	0.486***

Spearman's rank correlation of wave exposure indices are presented in Table 3.3.2 and Figure 3.2.2. The Ballantine Index correlated poorly with cartographically-based indices with the exception of the modified Burrows Index, which incorporated an approximation of shore gradient. This was not surprising considering the broad-scale of the Ballantine Index and the extreme exposure characteristic of most of the study sites – of the 41 study sites, 39 were rated as 1 or 2 on the Ballantine Index. Unsurprisingly, Thomas and Burrows Indices modified with further cartographic data correlated strongly with their unmodified indices. Want SQ Index, correlated strongly with Ballantine and Burrows Indices, and correlations improved with modified indices. This suggests that this semi-quantitative approach was successful in capturing the main facets of exposure. Note: Ballantine Index is negatively correlated with all indices because this scale alone is based on decreasing value with higher exposure.

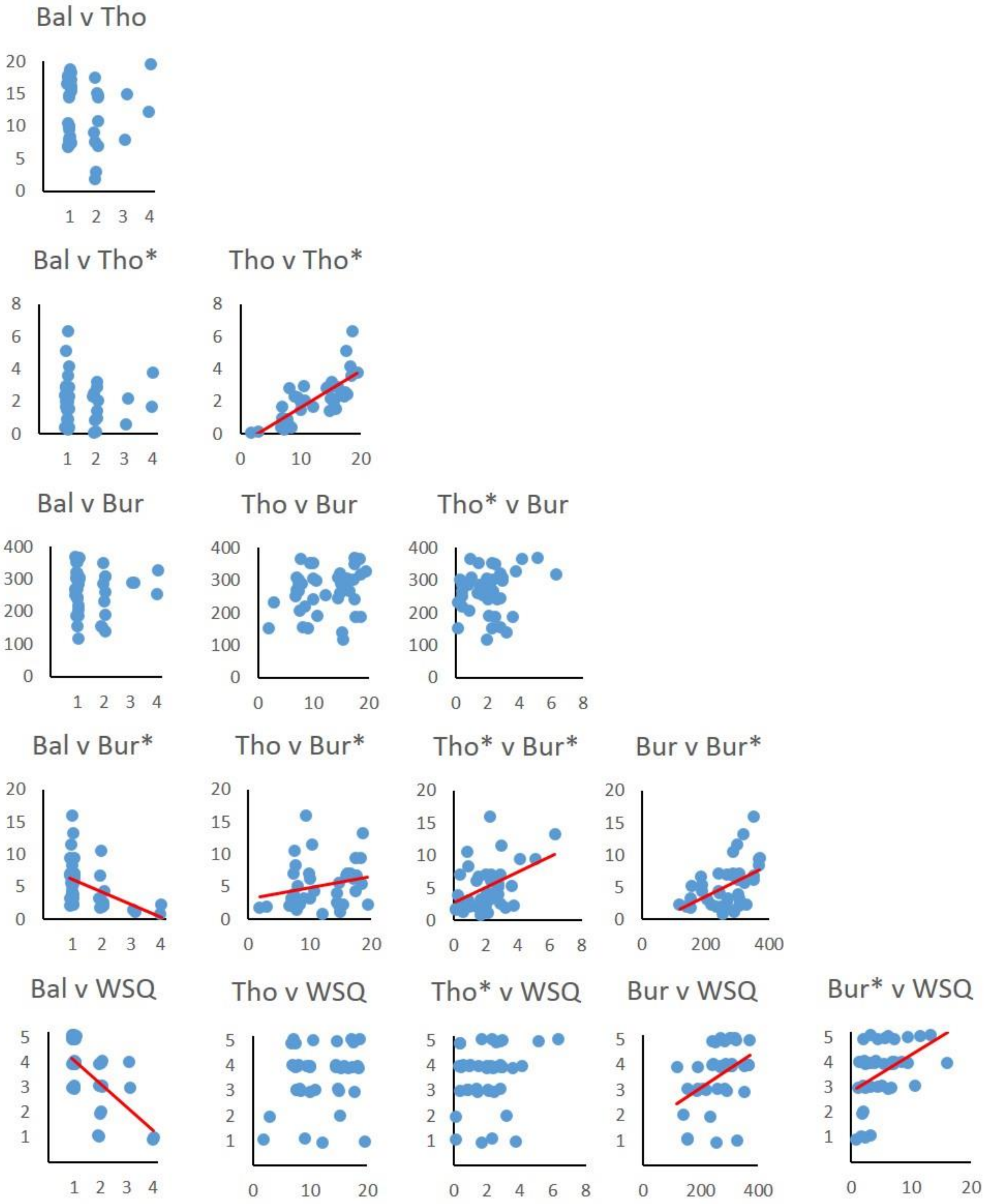


Figure 3.3.2: Correlations of wave indices abbreviated as follows: Ballantine (Bal); Thomas (Tho); Thomas modified (Tho*); Burrows (Bur); Burrows modified (Bur*); and Want semi-quantitative (WSQ). Line of best fit added to significant correlations. A ‘jitter’ function was applied to categorical scale data to separate coinciding data points in the graphs.

3.3.3 Principal component analysis:

Principal component analyses were performed on all combinations of faunal and floral data from WMO and Lewis. In all analyses, Principal component (PC) 1 appeared to represent an axis of exposure and explained approximately 30-42% of variation. Depending on the data subsets used, PC2 explained about 10-25% of the variance, and usually appeared to represent animal dominated shores. In Figure 3.3.3.1 species loadings for the first two PCs are plotted for faunal and floral data from WMO and Lewis. In PC1: the highest positive loadings were observed in high exposure species such as *Alaria esculenta*, *F. distichus anceps*, and 'red turf'; the highest negative loadings were observed in relatively lower exposure species including *Actinia equina*, *F. serratus*, and *Nucella lapillus*; in patellid limpet loadings, *P. ulyssiponensis* was positive, while *P. vulgata* was strongly negative. In PC2: the highest positive loadings were observed in the animals *Mytilus edulis*, *P. ulyssiponensis* and barnacles; the highest negative loadings were observed in the macroalgae *Himanthalia elongata*, *Palmaria palmata*, and *Sctyosiphon lomentaria*. In PC3: the highest positive loading was observed in the bladderless, high energy variant fucoid *F. vesiculosus* f. *linearis*; the highest negative loading was observed in the more moderate exposure form *F. vesiculosus*. It is not obvious what this component represents, although loadings of species beyond *F. vesiculosus* and modelling using exposure indices suggest that this component is not related to exposure. Loadings for individual species, and eigenvalues and proportion of variation explained by the first six PCs are presented in Table 3.3.3.1. Rocky shore survey sites were grouped according to broad geographic location and shore orientation. Site scores were plotted for the first two PCs and presented in Figure 3.3.3.2.

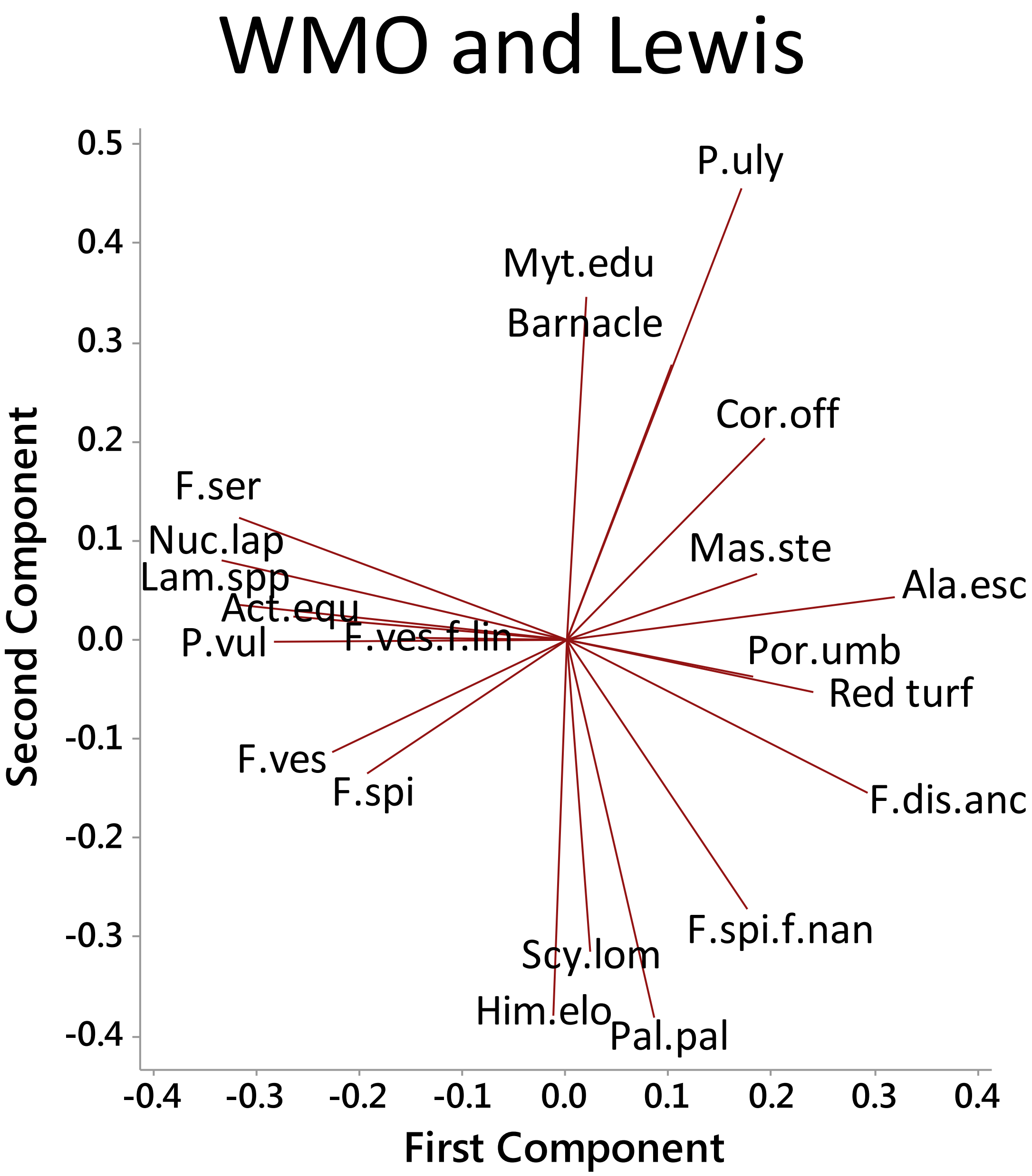


Figure 3.3.3.1 Principal component analysis: loading plot of faunal and floral abundance data from WMO and Lewis. Species are abbreviated as: *Actinia equina* (Act.equ); *Alaria esculenta* (Ala.esc); *Corallina officinalis* (Cor.off); *Fucus distichus anceps* (F.dis.anc); *Fucus serratus* (F.ser); *Fucus spiralis* (F.spi); *Fucus spiralis* f. *nanus* (F.spi.f.nan); *Fucus vesiculosus* (F.ves); *Fucus vesiculosus* f. *linearis* (F.ves.f.lin); *Himanthalia elongata* (Him.elo); *Laminaria* spp. (Lam.spp); *Mastocarpus stellatus* (Mas.ste); *Mytilus edulis* (Myt.edu); *Nucella lapillus* (Nuc.lap); *Palmaria palmata* (Pal.pal); *Patella ulyssiponensis* (P.uly); *Patella vulgata* (P.vul); *Porphyra umbilicalis* (Por.umb); and *Scytosiphon lomentaria* (Scy.lom).

Table 3.3.3.1 Principal component analysis: eigenvalues and the proportion of variation explained by the first six PCs for rocky shore faunal and floral data from WMO and Lewis. Loadings for 21 individual species are based on abundance data.

	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalue	7.050	2.076	1.880	1.501	1.353	1.100
Proportion	0.336	0.099	0.090	0.064	0.052	0.043
Cumulative	0.336	0.435	0.524	0.596	0.660	0.712
Barnacle spp.	0.103	0.277	-0.190	0.463	-0.139	-0.209
P. ulyssiponensis	0.170	0.457	-0.099	-0.060	-0.260	-0.039
P. vulgata	-0.282	-0.002	0.266	-0.122	0.112	-0.016
Mytilus edulis	0.019	0.346	0.260	-0.277	-0.426	0.086
Nucella lapillus	-0.335	0.080	0.006	0.007	-0.112	0.020
Actinia equina	-0.265	0.023	0.039	0.324	-0.319	0.165
F. distichus anceps	0.292	-0.155	-0.161	-0.131	0.049	-0.109
F. spiralis f. *nanus*	0.176	-0.272	0.001	-0.238	-0.179	0.122
F. spiralis	-0.193	-0.136	-0.328	0.035	0.098	0.465
F. vesiculosus f. *linearis*	-0.147	0.002	0.539	0.053	0.250	-0.055
F. vesiculosus	-0.227	-0.113	-0.375	0.157	-0.127	-0.017
F. serratus	-0.316	0.124	-0.123	-0.194	-0.030	0.078
Red turf	0.239	-0.053	-0.021	0.008	-0.250	0.027
Mastocarpus stellatus	0.186	0.067	-0.029	-0.368	0.220	0.199
Palmaria palmata	0.086	-0.383	-0.127	-0.124	-0.247	-0.326
Corallina officinalis	0.193	0.204	0.234	0.160	0.031	0.173
Himanthalia elongata	-0.013	-0.379	0.315	0.218	-0.114	-0.311
Alaria esculenta	0.318	0.043	0.108	0.209	-0.116	0.025
Laminaria spp.	-0.318	0.034	0.011	0.012	-0.105	-0.186
Scytosiphon lomentaria	0.024	-0.315	0.227	0.059	-0.414	0.525
Porphyra umbilicalis	0.181	-0.037	0.007	0.417	0.316	0.289

In Figure 3.3.3.2, scores for the first 2 PCs from sites orientated into broad geographic groupings are generally in close proximity to one another. On Lewis, sites mostly score positively with PC2, and northeast-orientated shores closely resemble WMO with regards to PC1. Sites on WMO typically score higher on the first axis, with the exception of relatively sheltered northeast and southwest-orientated shores. The WMO sites which score positively on PC1, tend to group with northwest-orientated shores scoring negatively and westerly-orientated shores scoring positively with respect to PC2. Closer examination of assemblage data between these two main coastal orientations studied on WMO reveals that species with median SACFOR abundances differing between the two groups by more than one category were: barnacles were more abundant on westerly-orientated WMO; and, *F. spiralis* f. *nanus*, *Palmaria palmata*, *Himanthalia elongata*, and *Scytosiphon lomentaria*, were more abundant on northwest-orientated WMO.

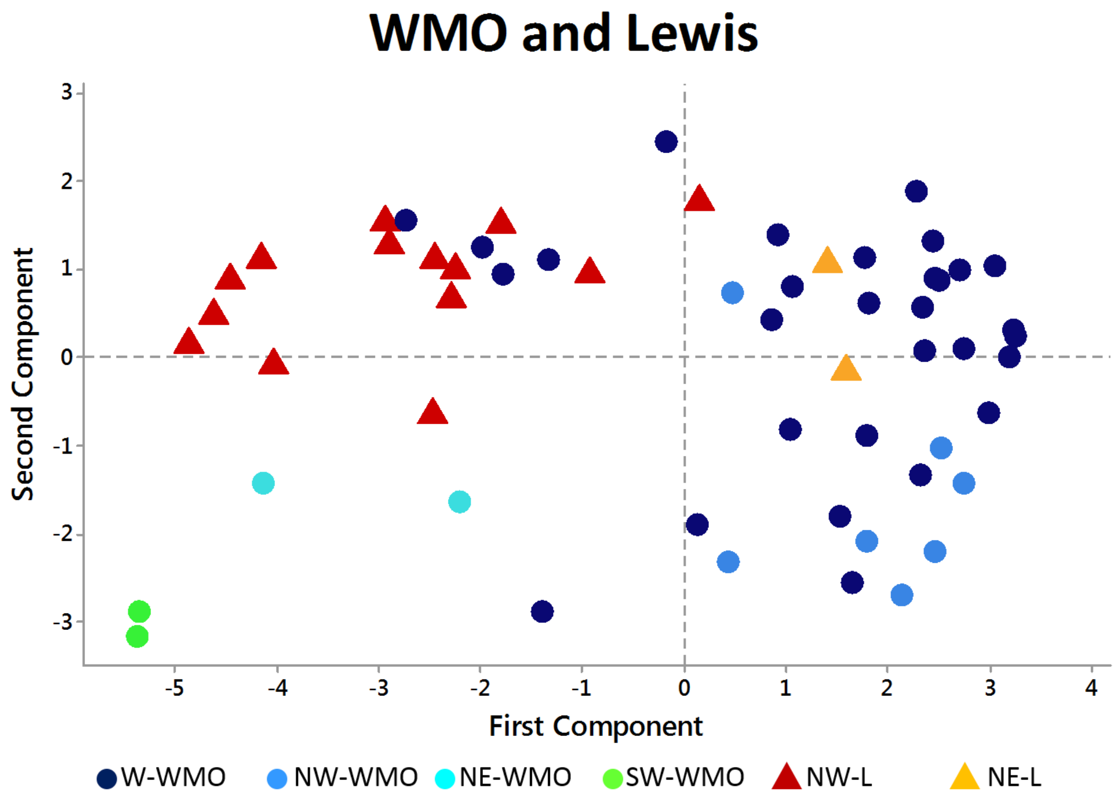


Figure 3.3.3.2 Principal component analysis: ordination of survey sites on WMO and Lewis using site scores with the first two principal components. Broad site groupings are abbreviated as: westerly-orientated WMO (W-WMO); north westerly-orientated WMO (NW-WMO); north easterly-orientated WMO (NE-WMO); south westerly-orientated WMO (SW-WMO); north westerly-orientated Lewis (NWL); and north easterly-orientated Lewis (NEL).

3.3.4 Annual variation on Lewis:

In Figure 3.3.4.1, species loadings for the first two PCs are plotted for faunal and floral data from Lewis recorded in 2013 and 2014. Loadings for individual species, and eigenvalues and proportion of variation explained by the first 6 PCs are presented in Table 3.3.4.1. PC1 appeared to represent an axis of exposure where: the highest negative loadings are observed in high exposure species such as *Alaria esculenta, F. distichus anceps,* and *F. spiralis* f. *nanus*; the highest positive loadings are observed in relatively lower exposure species including *F. serratus*, *F. vesiculosus* and *Nucella lapillus*; in patellid limpets loading, *P. ulyssiponensis* is negative, while *P. vulgata* is strongly positive. In PC2: the highest positive loadings are observed in *F. vesiculosus*, *Palmaria palmata,* and *P. ulyssiponensis*; the highest negative loadings are observed in *F. vesiculosus* f. *linearis, P. vulgata*, and *Sctyosiphon lomentaria*. Interpretation of this axis is not clear but the role of mid shore fucoids, such as *F. vesiculosus,* on assemblage patchiness observed on moderately exposed shores (Hawkins *et al*., 1992) and the strong correlation with the earlier successional species *Palmaria palmata* suggest that this axis may relate to assemblage stability.

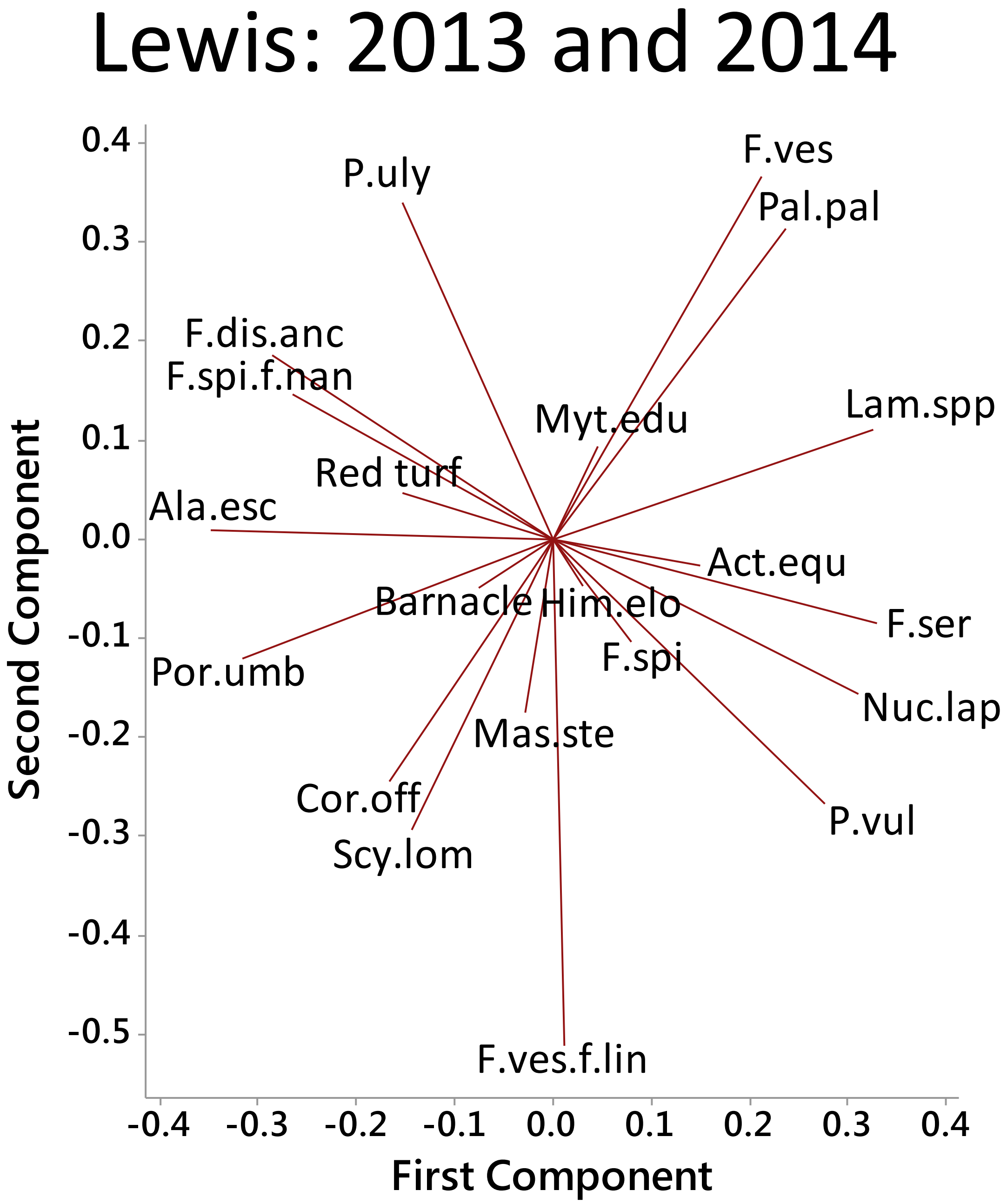


Figure 3.3.4.1 Principal component analysis: loading plot of faunal and floral abundance data from Lewis recorded in 2013 and 2014. Species are abbreviated as: *Actinia equina* (Act.equ); *Alaria esculenta* (Ala.esc); *Corallina officinalis* (Cor.off); *Fucus distichus anceps* (F.dis.anc); *Fucus serratus* (F.ser); *Fucus spiralis* (F.spi); *Fucus spiralis* f. *nanus* (F.spi.f.nan); *Fucus vesiculosus* (F.ves); *Fucus vesiculosus* f. *linearis* (F.ves.f.lin); *Himanthalia elongata* (Him.elo); *Laminaria* spp. (Lam.spp); *Mastocarpus stellatus* (Mas.ste); *Mytilus edulis* (Myt.edu); *Nucella lapillus* (Nuc.lap); *Palmaria palmata* (Pal.pal); *Patella ulyssiponensis* (P.uly); *Patella vulgata* (P.vul); *Porphyra umbilicalis* (Por.umb); and *Scytosiphon lomentaria* (Scy.lom).

Table 3.3.4.1 Principal component analysis: eigenvalues and the proportion of variation explained by the first six PCs for rocky shore faunal and floral data from Lewis. Loadings for 21 individual species are based on abundance data recorded in 2013 and 2014.

	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalue	6.404	3.105	2.268	1.722	1.604	1.352
Proportion	0.305	0.148	0.108	0.082	0.076	0.064
Cumulative	0.305	0.453	0.561	0.643	0.719	0.784
Barnacle spp.	-0.076	-0.049	0.029	-0.113	0.427	0.536
P. ulyssiponensis	-0.153	0.339	0.038	-0.312	-0.049	0.213
P. vulgata	0.277	-0.268	0.196	0.056	0.024	-0.179
Mytilus edulis	0.046	0.094	-0.135	0.433	-0.321	0.257
Nucella lapillus	0.312	-0.156	-0.189	0.095	-0.009	0.144
Actinia equina	0.149	-0.026	-0.493	-0.147	0.092	0.261
F. distichus anceps	-0.286	0.186	-0.096	0.280	-0.024	-0.147
F. spiralis f. *nanus*	-0.266	0.146	-0.257	0.286	0.151	0.086
F. spiralis	0.080	-0.103	-0.352	-0.239	-0.400	0.156
F. vesiculosus f. *linearis*	0.011	-0.512	0.195	0.052	0.064	0.063
F. vesiculosus	0.212	0.366	-0.064	-0.202	-0.137	-0.121
F. serratus	0.330	-0.084	-0.149	-0.064	0.103	-0.203
Red turf	-0.154	0.046	0.079	0.147	-0.222	-0.233
Mastocarpus stellatus	-0.028	-0.176	-0.109	0.029	-0.516	0.158
Palmaria palmata	0.238	0.313	0.166	-0.022	0.062	0.050
Corallina officinalis	-0.168	-0.245	0.156	-0.458	-0.151	0.032
Himanthalia elongata	0.030	-0.048	0.413	0.300	-0.180	0.461
Alaria esculenta	-0.349	0.008	0.033	-0.184	0.044	0.174
Laminaria spp.	0.326	0.111	0.064	-0.032	-0.117	0.142
Scytosiphon lomentaria	-0.144	-0.294	-0.392	0.150	0.186	-0.077
Porphyra umbilicalis	-0.318	-0.121	-0.010	-0.157	-0.247	-0.121

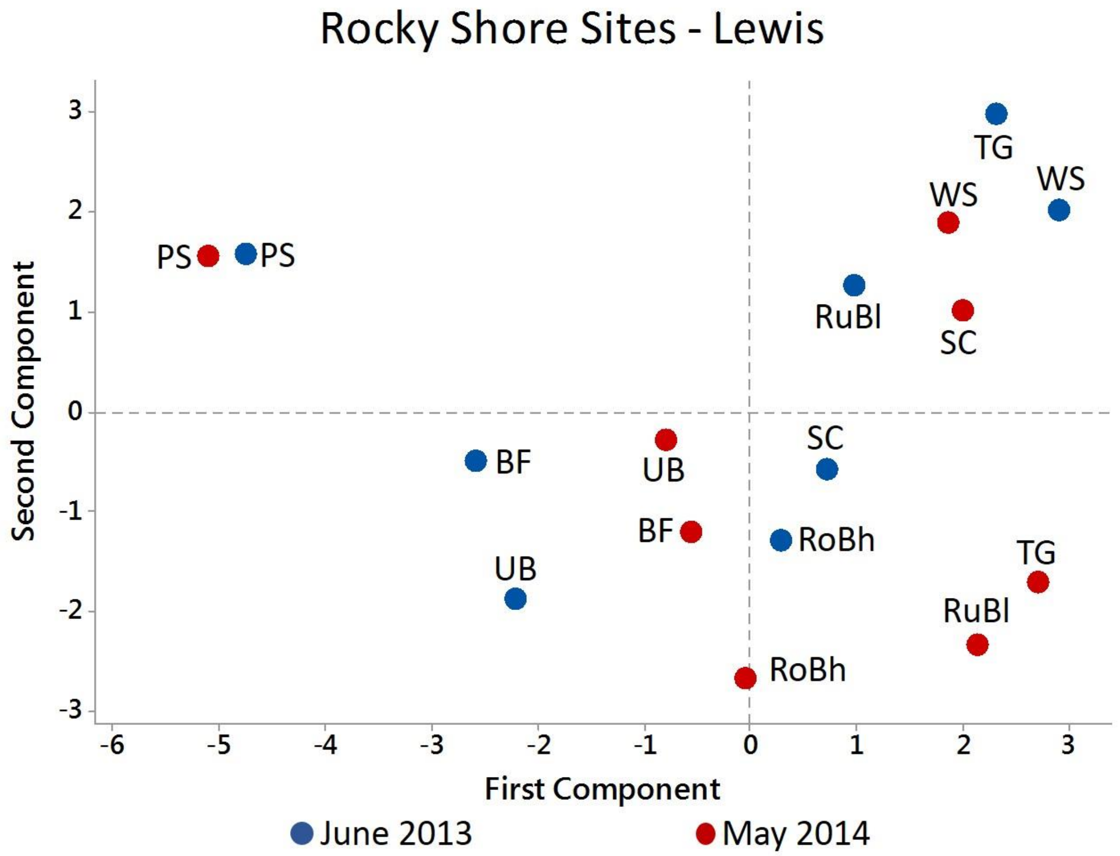


Figure 3.3.4.2 Principal component analysis: ordination of eight sites on Lewis recorded in June 2013 and May 2014 using faunal and floral scores with the first two principal components. Site locations are abbreviated as: Bad an Fhithich (BF); Port Stathanais (PS); Roinn a'Bhuic (RoBh); Rubha Blanisgaidh (RuBl); Sgeir Coidlt (SC); Tada Ghabhsainn (TG); Upper Barvas (UB); and West of Siadar (WS).

Annual variation in rocky shore communities on Lewis was examined by plotting scores from eight sites surveyed in 2013 and 2014 (Figure 3.3.4.2). At two sites (Port Stathanais and West of Siadar), scores from consecutive years were similar; at Bad an Fhithich, Sgier Coidlt, and Upper Barvas, scores shifted positively along the first PC axis; and, at Roinn a’Bhuic, Rubha Blanisgaidh, and Tada Ghabhsainn, scores substantially shifted negatively along the second PC axis. Upon closer examination, on the sites which shifted most notably on the first axis, the greatest differences in abundance between years were increases in *F. serratus* and *Nucella lapillus*, and decreases in *Alaria esculenta* and *Corallina officinalis* - all changes consistent with shifting on an axis towards lower exposure; on the two sites which shifted most notably on the second axis, the greatest differences in abundance between years were increases in *Nucella lapillus*, *Scytosiphon lomentaria*, and several fucoids (*F. serratus*, *F. spiralis*, and *F. vesiculosus* f. *linearis*) and decreases in *P. ulyssiponensis* and *F. vesiculosus* – some of these changes are suggestive of shifts in exposure (*Nucella lapillus* and lower energy fucoids), while others suggest seasonal patterns (*Scytosiphon lomentaria*) or cycling of key mid shore species (patellid limpets and fucoids). Overall, there are a range of differences in study sites between years which do not consistently follow a clear pattern. This may represent normal background stochasticity and do not appear indicative of a response to a known environmental event; scale of variation between years is generally less than the difference between northwest and northeast shore orientation.

3.3.5 Stepwise regressions of topographic variables:

Stepwise regression of PCA site scores and topographic variables recorded on WMO produced most parsimonious models using backward elimination (Table 3.3.5.1). The first PC was highly significantly correlated with complexity. In this model, sites featuring species most associated with high wave exposure were shores of reduced substrate complexity. The second PC was significantly correlated with reduced deviation of mean site bearing from the dominant wind energy direction. Sites orientated towards the dominant exposure direction tended to feature greater abundance of several animal species; sites orientated away from dominant exposure direction tended to feature greater abundance of several macroalgal species. The third PC was correlated highly significantly with aspect, and significantly with openness, the latter being negatively, i.e. associated with sites of reduced openness. Less open sites with substrate aspect orientated away from dominant exposure direction tended to feature greater abundance of *F. vesiculosus* f. *linearis*, *Himanthalia elongata,* and *P. vulgata*; more open sites with substrate aspect orientated towards dominant exposure direction tended to feature greater abundance of *F. vesiculosus*, *F. spiralis,* and *F. distichus anceps*.

Table 3.3.5.1: Stepwise regression (backward elimination; α = 0.1) of the first three PCA site scores and topographic variables from study sites on WMO. Regression coefficients of variables included in each model are included. Significance symbols: $^{+}$<0.10; *<0.05; **<0.01; ***<0.001.

Variable	PC1	PC2	PC3
Constant	3.220	0.470	2.110
Slope			
Openness			-0.019**
Bearing		-0.019**	
Aspect			0.018***
Complexity	-0.743***		
R^2	0.260	0.222	0.462

Stepwise regressions were also used to produce generalised linear models of PCA sites scores and topographic variables with the additional inclusion of different exposure indices used to describe rocky shore sites on WMO (Tables 3.3.5.2-5). Exposure indices were not included in the backward elimination procedure, i.e. they were specified as fixed model offsets, included in all candidate models. Models in which these indices would otherwise have been eliminated are indicated in grey text in Tables 3.3.5.2-5. Including scores from the ‘Ballantine Index’ produced a model featuring highly significant complexity and bearing which explained 83% of the variation in the first PC. This was not unexpected as the first axis is derived from species abundance on an exposure gradient and many of these same species are used to define the ‘Ballantine Index’. After accounting for exposure described by the ‘Ballantine Index’, a significant role of complexity was still identified, suggesting that this factor may be partially contributing to variation through ways beyond the elements of exposure accounted for by the 'Ballantine Index'. Unless forced, 'Ballantine Index' was not included in models examining the second and third PCs. When included, this exposure index did not contribute significantly to explaining variation and R^2 values were only marginally increased through the addition of this variable (Table 3.3.5.2) suggesting that factors other than exposure are accounting for variation in these scores.

Table 3.3.5.2: Stepwise regression (backward elimination; $\alpha = 0.1$) of the first three PCA site scores and topographic variables and 'Ballantine Index' from study sites on WMO. Regression coefficients of variables included in each model are included. Grey text indicates models where backward elimination removed exposure index (see Table 3.3.5.1 for preferred model). Significance symbols: $^+$<0.10; *<0.05; **<0.01; ***<0.001.

Variable	PC1	PC2	PC3
Constant	5.662	0.985	2.190
Slope			
Openness			-0.018*
Bearing	-0.011*	-0.020***	
Aspect			0.018***
Complexity	-0.259*		
Ballantine	-2.355***	-0.329	-0.157
R^2	0.830	0.251	0.470

Unless forced, 'Thomas Index' was not included in models examining the first three PCs. When included, this exposure index did not contribute significantly to explaining variation and R^2 values were only marginally increased through the addition of this variable (Table 3.3.5.3). This is not surprising when considering the open and generally straight shores of WMO because fetch-based exposure models such as the 'Thomas Index' are better at explaining coastlines of varying fetch distances and directions. Furthermore, as previously explained, gradient modifications were not applied to these analysis.

Table 3.3.5.3: Stepwise regression (backward elimination; α = 0.1) of the first three PCA site scores and topographic variables and unmodified 'Thomas Index' from study sites on WMO. Regression coefficients of variables included in each model are included. Grey text indicates models where backward elimination removed exposure index (see Table 3.3.5.1 for preferred model). Significance symbols: $^{+}$<0.10; *<0.05; **<0.01; ***<0.001.

Variable	PC1	PC2	PC3
Constant	2.470	0.602	2.330
Slope			
Openness			-0.017*
Bearing		-0.020*	
Aspect			0.016**
Complexity	-0.734***		
Thomas	0.060	-0.009	-0.035
R^2	0.274	0.222	0.470

Unless forced, 'Burrows Index' was not included in models examining the first three PCs. When included, this exposure index did not contribute significantly to explaining variation and R^2 values were only marginally increased through the addition of this variable (Table 3.3.5.4). This is not surprising when considering the open and generally straight shores of WMO because fetch-based exposure models such as the 'Burrows Index' are better at explaining coastlines of varying fetch distances and directions. Similar to regressions examining the 'Thomas Index', gradient modifications were not applied to these analysis.

Table 3.3.5.4: Stepwise regression (backward elimination; $\alpha = 0.1$) of the first three PCA site scores and topographic variables and unmodified ‘Burrows Index’ from study sites on WMO. Regression coefficients of variables included in each model are included. Grey text indicates models where backward elimination removed exposure index (see Table 3.3.5.1 for preferred model). Significance symbols: $^{+}$<0.10; *<0.05; **<0.01; ***<0.001.

Variable	PC1	PC2	PC3
Constant	3.290	-0.944	2.180
Slope			
Openness			-0.017*
Bearing		-0.018**	
Aspect			0.018***
Complexity	-0.747**		
Burrows	0.000	0.005	-0.002
R^2	0.260	0.270	0.466

Stepwise regression including scores from the ‘Want SQ Index’ produced a model featuring openness and the exposure index which explained 62% of the variation in the first PC. The relatively high coefficient of determination and high significance of this index provides further evidence that this semi-quantitative approach is able to capture several of the main facets of exposure prior to collecting biological data used in the PCA. Highly significant identification of reduced openness in this model of the first PC is harder to explain but may represent an additional factor contributing to species abundance beyond exposure. The ‘Want SQ Index’ was also significant in its inclusion in a model explaining the second PC. This suggests the axis of exposure may be orientated obliquely to the first and second PC axes which may complicate interpretation of these PCAs. Unless forced, ‘Want SQ Index’ was not included in a model examining the third PC. When included, this exposure index did not contribute significantly to explaining variation and R^2 value was only marginally increased through the addition of this variable, suggesting that PC3 is not related to exposure (Table 3.3.5.5).

Table 3.3.5.5: Stepwise regression (backward elimination; $\alpha = 0.1$) of the first three PCA site scores and topographic variables and ‘Want SQ Index’ from study sites on WMO. Regression coefficients of variables included in each model are included. Grey text indicates models where backward elimination removed exposure index (see Table 3.3.5.1 for preferred model). Significance symbols: $^{+}$<0.10; *<0.05; **<0.01; ***<0.001.

Variable	PC1	PC2	PC3
Constant	-0.240	-1.155	1.850
Slope			
Openness	-0.029**		-0.020**
Bearing		-0.016**	
Aspect			0.019***
Complexity			
Want SQ	1.565***	0.416*	0.114
R^2	0.621	0.317	0.471

3.3.6 Redundancy analysis:

Redundancy analysis was performed on faunal and floral abundance data and site scores for all sites on WMO (Table 3.3.6.1). Figure 3.3.6.1 shows a biplot of the first two RDA axes of WMO data constrained by complexity, slope and exposure. In common with the GLM models based on PCA scores, RDA supported the importance of complexity in explaining assemblage differences and the established role of including slope in improving exposure models. The ‘Want SQ Index’ was used to represent exposure after it was found to perform well in explaining assemblage variance when compared with other exposure indices. Each environmental variable is represented by a fitted arrow pointing in the direction of most rapid change and whose length is proportional to the correlation between the variable and ordination. As such, these vectors represent the direction and strength of the environmental gradient (Oksanen, 2014); sites scores and species loadings are ordinated in relationship to these variables. RDA results from WMO are consistent with other multivariate analyses performed in these studies: complexity and exposure are contrastingly related, where lower complexity sites are associated with species favouring higher exposure, such as *Alaria esculenta, F. distichus anceps,* and *P.*

ulyssiponensis; higher complexity sites are associated with species favouring lower exposure, such as *Laminaria* spp., *Nucella lapillus*, and *P. vulgata*; and steeper slopes favour greater abundance of *F. distichus anceps* and *Mastocarpus stellatus*, while patellid limpets do not correlate with slope (Figure 3.3.6.1). RDA was also performed using all topographic variables; this did not result in any noticeable difference in site or species ordination, or in the direction and strength of slope, complexity, or exposure vectors (results not shown).

Table 3.3.6.1 Redundancy analysis: top) eigenvalues and proportion of variation explained by the three RDAs and three PCs for rocky shore faunal and floral data from WMO, and loadings for individual species based on abundance data; bottom) eigenvalues and proportion of variation explained by the three RDAs and loadings for constraining environmental variables.

Species	RDA1	RDA2	RDA3	PC1	PC2	PC3
Eigenvalue	4.084	1.065	0.354	3.826	2.233	1.674
Proportion	0.195	0.051	0.017	0.182	0.106	0.080
Cumulative	0.195	0.245	0.262	0.444	0.551	0.630
Barnacle spp.	0.468	-0.005	0.031	0.588	-0.237	-0.590
P. ulyssiponensis	0.674	0.020	-0.085	-0.155	-0.449	-0.625
P. vulgata	-0.674	0.033	-0.098	0.250	-0.315	0.466
Mytilus edulis	0.300	0.278	-0.310	-0.343	-0.708	-0.286
Nucella lapillus	-0.712	0.086	0.163	0.785	-0.080	-0.083
Actinia equina	-0.497	0.293	-0.356	0.782	-0.127	0.051
F. distichus anceps	0.658	-0.212	-0.055	-0.563	0.380	0.048
F. spiralis f. *nanus*	0.173	0.282	0.080	-0.562	0.447	0.182
F. spiralis	-0.582	-0.184	-0.120	0.474	0.732	-0.190
F. vesiculosus f. *linearis*	-0.408	0.112	0.111	0.106	-0.589	0.643
F. vesiculosus	-0.546	0.065	0.099	0.712	0.398	-0.145
F. serratus	-0.556	-0.149	-0.041	0.746	0.265	-0.231
Red turf	0.386	0.300	0.131	-0.464	0.122	-0.438
Mastocarpus stellatus	0.475	-0.187	-0.076	-0.643	0.064	-0.108
Palmaria palmata	-0.184	0.238	0.173	-0.465	0.503	0.040
Corallina officinalis	0.371	0.318	0.125	-0.366	-0.553	-0.242
Himanthalia elongata	-0.476	0.580	-0.089	0.067	-0.104	0.601
Alaria esculenta	0.842	0.317	-0.117	-0.378	-0.196	-0.047
Laminaria spp.	-0.710	-0.230	-0.171	0.626	-0.168	0.183
Scytosiphon lomentaria	-0.155	0.536	-0.056	-0.230	0.287	0.130
Environmental	RDA1	RDA2	RDA3	PC1	PC2	PC3
Eigenvalue	4.084	1.065	0.354	-	-	-
Proportion	0.742	0.194	0.064	-	-	-
Cumulative	0.742	0.936	1.000	-	-	-
Exposure (Want SQ)	0.985	0.163	-0.062	-	-	-
Complexity	0.284	-0.948	-0.148	-	-	-
Slope	-0.654	-0.088	-0.751	-	-	-

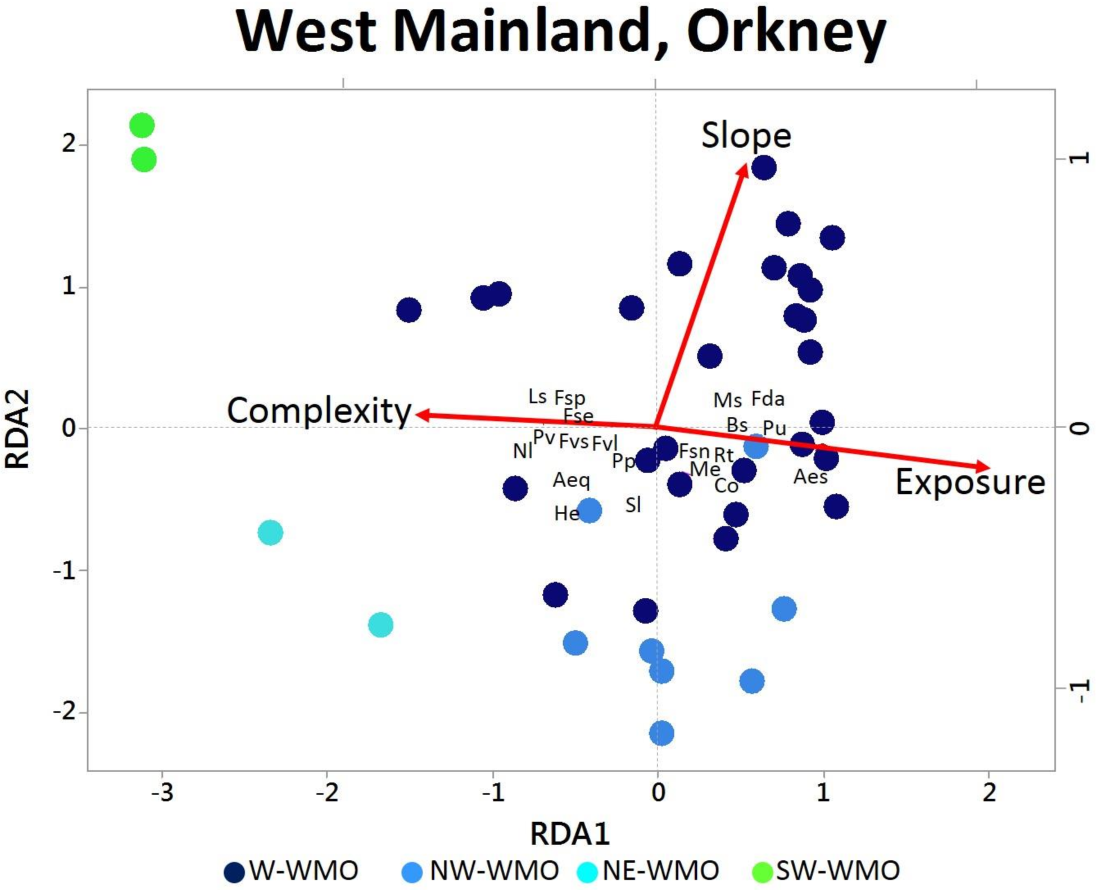


Figure 3.3.6.1 Redundancy analysis: ordination of survey sites on WMO using faunal and floral scores constraining with three environmental variables: complexity, slope and exposure. Broad site groupings are abbreviated as: westerly-orientated WMO (W-WMO); north westerly-orientated WMO (NW-WMO); north easterly-orientated WMO (NE-WMO); and south westerly-orientated WMO (SW-WMO). Species are abbreviated as: *Actinia equina* (Aeq); *Alaria esculenta* (Aes); *Corallina officinalis* (Co); *Fucus distichus anceps* (Fda); *Fucus serratus* (Fse); *Fucus spiralis* (Fsp); *Fucus spiralis* f. *nanus* (Fsn); *Fucus vesiculosus* (Fvs); *Fucus vesiculosus* f. *linearis* (Fvl); *Himanthalia elongata* (He); *Laminaria* spp. (Ls); *Mastocarpus stellatus* (Ms); *Mytilus edulis* (Me); *Nucella lapillus* (Nl); *Palmaria palmata* (Pp); *Patella ulyssiponensis* (Pu); *Patella vulgata* (Pv);) and *Scytosiphon lomentaria* (Sl).

3.3.7 Generalised linear modelling of rocky shore species and topography – *Patella ulyssiponensis*:

Using backward elimination of topographical variables, linear regression of *Patella* spp. abundance data removed all variables from the model. This is perhaps unsurprising, histograms of ubiquitous *Patella* spp. abundance on WMO reveal considerable homogeneity: 38 of 41 survey sites had SACFOR rankings of either ‘abundant’, ‘common’, or ‘frequent’; and no sites were studied where limpets were not recorded. However, when separated into species using proportional data, greater abundance ranges were displayed including 18 sites where only one of the species was recorded (Figure 3.3.7.1).

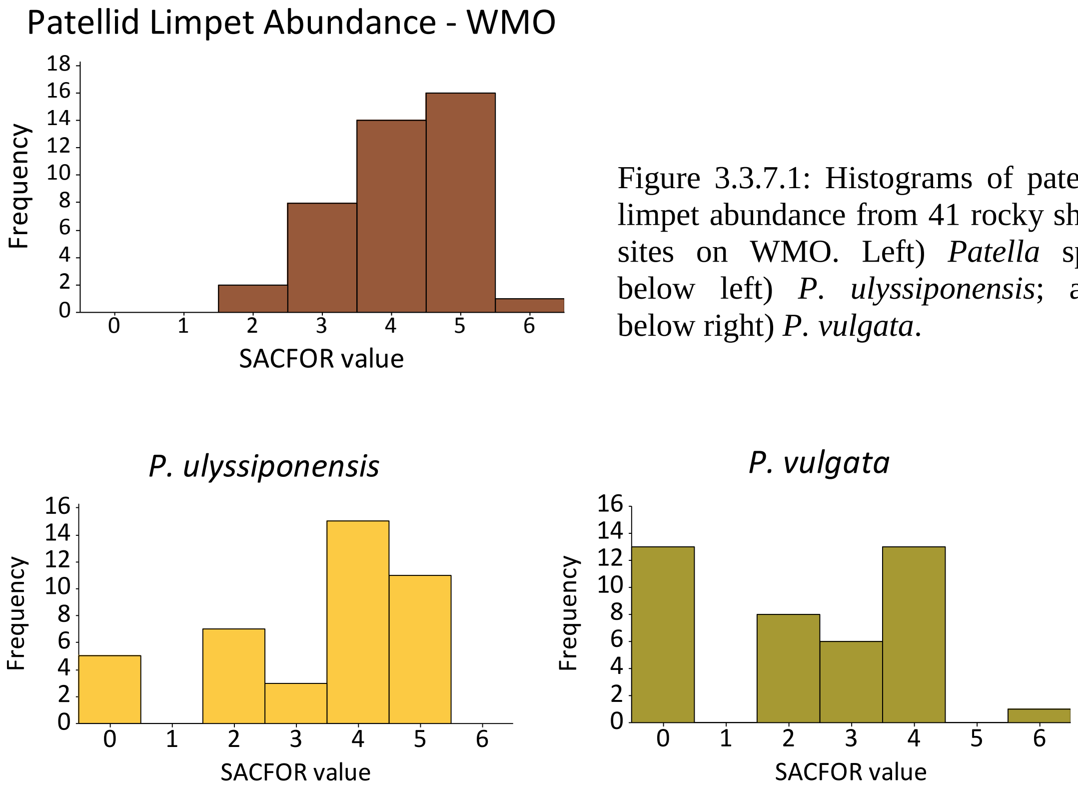


Figure 3.3.7.1: Histograms of patellid limpet abundance from 41 rocky shore sites on WMO. Left) *Patella* spp.; below left) *P. ulyssiponensis*; and, below right) *P. vulgata*.

Logistic regression of patellid proportional data and topographic variables produced the most parsimonious model using survey site slope, complexity, openness, bearing, and aspect ($R^2 = 0.273$). In this model: complexity and bearing were highly significant; openness was significant (Table 3.3.7.1). These findings are consistent with expectations of increased proportions of *P. ulyssiponensis* on more exposed rocky shores. Specifically, substrates of low complexity, open to a wider angle of fetch, and with bearing orientated towards the dominant direction of wave energy were identified in the model as significant, and are associated with higher exposure. While slope was included in this model, it was found to be the least significant of the topographic variables in explaining proportion of *P. ulyssiponensis.*

Table 3.3.7.1: Logistic regression (backward elimination; $\alpha = 0.1$) of *P. ulyssiponensis* proportion (out of total *Patella* spp.) and topographic variables from 41 samples sites on WMO.

Source	Coefficient	SE Coefficient	Chi-Square	*P*-value
Constant	1.1260	0.5990		
Slope	0.0423	0.0248	2.96	0.085
Complexity	-0.4122	0.0557	59.84	<0.001
Openness	0.0075	0.0032	5.46	0.020
Bearing	-0.0178	0.0036	24.22	<0.001
Aspect	0.0056	0.0032	3.01	0.083

Logistic regressions of patellid proportional data and topographic variables were also produced with inclusion of different exposure indices used to describe rocky shore sites on WMO (Table 3.3.7.2-5). Using scores from the ‘Ballantine Index’ of exposure produced the most parsimonious model using survey site complexity, openness, bearing, and ‘Ballantine Index’ ($R^2 = 0.450$). These findings are consistent with expectations of increased proportions of *P. ulyssiponensis* on more exposed rocky shores. Specifically, substrates of low complexity, open to a wider angle of fetch, and with bearing orientated towards the dominant direction of wave energy were identified in the model as highly significant, and are associated with higher exposure (Table 3.3.7.2). The biologically-based 'Ballantine Index' categorises assemblages on a hydrodynamic gradient, whereas the topographic variables are physical factors contributing to this gradient. Increased coefficient of determination and elimination of slope, in the model including 'Ballantine Index' are not unexpected, the latter being an important contributing factor in the relationship between biological assemblages and exposure.

Table 3.3.7.2: Logistic regression (backward elimination; $\alpha = 0.1$) of *P. ulyssiponensis* proportion (out of total *Patella* spp.) and topographic variables with 'Ballantine Index' from 41 samples sites on WMO.

Source	Coefficient	SE Coefficient	Chi-Square	*P*-value
Constant	1.2870	0.5740		
Complexity	-0.2090	0.0596	12.35	<0.001
Openness	0.0190	0.0037	27.65	<0.001
Bearing	-0.0218	0.0026	85.35	<0.001
Ballantine	-1.1750	0.1260	98.33	<0.001

Logistic regression of patellid proportional data and topographic variables including the 'Thomas Index' of exposure produced the most parsimonious model using survey site complexity, bearing, aspect, and 'Thomas Index' ($R^2 = 0.278$). In this model: complexity and bearing were highly significant; aspect was significant (Table 3.3.7.3). These findings are mostly consistent with expectations of increased proportions of *P. ulyssiponensis* on more exposed rocky shores. Specifically, substrates of low complexity, with bearing orientated towards the dominant direction of wave energy are associated with higher exposure. In contrast, aspect, the least significant variable identified, showed a positive correlation, i.e. greater deviation from mean direction of wave energy. Inclusion of the 'Thomas Index' resulted in elimination of slope and openness but did not improve the model. Elimination of slope is not surprising given that the 'Thomas Index' includes an estimate of offshore gradient which might be expected to correlate with littoral slope.

Table 3.3.7.3: Logistic regression (backward elimination; $\alpha = 0.1$) of *P. ulyssiponensis* proportion (out of total *Patella* spp.) and topographic variables with unmodified 'Thomas Index' from 41 samples sites on WMO.

Source	Coefficient	SE Coefficient	Chi-Square	*P*-value
Constant	1.6520	0.3820		
Complexity	-0.4213	0.0544	64.58	<0.001
Bearing	-0.0157	0.0038	17.85	<0.001
Aspect	0.0068	0.0033	4.30	0.038
Thomas	0.0771	0.0234	10.92	0.001

Logistic regression of patellid proportional data and topographic variables including the 'Burrows Index' of exposure produced the most parsimonious model using survey site slope, complexity, openness, bearing, aspect, and 'Burrows Index' ($R^2 = 0.338$). In this model: complexity, bearing, and aspect were highly significant; slope and openness were approaching significance (Table 3.3.7.4). These findings are mostly consistent with expectations of increased proportions of *P. ulyssiponensis* on more exposed rocky shores. Specifically, substrates of low complexity, with bearing orientated towards the dominant direction of wave energy are associated with higher exposure. In contrast, openness and aspect showed a positive correlation, i.e. both variables suggest less exposed conditions. Coefficient of determination was only marginally increased through the addition of this unmodified, fetch-based exposure index.

Table 3.3.7.4: Logistic regression (backward elimination; $\alpha = 0.1$) of *P. ulyssiponensis* proportion (out of total *Patella* spp.) and topographic variables with unmodified 'Burrows Index' from 41 samples sites on WMO.

Source	Coefficient	SE Coefficient	Chi-Square	*P*-value
Constant	0.3610	0.6310		
Slope	0.0465	0.0254	3.40	0.065
Complexity	-0.2662	0.0607	19.95	<0.001
Openness	-0.0080	0.0043	3.45	0.063
Bearing	-0.0226	0.0038	35.87	<0.001
Aspect	0.0104	0.0034	9.44	0.002
Burrows	0.0102	0.0018	34.33	<0.001

Logistic regression of patellid proportional data and topographic variables including the ‘Want SQ Index’ of exposure produced the most parsimonious model using survey site bearing, and ‘Want SQ Index’ ($R^2 = 0.412$). These findings are consistent with expectations of increased proportions of *P. ulyssiponensis* on more exposed rocky shores. Inclusion of the ‘Want SQ Index’ resulted in elimination of complexity, slope, and openness from the model (Table 3.3.7.5). This is unsurprising. While the ‘Want SQ Index’ does not include direct input of values from these topographic variables, the index is informed by an overarching assessment of these features (see Table 3.2.1.2).

Table 3.3.7.5: Logistic regression (backward elimination; α = 0.1) of *P. ulyssiponensis* proportion (out of total *Patella* spp.) and topographic variables with ‘Want SQ Index’ from 41 samples sites on WMO.

Source	Coefficient	SE Coefficient	Chi-Square	*P*-value
Constant	-1.6140	0.3060		
Bearing	-0.0154	0.0025	42.92	<0.001
Want SQ	0.8750	0.0814	142.04	<0.001

3.3.8 Generalised linear modelling of rocky shore species and topography – *Fucus distichus anceps*:

Linear regression of *F. distichus anceps* abundance data and topographic variables from WMO surveys produced the most parsimonious model using site slope and complexity ($R^2 = 0.215$). In this model, both variables were found to be significant (Table 3.3.8.1). These findings are consistent with expectations of increased abundance of *F. distichus anceps* on more exposed rocky shores. Specifically, substrates of high slope and low complexity, both associated with higher exposure, were identified in the model as significant.

Table 3.3.8.1: GLM (backward elimination; α = 0.1) for *F. distichus anceps* abundance compared with topographic variables from 41 survey sites on WMO.

Source	Coefficient	SE Coefficient	*t*-value	*P*-value
Constant	3.050	1.000		
Slope	0.180	0.076	2.36	0.024
Complexity	-0.464	0.209	-2.21	0.033

Linear regression of *F. distichus anceps* abundance data and topographic variables including the 'Ballantine Index' of exposure produced the most parsimonious model using survey site aspect, and 'Ballantine Index' (Table 3.3.8.2). Inclusion of the 'Ballantine Index' resulted in removal of slope and complexity from the model, and improved the coefficient of determination ($R^2 = 0.581$). These findings are consistent with expectations of increased abundance of *F. distichus anceps* on more exposed rocky shores: substrate complexity and decreased slope contribute to greater energy dissipation; similar conditions are represented on the 'Ballantine Index' by assemblages associated with greater shelter.

Table 3.3.8.2: GLM (backward elimination; α = 0.1) for *F. distichus anceps* abundance compared with topographic variables and 'Ballantine Index' from 41 survey sites on WMO.

Source	Coefficient	SE Coefficient	*t*-value	*P*-value
Constant	7.033	0.590		
Aspect	-0.015	0.006	-2.62	0.013
Ballantine	-2.111	0.302	-6.99	<0.001

Linear regression of *F. distichus anceps* abundance data and topographic variables including the ‘Thomas Index’ of exposure produced the most parsimonious model using survey site slope, complexity, openness, bearing, and ‘Thomas Index’. These findings are mostly consistent with expectations of increased abundance of *F. distichus anceps* on more exposed rocky shores. Specifically, steep slope and substrates of low complexity were highly significant and are associated with higher exposure. In contrast, reduced openness and bearing deviating away from the dominant direction of wave energy were found to be significant and are associated with lower exposure (Table 3.3.8.3). Coefficient of determination was increased through the addition of this unmodified, fetch-based exposure index and additional topographic variables ($R^2 = 0.362$). It might be expected that models featuring the ‘Thomas Index’ would eliminate slope owing to the inclusion of off-shore gradient in this index. That slope was not eliminated in this model is difficult to interpret. It may be that correlation between *F. distichus anceps* and slope is highly site-specific to the littoral zone, and this is not captured using off-shore gradient estimates of slope.

Table 3.3.8.3: GLM (backward elimination; $\alpha = 0.1$) for *F. distichus anceps* abundance compared with topographic variables and unmodified ‘Thomas Index’ from 41 survey sites on WMO.

Source	Coefficient	SE Coefficient	*t*-value	*P*-value
Constant	4.150	2.380		
Slope	0.243	0.085	2.86	0.007
Complexity	-0.602	0.205	-2.94	0.006
Openness	-0.028	0.014	-2.07	0.046
Bearing	0.027	0.012	2.25	0.031
Thomas	0.171	0.092	1.86	0.072

Linear regression of *F. distichus anceps* abundance data and topographic variables including the 'Burrows Index' of exposure produced the most parsimonious model using survey site slope, complexity, and 'Burrows Index' ($R^2 = 0.226$). This model was created by forcing the inclusion of this exposure index, i.e. without forcing, the index was eliminated. These findings are consistent with expectations of increased abundance of *F. distichus anceps* on more exposed rocky shores. Specifically, steep slope and substrates of low complexity were significant and are associated with higher exposure (Table 3.3.8.4). Coefficient of determination was only marginally increased through the addition of this unmodified, fetch-based exposure index.

Table 3.3.8.4: GLM (backward elimination; $\alpha = 0.1$) for *F. distichus anceps* abundance compared with topographic variables and unmodified 'Burrows Index' from 41 survey sites on WMO.

Source	Coefficient	SE Coefficient	*t*-value	*P*-value
Constant	4.250	1.950		
Slope	0.185	0.077	2.40	0.021
Complexity	-0.528	0.229	-2.31	0.027
Burrows	-0.004	0.005	-0.72	0.477

Linear regression of *F. distichus anceps* abundance data and topographic variables including the 'Want SQ Index' of exposure produced the most parsimonious model using survey site slope, openness, bearing, aspect, and 'Want SQ Index' (Table 3.3.8.5). Improvement of the coefficient of determination ($R^2 = 0.525$) and elimination of complexity from the model are not unexpected; complexity plays an important role in the overarching assessment used in the 'Want SQ Index' (see Table 3.2.1.2). These findings are mostly consistent with expectations of increased abundance of *F. distichus anceps* on more exposed rocky shores. Specifically, steep slope and sites with aspect towards the dominant direction of wave energy were identified in the model as significant, and approaching significance, respectively, and are associated with higher exposure. In contrast, reduced openness and bearing deviating away from the dominant direction of wave energy were found to be significant and are associated with lower exposure. It is a difficult to interpret why slope was not eliminated from this model with the 'Want SQ Index', while slope was eliminated in logistic regression of *P. ulyssiponensis* including this index. The occasionally puzzling inclusion or exclusion of certain topographic variables when exposure indices are considered may indicate the complicated multi-factorial nature of exposure. These indices may not fully capture the contribution of these factors; greater ability to quantify topographic variables may lead to improved exposure indices.

Table 3.3.8.5: GLM (backward elimination; α = 0.1) for *F. distichus anceps* abundance compared with topographic variables and 'Want SQ Index' from 41 survey sites on WMO.

Source	Coefficient	SE Coefficient	*t*-value	*P*-value
Constant	1.020	2.030		
Slope	0.194	0.074	2.61	0.013
Openness	-0.028	0.011	-2.45	0.019
Bearing	0.032	0.013	2.55	0.015
Aspect	-0.019	0.011	-1.75	0.088
Want SQ	1.198	0.241	4.97	<0.001

3.4 Discussion:

The studies reported here provide a record of rocky shore assemblages along coasts where large-scale extraction of wave energy may occur in the near future. The selection of survey sites allowed assessment of areas close to leasing sites for device deployment, where impacts are to be most expected, as well as areas distant from development, which may function as control sites. These studies also examined the role that wave exposure plays in determining rocky shore communities and how topographic features of the coast may be expected to modify dissipation of wave energy. Biological and topographic data from WMO and Lewis suggest that:

- exposure is the main contributing factor to observed differences in rocky shore assemblages;
- topographic variables, especially structural complexity of the substrate, are important modifiers of littoral exposure;
- despite similar off-shore wave resources, the littoral communities of WMO and Lewis differ owing to topographically-mediated dissipation of wave energy, especially through greater complexity on Lewis shores;
- differences in assemblages between rocky shore sites on Lewis are primarily created by topography, although annual changes of smaller magnitude are also apparent;
- exposure indices are improved when modified with topographic data;
- *in situ* recording of topography at individual site-scale will provide additional data, not captured through cartographic assessment, which may improve exposure modelling;
- when compared with *P. vulgata*, *P. ulyssiponensis* is found on more exposed shorelines, especially those of low topographic complexity providing fewer microhabitats of relative shelter;
- the presence of *F. distichus anceps* on WMO is strongly related to a habitat characterised by a narrow set of topographic factors; *F. distichus anceps* thrives on high exposure shores with steep slopes and low complexity.

The surveys conducted here may also provide baseline data allowing future assessment of other long-term environmental forcing agents such as climate change, manifest through increased temperatures and, potentially, increased storm activity. Comparisons of inter-annual and between site variation in rocky shore community assemblages suggest that using the survey approach described in the current studies it may be possible to identify long-term environmental responses against a background of natural change. This is a fundamental requirement in BACI-style studies. A novel index is being developed to explore the practicality of modifying wave or fetch-based exposure models using topographic variables recorded during site-specific studies (see Appendix 6). The hypotheses identified in 3.1.2 are addressed below.

Topography and exposure:

In spite of the well-known importance of wave energy in structuring rocky shore communities (Ballantine, 1961; Lewis, 1964), remarkably little is known of the specific facets of exposure that form this relationship (Thomas, 1986; Denny, 1999; Gaylord, 2000). Cartographic, fetch-based models of wave exposure have proved useful in rocky shore ecological studies, especially when informed with wind data. These models improved when modified by estimates of gradient (Thomas, 1986; Burrows *et al*., 2008; Sundblad *et al*., 2014). In the studies reported here, an approach has been developed to capture several features of wave energy dissipation which may be the main source of variability in exposure on shores with similar offshore wave resource. These relate to local topography at the scale of metres rather than a broader approach based solely on fetch or using cartographic measurements. The current studies support the postulation that topographically determined variation in exposure is a major determinant of observed differences in the littoral community at study sites on WMO and Lewis. Principal component analysis demonstrates that the dominant direction of variability in WMO rocky shore assemblages is related to exposure (Table 3.3.3.1). Secondary direction of variability identifies the relationship of high exposure shores with increased animal dominance, representing a net consumption trophic level (Hawkins *et al.*, 1992). On the most extreme exposed shores observed in these studies: most mobile animals are absent or have reduced abundance; animals capable of survival tend to be filter-feeders, e.g. barnacles and small mussels; and, macroalgae are limited to ‘dwarf’ fucoids and a few low profile plants. On more moderately exposed shores, patches of fucoids form mosaics with patellid limpets and barnacles which have been shown to cycle relative to one another (Hawkins *et al.*, 1992) (see Section 1.4: Fucoid-barnacle-patella complex). Studies in Orkney by Baxter *et al.* (1985) suggest that these fluctuations occur less rapidly at higher latitudes. In the current study, only four sites on WMO and seven on Lewis are considered to be moderately exposed, and only the Lewis sites were compared between years. While established cycling may underlie the relationship between major components of the rocky shore community, there is not the current scope in these studies to describe community dynamics with any certainty, although abundance changes in key species, i.e. *P. ulyssiponensis* and several fucoids, between years at some Lewis sites suggest mid shore cycling (Figure 3.3.3.2).

While the dominant direction of variability in assemblage composition was best explained by differences in exposure, evidence suggests that exposure may, at least partially, explain other directions of variability (Table 3.3.5.5). This underlines the importance of recognising that processes affecting species composition are complicated and at times it may be hazardous to make interpretations based on a single factor. Improved correlation with inclusion of the ‘Want SQ Index’ with both PC1 and PC2 scores suggests that an axis representing exposure may be orientated obliquely to PC axes and contribute to explaining both PCs. These findings are consistent with the established relationship between higher exposure and animal domination of rocky shores in the North Atlantic

(Hawkins *et al*., 1992). Further components of variability identified in the analysis are more challenging to interpret. A contrast between *F. vesiculosus* f. *linearis* and *F. vesiculosus* after the effects of exposure are already accounted for (Table 3.3.3.1), suggests that additional habitat modifiers may be relevant. While difficult to establish certainty, substrate complexity is the most obvious candidate and explained more of the variance than other variables when constructing models with topographic input (Table 3.3.5.1).

On westerly-facing study sites along WMO, from the Billia Croo to the Brough of Birsay, the combination of coastline orientation and the westerly dip of Orcadian sandstone creates planar rocky platforms at the base of cliffs facing the dominant incoming wave direction. Typically, little refraction occurs as waves break while running up these slopes. On this type of shoreline, a relatively homogeneous dissipation of energy might be expected, from the waves to the bottom substrate (Denny, 1995). In contrast, from Birsay to Costa Head, the coastline of WMO is orientated to the NW, oblique to the bedrock dipping west. Instead of the frequently elegant and uniform planar platforms characteristic of the westerly-orientated coast, below the cliffs of NW WMO a series of coarsely-stepped reefs are often formed. Depending on wave height and water depth (owing to the timing of the tidal cycle), stepping of these obliquely orientated shores will tend to promote shoaling of the incoming, and refracting, waves (Folley and Whittaker, 2009). As these shores deviate from planar surfaces, increasing structural complexity of the sea bottom will increase dissipation. Rather than a continuous rate of energy dissipation, stepping might be expected to create punctuated energy loss as waves shoal over rapidly decreasing depths (Denny, 1995). That the rocky shore assemblages on westerly and north-westerly orientated coasts on WMO feature mostly the same key species associated with extreme wave energy suggests that, in this case, the net consequences of orientation and topographic variation is, broadly-speaking, a similar level of littoral exposure. That these sites appear to group separately after the primary effects of exposure are accounted for (Figure 3.3.3.2), suggests however that orientation of these cliffs is important. Sites on NW WMO feature greater abundance of *F. spiralis nanus*, *Palmaria palmata*, and *Scytosiphon lomentaria*; sites on W WMO feature greater abundance of barnacles (Table 3.3.3.1). The precise mechanism accounting for species differences observed between W WMO and NW WMO are not clear. Barnacle-dominated shores are characteristic of the relatively greater stability seen in higher latitude locations, such as Orkney, compared with greater fluctuations seen in rocky shore assemblages at lower latitudes (Baxter *et al*., 1985; Hawkins *et al*., 1992) (see Section 1.4: Fucoid-barnacle-patella complex). On NW WMO, greater abundance of small fucoids (i.e. *F. distichus anceps* and *F. spiralis* f. *nanus*) and stands of *Palmaria palmata*, as well as more ephemeral species such as *Scytosiphon lomentaria*, might be indicative of less stable or recently disturbed habitats. This topic is described in greater detail in Chapter 4 (Discussion – Exposure limits and vertical surfaces). It should be noted again that any interpretation of NW WMO shore must be met with caution owing to the low number of survey sites.

Additional coastal orientations on WMO included in this work were limited to two sites facing SW and two sites facing NE (Figure 3.2.1.1). SW facing sites featured more complex, broken shores and were orientated towards the high island of Hoy, therefore with much reduced fetch; NE facing sites were shallow-sloped and orientated towards the island of Rousay, also resulting in much reduced fetch. SW sites were dominated by moderately exposure fucoids; NE sites featured modestly more exposed species, and were less fucoid-dominated (Figure 3.3.3.2).

WMO v Lewis:

When compared against the extreme exposure assemblages found on most of WMO, the littoral community on Lewis is associated with more moderate levels of exposure (Figure 3.3.3.2). This is in spite of the high wave energy resource found off Lewis; in fact, relative sheltering of WMO from more southerly winds owing to the presence of the Outer Hebrides and the Scottish mainland, reduces gross off-shore wave resource compared with the Western Isles (Folley *et al*., 2010). On NWL, most survey sites suggest a general pattern towards more moderate exposure and greater abundance of faunal species (Figure 3.3.3.2 . As a general statement, these shores feature well-developed barnacles zones, and abundant patellid limpets and mussels. When compared with WMO shores, NWL featured greater abundances of other animals such as *Actinia equina* and *Nucella lapillus*, as well as additional grazing species absent from much of WMO, i.e. littorinid and trochid snails. The greater variety of rocky shore species on NWL may result from greater substrate complexity where more extreme contrasts in exposure are created at highly localised scales in close proximity (Burrows *et al*., 2014). In contrast, the single site on NEL, was topographically similar to much of WMO and featured greater abundances of species associated with high exposure. The steep, planar platforms on this short coastal section (from the Butt of Lewis to Port Stathanais) are home to a population of *F. distichus anceps* and *F. spiralis* f. *nanus.*

Slope:

Slope is an important modifier of exposure in two important ways: firstly, at site-specific scale, differing hydrodynamic forces are created by breaking waves in the surf-zone, with steeper shores tending to produce more powerful collapsing or surging waves; and secondly, at a broader scale, the gradient of the nearshore modifies dissipation of energy through bottom friction, from wave to substrate, with shallower slopes resulting in less energy reaching the surf-zone (Peregrine, 1983; Smith, 2003). The presence of littoral organisms typical of high wave energy shores correlates with slope steepness, although this relationship becomes weaker with increasing tidal range, presumably owing to the decreasing relative role of wave exposure on vertical zonation (Thomas, 1986).

Cartographically-based derivation of shoreline gradient, using nearshore bathymetry or littoral shore extension measurements, is a convenient way to estimate slope at a broad-scale without direct assessment of the site. The 'Thomas' and 'Burrows' indices explored in the current study are improved by using estimates of offshore and foreshore gradients as modifiers (Table 3.3.2); these estimates may capture general variability in gradients important to wave energy dissipation. However, without finer scale measurement directly at the site, these indices might not capture the specific slope of a platform or rock feature where the waves break in the intertidal zone and hydrodynamic forces are at their maximum (Gaylord, 2000). On the other hand, using only slope measured in the intertidal survey area may be 'myopic' in overall assessment of wave dissipation, missing the overall characterisation of shoreline gradient. Preliminary investigation of bathymetric data from westerly-orientated WMO suggests that offshore and littoral shore slope correlate very closely (data not shown). Future development of exposure indices might benefit from including slope modifiers at two different scales: site-scale determination of slope in the littoral zone where waves break; and broader-scale determination of nearshore slope where wave dissipation to the substrate begins.

On WMO, platform slope varies from about 3°-20°; there are no observed littoral surfaces angled between approximately 20° and essentially vertical cliff faces. With the exception of surge gullies, subject to large sediment scour, there are no areas observed to be too energetic for survival of macroalgae and barnacles. The extreme regular planar platforms typical of WMO are found on only a few other coastlines in Britain and Ireland, e.g. parts of Caithness, County Clare and Donegal Bay (Lewis, 1964); similar topography was observed in the current studies on the north-easterly orientated shores near the Butt of Lewis. With the exception of Donegal Bay, all of these locations feature *F. distichus anceps* (Powell, 1957a).

In the present study, slope was not included in the most parsimonious models produced to explain assemblage variation (Table 3.3.5.1). Furthermore, topographic variables were compared with *P. ulyssiponensis* data; using different exposure indices, slope was generally eliminated from models or was the least significant amongst the other topographic variables (Tables 3.3.7.1, 3.3.7.2, and 3.3.7.4). However, comparisons of exposure indices showed improvement in 'Thomas' and 'Burrows' indices when modified with shore slope (Table 3.3.2). Furthermore, when applied to *F. distichus anceps* data using the same exposure indices, slope was identified as significant in all models except the 'Ballantine Index' (Tables 3.3.8.1, 3.3.8.3, 3.3.8.4, and 3.3.8.5). These results show that *F. distichus anceps* is typically found, and in greatest abundance, on platforms and off-shore skerries at steeper angles as long as the shoreline is subjected to high-wave energy. Shallow gradient platforms on more exposed shores and steep slopes on less-exposed shores tend to be populated by relatively lower energy fucoids, such as *F. vesiculosus* f. *linearis* (Figure 3.3.1.2). This distribution pattern is consistent with previous research in Iceland where *F. distichus anceps* was found to become more abundant with steeper, more exposed shores (Munda, 2004). RDA using slope as a constraining variable confirms that, on WMO, steeper littoral gradients correlate with higher exposure sites but not strongly (Figure 3.3.6.1), and that species associated with high exposure are not necessarily correlated with slope. As the current studies show, a simple monotonic relationship does not always exist between slope and high-exposure organisms; while steeper slopes are generally subject to more energetic hydrodynamic conditions and are typically associated with species favouring high exposure (Figure 3.3.1.2), additional factors related to slope (see page 62) may be important to certain species including *P. ulyssiponensis* (see page 127 for further discussion on this species).

Openness:

The openness of a shore will modify wave exposure by varying the total angle of approaching fetch. Headlands are battered by waves, and embayments are sheltered from waves, because of differences in openness, as well as bathymetric features which produce shoaling and refraction (Smith, 2003; Folley *et al*., 2010). Versions of this metric have informed the earliest attempts at cartographically-determined wave indices (Baardseth, 1970) and were used to summate fetch from directional sectors in models explored in this study (Thomas, 1986; Burrows *et al*., 2008). These models create a coarse-scale of openness depending on the selected size of sectors and the directional precision of meteorological data. In the current study, openness has been considered as an additional variable because site-scale topographic surveying allows a more precise determination of this factor, although openness can also be determined cartographically.

Owing to the mostly straight coast of much of WMO, in this study, as a general statement, openness did not vary a great deal between sites. Interestingly, the extremes of openness on WMO, at Borwick (98°) and Breckness (224°), do not correlate with exposure. In these examples, however, this is unsurprising: despite the relative embayment at Borwick, this site is in all other ways typical of an extreme exposure shore; and the headland at Breckness has one of the most extensive foreshores on WMO and is orientated south-west towards the high island of Hoy, resulting in much reduced fetch. These examples emphasise the importance of a multifactorial approach to representing exposure. In the current study, the proportion of limpets that were *P. ulyssiponensis* was seen to be positively related with openness (Table 3.3.7.1), consistent with an association with higher exposure shores. However, in general, openness did not explain variance using GLMs of PC site scores or when examining *F. distichus anceps* abundance; indeed, in one model, openness was unexpectedly correlated negatively with exposure (Table 3.3.5.5). As with the examples from Borwick and Breckness, the theoretical importance of openness may be over-shadowed in practice by other factors. The generally poor correlation between openness and exposure may be in part due to a reduction in directional distribution in energy which occurs as approaching waves refract in the nearshore (Folley *et al*., 2010). This will focus wave energy into local 'hot spots' or 'cold spots' based on bathymetry and coastal orientation. While even small changes in fetch have been shown to induce morphological variation in fucoids (Ruuskanen *et al*., 1999), the orientation of the shore towards maximum fetch distance may be more important than 'openness' to fetch, per se.

Mean site bearing and substrate aspect:

The rocky shores on WMO from the Billia Croo to Birsay are predominantly orientated in a westerly direction (Figure 2.3.1). As such, waves approaching from the west – which is both the dominant wind direction and the longest fetch – tend to refract little as they interact with the underlying bedrock and thus subject the shore to, practically, the full force of the sea. In this manner, the aspect of the coast is of critical importance in the hydrodynamic relationship between sea and shore (Thomas, 1986). Whereas, the interaction between hydrodynamic forces and shoreline topography is typically complex (Smith, 2003), on WMO the ‘co-orientation’ of dip with bearing and aspect, as well as the extreme uniformity of much of the rocky platforms of WMO create an unusual set of circumstances where much of the rocky platforms are far simpler, and far more exposed, than most coastal configurations.

While mean site bearing and aspect refer to different facets of coastline orientation, these indices share similar origin in that both are defined by angular deviations from the same dominant wave energy direction. In the case of westerly-orientated WMO, where the bedrock also dips in a westerly direction, both indices are generally similar. The process of refraction, accompanied by shoaling in shallowing waters, attenuates waves; greater refraction and shoaling will dissipate more wave energy. Previous wave exposure indices do not take into account aspect and its modifying effect through wave refraction. The importance of wave refraction to coastal hydrodynamics is illustrated in the shoreline surrounding the study site at the Hole o’Row (Figure 3.4.1). In a relatively compact area, waves entering Skaill Bay will shoal, dissipating energy as they refract around the headland. Mid shore organisms at the most exposed reefs (used for the study site itself) include the fucoids *F. distichus anceps* and *F. spiralis* f. *nanus*; rocky platforms inshore from the outer-most reefs will tend to feature *F. vesiculosus* f. *linearis*; and, further into the embayment, the fucoid zone is comprised of larger *F. vesiculosus* and *F. spiralis* without high-exposure morphological adaptations.

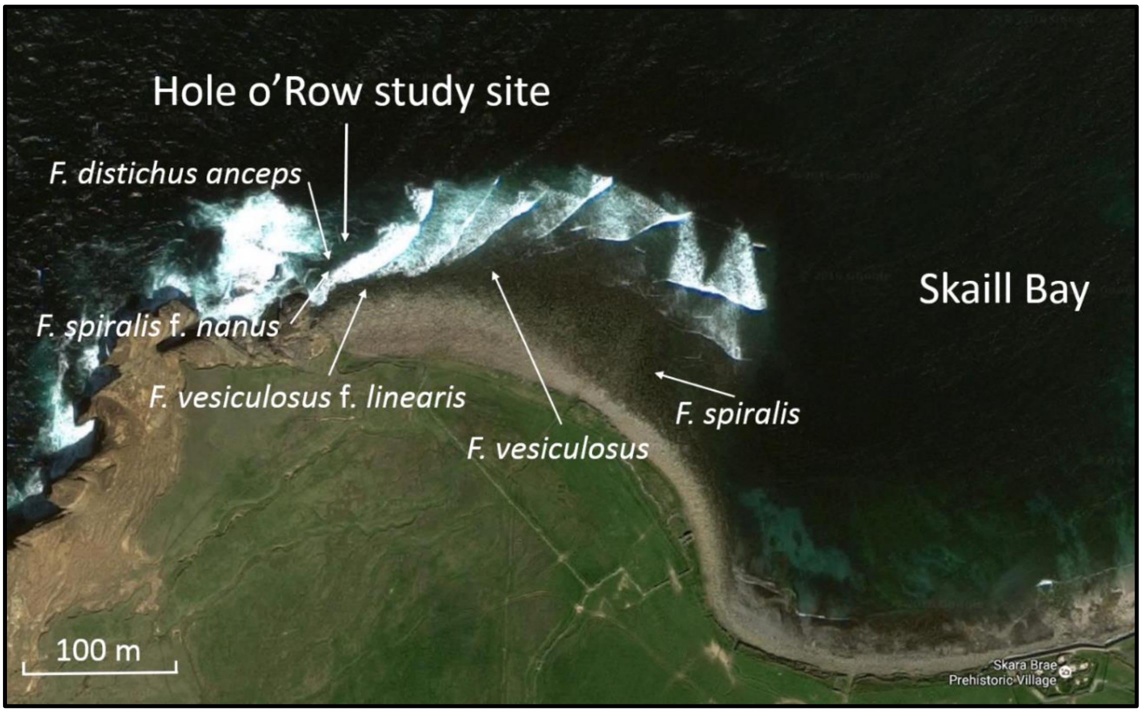


Figure 3.4.1: Satellite image of refraction as waves pass Row Head to enter Skaill Bay, WMO, and general distribution of fucoid algae (Google Earth, 2016). Notice the changing angle of successive wave fronts from the open ocean (left of image) to the relatively perpendicular orientation of the final breaking wave in this series.

In the current study, while mean site bearing was frequently identified in models and was found to be highly significant in explaining *P. ulyssiponensis* proportion on WMO (Table 3.3.7.1), in some models, contrary to expectations, greater deviation of bearing from dominant energy direction was correlated with *F. distichus anceps* abundance. Similarly, substrate aspect was infrequently identified in models produced when comparing exposure indices with topographic variables, and some models found a contradictory relationship with exposure.

Mean site bearing and substrate aspect are defined in the present studies based on dominant wave energy direction determined from wind data (direction and speed) at Billia Croo over 3 years (Chapter section 2.5). Because oceanic swell may form far from the shores it is destined to reach, wind records alone may not always accurately represent wave energy direction (EMEC, 2006). When possible, determining angle of wave incidence directly from wave data may be preferred. Similar to analysing wind data, wave direction, height, and period can be used to determine dominant wave energy direction; in the current study, wave directional data were not readily available. Clearly, the angle of deviation from fixed topographic features, will vary as angle of wave incidence shifts. Temporal variation in dominant wave energy might be expected to occur seasonally and over longer time periods. Thus, it is important to be cognisant of the changeability of energy directionality when evaluating bearing and aspect. Perhaps the importance of shoreline orientation was not apparent in the current studies because of spatial and temporal imprecision created by assigning a single dominant energy direction, albeit based on sound reasoning and wind data spanning several years. This may provide an explanation for the occasional contradictory findings as possible spurious associations based on current limitations in defining energy directionality. More sophisticated modelling in future studies may better capture temporal change in these exposure-modifying factors; use of nearshore wave directional data may better capture spatial changes in wave energy resource.

Substrate complexity:

Results of GLMs of PCA sites scores and topographic variables, in the present study, suggest that substrate complexity is a major determinant of differences in rocky shore assemblages between sites with similar off-shore wave environments (Table 3.3.5.1). Complex substrates tend both to dissipate wave energy, where shoaling and substrate porosity increase bottom friction (Mork, 1996; Ferrario *et al*., 2014), and to complicate the interaction with hydrodynamic forces and the benthic community, the latter leading to littoral micro-habitats of greater exposure and relative shelter. Variations in substrate complexity between WMO and Lewis appear to be manifest in assemblage differences between these shores. As noted before, despite the openness of the north coast of Lewis to a high wave energy resource offshore, greater topographical complexity is correlated with reduced exposure in the littoral zone and is associated with species typically found on more sheltered shores. The importance of complexity in explaining abundance differences between sites may not be entirely due to exposure, Johnson *et al.* (2003) found that substrate complexity may increase species richness owing to increases in habitat diversity and surface area, and greater variation in environmental factors, such as wetness. In contrast, much of WMO coastline more closely resembles idealised planar surfaces where the lack of complicating features dissipates less wave energy approaching the shore and creates greater homogeneity in exposure. Overall species richness was reduced on these shores when compared with the Lewis sites. As well as best explaining assemblage variance with exposure (Table 3.3.5.1), complexity was found to be highly significant in explaining *P. ulyssiponensis* proportion (Table 3.3.7.1), and significant in explaining *F. distichus anceps* abundance (Table 3.3.8.1). The importance of complexity was further supported in many of the GLMs examining topographic variables and exposure indices, and RDA of WMO biological and site data showed a strongly opposing relationship between the selected variables of complexity and exposure (Figure 3.3.6.1).

Using the semi-quantitative approach to determining substrate complexity used in this study, it is possible to rank sites in relationship to one another; species abundance data confirm the relationship between increased complexity and decreased exposure. However, this scale does not address the linearity of the relationship. Established methods for determining substrate complexity include indirect and direct techniques: indirect methods reproduce surface profile using techniques such as stereo imagery, profile gauging, and plaster casting (Frost *et al.*, 2005); direct methods include *in situ* physical assessments using such tools as chain links, dividers, and distance wheels (Wilding *et al.*, 2010). Limitations in time and personnel in the current study, prevented the use of these methods. In future, complexity may be quantifiably defined, e.g. as a mathematically described deviation from a planar surface using georeferenced imagery to construct 3-dimensional shore profiles (e.g. Agisoft, 2016). Imagery captured using unmanned aerial vehicles (UAV) is becoming an important tool in ecological studies, including rocky shore characterisation (Anderson and Gaston, 2013; Bryson *et al*., 2013). In addition to the application of new technologies in refining data collection, further development of a complexity scale may also require further refinement in the definition of this variable. As reviewed by McCoy and Bell (1991), the use of terms such as ‘roughness’, ‘heterogeneity’, and ‘complexity’ are not always applied consistently, are frequently interchanged, and their definitions are highly dependent on scale.

***Patella ulyssiponensis* and *Fucus distichus anceps*:**

Abundance of *Patella* spp. appeared unrelated with the topographic variables recorded in this study. This may be because abundance of *Patella* spp. was generally homogenous on these shores; when separated into species based on proportional data, much greater variation and segregation was observed between study sites (Figure 3.3.7.1). Principal component analysis of rocky shore assemblages on WMO and Lewis segregated patellid limpets on the first axis, where *P. ulyssiponensis* is typically associated with high exposure shores, and *P. vulgata* is typically associated with relatively lower exposure shores (Figure 3.3.3.1). Recent analysis by Burrows *et al*. (2014) found that out of almost 60 representative rocky shore species in the UK, *P. ulyssiponensis* showed the strongest positive correlation with wave fetch. In the current study, logistic regression of *P. ulyssiponensis* proportional data and topography produced a most parsimonious model including most of the topographic variables (Table 3.3.7.1). Limpet proportions correlated most strongly with substrate complexity; *P. ulyssiponensis* is associated with shores of low complexity. This is consistent with the known relationships between this species and exposure, and between complexity and wave energy dissipation. Significant correlations were also identified between *P. ulyssiponensis* proportion and mean site bearing and openness, both consistent with increased fetch and high exposure conditions. Interestingly, of the variables selected in this model, slope was the least significant. When *P. ulyssiponensis* proportion was compared with topography and exposure indices, slope was either eliminated from the models or was found to be the least significant variable.

P. ulyssiponensis is associated with wetter surfaces favouring encrustation by calcareous red algae (Firth and Crowe, 2010). In the present study, the abundance of encrusting algae was not determined and species identification was not attempted; hereafter, these organisms are collectively referred to as 'lithothamnia'. On WMO, rock pools in the mid shore are typically lined with 'lithothamnia' which may help explain the presence in the mid shore of *P. ulyssiponensis*, more typically found on the lower shore (Delany *et al.*, 1998). Steep shore gradients drain faster than more gradual slopes and may result in greater desiccation stress in certain species (Benedetti-Cecchi *et al*., 2000). Sensitivity to desiccation by *P. ulyssiponensis* or 'lithothamnia' may explain why *P. ulyssiponensis* is not associated with steep gradients, despite favouring higher exposure conditions. That this organism can still be found on some of the steeper slopes may owe to the mitigating effects on desiccation resulting from splash on high exposure shores, as well as the overcast, frequently foggy conditions experienced on Orkney shores emerging from spring lows late in the afternoon, when insolation stress is reduced (Baxter *et al*., 1985). On these steeper slopes, on the open rock faces away from mid shore pools, *P. ulyssiponensis* individuals are typically large adults (A. Want, pers. obs.). Large size might allow sufficient protection from desiccation to allow such individuals to migrate from lower shores or rock pools and survive on steeper, open rock surfaces. Any speculations however, must be tempered with the recognition that rocky shore surveys described in this chapter were not experimental in design, and by necessity, were limited to a single observer constrained by boat-based access timings to record a single 1m x 1m patellid quadrat per site. In comparison, the rocky shore survey protocol adopted in the MarClim project standardised effort for each site to two people over 2 hours (Burrows *et al*., 2014). Differences in effort are somewhat mitigated by the typically smaller geographic scale of sites in the present study.

In contrast to the weak correlation between *P. ulyssiponensis* and shore gradient, linear regression of *F. distichus anceps* abundance on WMO positively related to slope and negatively related to substrate complexity (Table 3.3.8.1). In addition, a number of other analyses corroborated the importance of slope and complexity for *F. distichus anceps* abundance on WMO (e.g. Figure 3.3.6.1). Occasionally, some of the models identified an unexpected, contradictory response to a topographic variable, e.g. a typically high-exposure species correlating more strongly with orientation away from dominant energy direction. As described earlier, these may be spurious correlations associated with weaker signals or may be caused by insufficient spatial or temporal resolution of dominant energy direction.

This research has revealed a strong relationship between *F. distichus anceps* and uncomplicated, steeply-sloped platforms on highly exposed rocky shores. Plants are found on surfaces facing the dominant wave direction that are fully emerged at low spring tide, although still subject to frequent wave action even at low water. At some sites, vertical zones of *Ulva intestinalis*, associated with fresh-water run-off from fields above the shore, are found passing perpendicularly through horizontal zones of *F. distichus* *anceps* and other macroalgae. This suggests that *F. distichus anceps* cannot tolerate low salinity or cannot compete for space resource with *U. intestinalis* under these conditions. Studies on less exposed shores by Jonsson *et al.* (2006) found that grazing by *P. vulgata* limits establishment of fucoids but, once established, wave action affects persistence of fucoids. How the relationship between patellid limpet grazing and fucoid canopy establishment is manifest on the extreme exposure shores of WMO, where the groups in question are represented by less studied species like *P. ulyssiponensis* and *F. distichus anceps*, remains to be seen; the correlation between *F. distichus anceps* and steep slopes may be related to hydrodynamic forces or reduced grazing pressure. The results from research described in this chapter support the selection of *F. distichus anceps* as a potentially important indicator species for high exposure on these shores. In Chapter 4, studies of this species, and its congener *F. vesiculosus* f. *linearis*, are described in greater detail including additional factors important in establishment of zones.

Indices of exposure:

The relative simplicity of WMO may provide an ideal location to develop a topographically-informed, fetch-based exposure index, where the offshore wave resource is expected to be essentially the same for all westerly-facing sites. As such, differences in exposure as waves reach the littoral zone, would be expected to result from topographically-mediated dissipation, and variation in assemblages might be best explained in terms of these topographic variables. While the geomorphology of the skerries, reefs and platforms on WMO are typically similar, the precise slope, orientation and configuration of coastal features are not identical. Using WMO for study sites also allows exploration of existing indices, used to characterise exposure, towards the highest end of the hydrodynamic gradient. These indices may not have sufficient resolution to describe exposure at a scale necessary to inform the renewable energy industry of potential ecological consequences following wave energy extraction. Additional research into species occurring in extreme wave locations, such as *F. distichus anceps*, may be valuable in assessing ecological responses to changes in exposure owing to energy extraction or other long-term forcing agents.

Application of the ‘Want SQ Index’ was performed by the same observer and informed by prior quantitative field data from three sites on WMO. This approach appears to have successfully captured most facets of rocky shore exposure (Table 3.3.5.5). When compared with the other exposure indices, ‘Want SQ Index’ performed well against the ‘Ballantine Index’, and correlations with fetch-based models improved when a gradient estimate was applied to the latter. The ‘Ballantine Index’ is of great historical importance and concepts described therein have been developed to improve exposure indices; Ballantine (1961) recognised that fetch and topographic modifiers, such as slope, were essential factors to be included in understanding exposure. The circularity of assessing exposure based on species associated with arbitrarily defined exposure levels results in an unsurprisingly strong correlation with assemblage data on WMO (R^2 = 83%) in modelling with topographic variables (Table 3.3.5.2). However, on the high exposure sites along WMO, the scale of the ‘Ballantine Index’ was found to be too coarse to capture more subtle differences in assemblages found at the extreme end of the hydrodynamic gradient; changes in rocky shore assemblages following energy extraction might not be captured using such a broad scale.

In the current studies, fetch-based indices did not perform as well as the ‘Ballantine Index’ or the ‘Want SQ Index’ but improved when gradient estimates were applied. Previous studies have shown that fetch-based indices are sensitive enough to identify differences in response to exposure (Thomas, 1986; Ruuskanen and Nappu, 2005) and work well in describing broad scales, especially those featuring complicated coastlines where differences in fetch play a major role in community variation (Burrows *et al*., 2008; Sundblad *et al*., 2014). On the west coast of Scotland, renowned for its numerous islands and intricate coast, modification of the ‘Burrows Index’ has also been successfully applied to sublittoral community characterisation (Burrows, 2012). In the current comparisons, the ‘Thomas Index’ performed better than the ‘Burrows Index’ (Tables 3.3.2, 3.3.5.3 and 3.3.5.4) but this may be a reflection of the ‘stripped-down’ application of the latter; for these studies, the foreshore gradient estimate, i.e. a direct alternative for shore slope, was not included in ‘Burrows Index’, while the ‘Thomas Index’ retained modification using nearshore gradient estimate determined to the 6 m depth contour, i.e. this variable was considered to be sufficiently distinct from shore slope. Furthermore, while fetch-only indices can perform as well as those informed with wind data (Burrows *et al*., 2014), when differentiating exposure on high-energy shores with similar fetch, as on WMO and Lewis, modification using directional wind data may be a necessary addition to distinguish between sites.

Annual variation in rocky shore assemblage – Lewis 2013 and 2014:

Evaluation of a limited set of data collected at eight rocky shore sites on Lewis did not identify a clear pattern of changes in the biological community between 2013 and 2014. Two survey sites were similar between years but at the remaining six survey sites noticeable shifts occurred: at three sites species generally shifted towards those associated with reduced exposure; and at the other three sites species generally shifted to key species generally associated with less stable communities including most fucoid species and the animals *Nucella lapillus* and *P. ulyssiponensis* (Figure 3.3.4.2). Site-scale fluctuations of fucoid abundance on moderately exposed shores, such as the low gradient, broken shores of NWL, might be attributed to mid shore cycling as described by Hawkins *et al*. (1992). It is also possible that the lack of obvious pattern may represent background variation or stochastic changes and are not indicative of any environmental response. Using data from only eight sites makes interpretation difficult but may serve to help establish ranges of normal variation without environmental interventions by which to compare future long-term forcing agents. The inter-annual variation appears to be less than the variation between sites. Therefore, it should be possible to detect variation at a scale that exists between sites within a BACI-style study.

Other long-term variations in exposure on rocky shore assemblages:

While wind and wave data have been used in studies to determine dominant direction of energy approaching the coasts of WMO and Lewis (Folley and Whittaker, 2009; Vogler *et al*., 2013), it is also evident that dominant direction varies seasonally, and possibly over longer periods of time; spatial and temporal variation in exposure is expected to be unique to any given location. It has been shown that in extreme events, over 10% of annual wave energy can arrive offshore in a storm lasting less than 24 hours (Folley and Whittaker, 2009). To what extent an organism's adaptations and presence on wave-exposed rocky shores are influenced by average (or chronic) energy regime versus seasonal patterns of exposure versus extreme (or acute) storm events is poorly understand (Thomas 1986); it is entirely plausible that different members of the rocky shore community will respond differentially to these broad categories of wave energy. In theory, mobile organisms will be less tolerant of higher hydrodynamic forces than sessile species (Menge and Sutherland, 1987) but may mitigate against dislodgement behaviourally by adjusting timing of foraging and retreat to safer areas. In studies of shallow subtidal consumers (in this case, echinoderms), Siddon and Witman (2003) reported that zonation was maintained by water flow far below displacement levels – this could be interpreted as evidence that mean exposure levels determine zonation. In contrast, studies of the seaweed *Pelvetiopsis limitata* in the Pacific reported size limitations imposed seasonally by extreme storm events (Wolcott, 2007).

Understanding responses to extreme events are particularly important in light of climatic models which predict that increasing temperatures may result in greater frequency and intensity of storm activity (Collins *et al*., 2013; Woolf and Wolf, 2013). Globally, extreme wind speeds and, to a lesser degree, extreme wave heights have increased during a 23-year (1985-2008) study period (Young *et al*., 2011). On the other hand, assessment at fine scale by Helmuth and Denny (2003) demonstrated that, on most of their evaluated sites, definable limits to force were reached as wave height increased, suggesting that extreme events offshore may not translate proportionally to extreme hydrodynamic forces in the intertidal zone. Similarly, nearshore features affecting processes such as refraction and bottom friction may sufficiently dissipate wave energy that littoral exposure increases are minimised during extreme storm events (Folley and Whittaker, 2009). The consequences of global rise in temperature for shoreline exposure remain unresolved. In addition, any long-term monitoring of littoral zones must be cognisant of the potential complicating factor of sea level changes, either through isostatic rebound (Rennie and Hansom, 2011) or through increased input of glacial melt-water (Church *et al*., 2013).

WECs and reduced exposure:

Comparisons between sites of varying exposure might provide the ability to predict impacts on littoral organisms following changes in hydrodynamic conditions. On very regular rocky platforms, like those seen on WMO, differences in topography may provide examples of how communities will respond to changes in exposure. Graphic representation of assemblage differences on two shores of varying slope but otherwise similar topography and off-shore wave resource provides a coarse representation of how expected changes in assemblages might be manifest following long-term shifts in exposure (Figure 3.3.1.2). Using this example, it can be argued that assemblages found on the lower gradient slope might be indicative of expected changes to the higher gradient slope if exposure was reduced. Importantly, however, this example features only one factor in energy dissipation and, as the current studies have shown, different members of the littoral community may be more or less responsive to specific topographic variables. Furthermore, the complex interaction between community members, which may be responding differentially to changes in exposure, requires that any interpretation be delivered with considerable caution.

When trying to predict any effect of reduced wave energy it is important to take WEC technology into consideration; alteration to the wave regime downstream of WEC arrays will be produced by the operational characteristics of all the devices that make up the array. Although small changes in fetch have been shown to produce morphological differences in fucoids (Ruuskanen *et al*., 1999), and similar such consequences might be expected from wave extraction, it is not correct to assume that WEC deployment results in a permanently limited or constrained level of exposure (analogous to fetch reduction) for the duration of a development's presence. In the example of WECs designed to minimise interactions during high energy storms, enabling them to survive the high stresses imposed, this will allow the usual winter storm waves to reach the shoreline with minimal anthropogenic attenuation. This will effectively increase the difference in shoreline wave action between lowered energy in summer and unaffected high energy in winter. This could have consequences on species with highly seasonal patterns of growth where life processes during less energetic seasons are critical for persistence. On the other hand, for species whose presence and abundance are primarily driven by acute, extreme events, extraction of wave energy during only more moderate conditions may have little direct consequence.

The chaotic nature of breaking waves (Peregrine, 1983) has resulted in the common approach in wave modelling of parameterising to account for macro-scale effects of this complicated process (Janssen and Battjess, 2007). Certain variables included in the current studies, i.e. slope and substrate complexity, may serve as proxies for energy dissipation. Currently, the inability to quantify wave exposure at a biologically meaningful scale on littoral shores, and the paucity of *in situ* studies examining energy profiles of specific organisms, limits the capacity to predict responses to changes in exposure. Pelamis, the largest capacity WEC tested so far at Billia Croo, has an electricity-generation rating of 800 kW (EMEC, 2017). However, owing to the early stage of WEC technology, the complexity of array configuration on energy extraction, and issues of commercial confidence, specific performances of WECs *in situ* are not readily available (Neill *et al.*, 2014). In the meantime, long-term field studies may be required to effectively monitor changes in wave action on littoral communities.

Development and application of the ‘Want Index’ of exposure:

Exposure indices and topographic variables examined in this research have resulted in preliminary development of the ‘Want Index’ – a novel, topographically-informed, fetch-based index to compare exposure on rocky shores (Appendix 6). This index aims to modify measures of off-shore wave resource using the dissipating variables explored in these studies to produce an ecologically meaningful value of exposure at individual site scale. Discussions with hydrodynamicists confirmed that the topographic variables recorded during rocky shore site surveys appear to be a promising approach to developing this index. As the present studies have shown, quantifying some of these environmental variables is challenging and some variables appear to play a greater role in modifying wave energy than others. As such, a weighting factor (λ) may be assigned to adjust the relative importance of each variable to a given application. Currently, the relative role of each topographic modifier has not been quantified and the linearity of the relationship between modifier and exposure is not always known. The intention is that this index can be improved by populating weighting factors for each topographic variable with increasingly meaningful values determined through hydrodynamic and ecological study.

Findings from the current studies support the inclusion of these topographic factors but have high-lighted some important issues with their application. The inclusion of both survey-determined shore slope and bathymetrically-determined nearshore gradient should improve the ‘Want Index’. Response differences in organisms to individual variables, such as slope, illustrate some of the challenges in developing indices to describe such complicated habitats. Orientation of coastline through mean site bearing and aspect may be up-weighted relative to openness. In the current studies, mean site bearing and aspect were defined relative to a dominant energy direction determined from several years of meteorological data; to better understand the role of nearshore processes during seasonal and acute storm events, it may be necessary in future development of the ‘Want Index’ to define mean site bearing and aspect spatially and temporally. The semi-quantitative complexity scale used in the current study appears to suitably rank survey sites based on structural complexity of the substrate; substrate complexity as characterised using this scale has been shown in these studies to be of great importance in describing rocky shore exposure. In previous studies, complexity has been found to be difficult to quantify and hard to universally define (McCoy and Bell, 1991). Development of the ‘Want Index’ aims to better define substrate complexity through the use of emerging image-capture and processing technologies.

Transferability of the ‘Want Index’ to other shores is dependent on presumptions that topographic modifications apply universally. While such general assumptions may be valid, local differences in the relative importance of topographic variables may apply. Energy dissipation on topographically similar environments may vary, for example, between: kelp forest and coral reef, owing to differences in bottom friction created by wave interactions with the substrate not described by these studies, i.e. substrate porosity; and, slopes of similar gradient and aspect found at different latitudes or climates may be subject to varying levels of insolation stress, thus, affecting other processes linked to topographic variance. Potential application beyond the current studies might see the addition of a local modifier to each λ value to account for site-specific phenomena.

Summary:

The eventual scale, exact site locations, and installation schedules of WEC development off the coast of Orkney remain unknown. To date, only testing of individual devices has been conducted at the EMEC wave test area off Billia Croo. The consequences of large-scale extraction of wave energy remain to be assessed in practice. The current studies provide a detailed pre-development assessment including areas never before described, scientifically. In addition, these studies may also be a valuable record of biological conditions for comparison following other anticipated long-term changes, such as through increased sea surface temperature or more frequent acute storm events, as projected by meteorological models (Collins *et al*., 2013; Woolf and Wolf, 2013). At present, exposure indices, like the novel one described here, can be developed to identify key factors which modify quantifiable off-shore energy and allow evaluation of littoral exposure on a biologically meaningful scale. From a management point of view, a quantitative value of wave action associated with classified biotopes, capable of being measured in the field, would allow prediction of how biotic assemblages at certain locations might respond to changes in wave energy (see Section 1.3: Community classification).

Wave exposure in the littoral zone is strongly related to topographic variables which affect energy dissipation – in particular, substrate complexity. Direct measurement in the littoral zone of shore gradient and semi-quantifiable assessment of complexity will improve fetch or wind-based exposure models. At this stage it is not computationally feasible to use hydrodynamic models to assess the wave-induced forces acting at the spatial scale of individual rocky shore sites, even if bathymetric data were able to populate these models at sufficient resolution or accuracy. However, bathymetric data can be used to improve existing exposure indices: fetch-based models have been recently developed by applying an algorithm for estimating attenuation of wave energy in the nearshore (Hill *et al.*, 2010; Sundblad *et al.*, 2014). Analysis of high-resolution bathymetric data can allow more detailed quantification of nearshore gradient, and substrate complexity (or rugosity) can be mathematically described (Pirtle *et al.*, 2015), although issues of scale remain unresolved (McCoy and Bell, 1991). Furthermore, bathymetry can also be used to create a wave focussing variable capable of identifying exposure ‘hot-spots’ and ‘cold-spots’ (Folley *et al.*, 2010). In future, measurements of fine-scale *in-situ* wave forces and directions may become available for reliable determination of how wave energy interacts with the benthic community. High resolution instrumentation might provide essential data for predicting consequences following installation of WEC arrays.

Improvements in field data collection for future research on the exposed rocky shores of WMO have been identified in this study. With sufficient time and budget, additional collection of data and complementary studies of fucoids, barnacles and limpets would help explain the relative roles of these key community members at high latitudes, on high exposure shores, and featuring species less represented in previous research. Collection of topographic data would be enhanced through use of remote (UAV) technology (Anderson and Gaston, 2013; Bryson *et al.*, 2013). Similar approaches to habitat and biotope mapping have been applied in comparable marine environments using aerial photographs, satellite imagery and other remote sensing data (e.g. Mumby *et al.*, 1997). Further improvements can be made in modelling resource data used in exposure indices; while wind data continue to be applied to good effect, direct use of wave data, including directional incidence, will improve exposure models, although highest resolution data are not always easy to source (Hill *et al.*, 2010). Regardless of whether exposure indices are informed by wind or wave data, more sophisticated modelling of exposure is possible by applying subsets of meteorological data based on seasonal or other periods. Mean site bearing and aspect are important variables in littoral exposure by modifying refraction and shoaling of incoming waves. Assessment of the role played by fixed shore orientation requires more flexible input of meteorological data which reflects seasonal variance, as well as extreme storm events. This may help address some of the uncertainty regarding the effects of acute versus chronic exposure on structuring littoral communities, which, in turn, may be necessary in studying the consequences of wave energy extraction.

Chapter 4 - Assessment of *Fucus distichus anceps* as an indicator species of wave exposure and climatic change:

4.1 Introduction:

Fucus distichus (L.) is a monoecious littoral brown alga found in a variety of forms in the Northern Hemisphere across a wide-range of exposure levels (Powell, 1957a; Coyer *et al*., 2006). Only one morphological form has been identified in Orkney and described by Powell (1957a) as *F. distichus anceps*[1] (Figure 4.1). In this chapter, references will be specified to either *F. distichus anceps* or more broadly to *Fucus distichus* for some earlier studies. In the British Isles, *F. distichus anceps* is limited to a few rocky shores exposed to extreme wave conditions on northern and western coasts of Scotland and Ireland with substantial populations identified on the northern Scottish island groups of Orkney and Shetland. The British distribution of *F. distichus* does not extend below the 13˚C summer isotherm - excepting the St. Kilda population (Hiscock *et al*., 2004) - but this may be due to photoperiod, desiccation or another factor rather than temperature per se, as *F. distichus anceps* is also found in isolated populations in the south of County Clare and Kerry Head, Ireland (Powell, 1957a; Twigg, 2011).

Fucoids play an important ecological role in rocky shore communities, providing canopy cover for numerous plants and animals (Lewis, 1964; Raffaelli and Hawkins, 1996). Compared with larger macroalgae such as *F. vesiculosus* and *Ascophyllum nodosum,* studies in Iceland found *F. distichus anceps* canopies had fewer associated species but

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[1] Powell (1957b) described subspecies within the *F. distichus* complex in terms of morphological adaptations to environmental conditions. In this document, in agreement with this pioneering work conducted in Orkney, the subspecies epithet will be used. The reader interested in morphometric and genetic taxonomy of this organism is directed to work by Rice and Chapman (1985) and Coyer, *et al*. (2006).

retained an important canopy-providing role on rocky shores (Munda, 2004). While the stands of *F. distichus anceps* and other dwarf forms on highly exposed shores do not produce the same degree of canopy formation as the mid shore fucoid belt on more sheltered shores, in this habitat these plants play an important role in community dynamics providing a food source for grazers and a refuge for many species (Jenkins *et al*., 1999).

Figure 4.1: *F. distichus anceps*: individual at Hole o'Row, Skaill Bay; and zone on typical habitat at Choldertoo Skerry

The typical habitat of *F. distichus anceps* has been used to illustrate examples of extreme wave exposure on rocky shores (Lewis, 1964) and this species has been considered as a potential indicator for changes in both sea temperature (Hiscock *et al*., 2004) and wave energy (Burrows *et al*., 2014). Despite the recognition of the potential importance of *F. distichus anceps* as an indicator species, only a limited number of macroalgal studies have been conducted in Orkney or Shetland (Russell, 1974; Wilkinson, 1975; Wells *et al*., 2003) presumably owing to the difficulties in accessing much of its habitat. For this reason, much of the autecology of *F. distichus anceps* remains poorly understood (Twigg, 2011). Important ecological work on forms of *F. distichus* occurring on more sheltered shores have been reported (Edelstein and McLachlan, 1975; Ang, 1991; Pearson and

Brawley, 1996) but these may be of limited application to *F. distichus anceps* and the relationship with high exposure environments.

Removal of energy by WECs and warming seas associated with climatic change might be expected to have unfavourable consequences for *F. distichus anceps*, especially at the southern limit of its distribution. Jonsson *et al.* (2006) predicted that rising global temperature will see fucoids in the north becoming increasingly limited to more sheltered locations owing to increased pressure from desiccation and limpet grazing. This phenomenon has already been reported in southern Europe (Ladah *et al*., 2003). The consequences of climatic change however are complicated by predictions of increased storm events with temperature increases (Young *et al*., 2011; Collins *et al*., 2013; Woolf and Wolf, 2013). This may have a mitigating effect depending upon how much average wave energy versus extreme storm events dictates the presence of *F. distichus anceps* – the precise relationship remains unknown.

F. distichus anceps reaches reproductive maturity in two years, during a life span of typically 2-3 years (Powell, 1957a). Reproductive receptacles begin developing in January and are fertile between April and August. Peak fruiting appears to vary by latitude with southern populations peaking earlier (Powell, 1957a). In Orkney, *F. distichus anceps* is confined to the extremely exposed Atlantic-facing west coast (Wells *et al*., 2003), in particular below westward orientated cliffs on uncomplicated platforms dipping ~12° seawards with sufficient emersion at low tide (A. Want, pers. obs.) (see Section 3.4 Discussion – *Patella ulyssiponensis* and *Fucus distichus anceps*). This combination of exposure and topography appears to be the main factor in determining the presence of *F. distichus anceps* in Orkney and Caithness (Powell, 1963). Whereas stands of other fucoid species may experience localised fluctuations over time (Lewis, 1964), *F. distichus* *anceps* at several of these locations appears to remain stable over many decades (Powell, 1957b; Powell, 1963; Wilkinson, 1975). Observations of fucoids, barnacles and limpets suggest that high-energy assemblages may possess greater stability relative to those on more moderately exposed coasts owing to a greater equilibrium in the complex relationship between these organisms (Southward and Southward, 1978; Hartnoll and Hawkins, 1985).

While fucoids play a dominant ecological role in many NE Atlantic rocky shores, they are only able to survive on high wave-energy exposed shores as ‘dwarf’ forms (Powell 1957a, Lewis 1964, Russell 1974). In addition to lower overall height, these forms typically feature restricted frond width, stiffened stipes and broad discoid holdfasts when compared with other fucoids – these characteristics help the forms survive against tremendous hydrodynamic forces (Denny, 1987; Gaylord, 2000). The frond width in *F. vesiculosus* will narrow in response to increased exposure (Back, 1993). *F. gardneri* have reduced thalli and smaller overall size in exposed conditions (Blanchette, 1997) while responding with more holdfast perennations (Ruuskanen and Nappu, 2005). Similar reductions in size associated with increased wave action have been reported for the fucoids *Pelvetia compressa* and *Hesperophycus californicus* (Blanchette *et al*., 2000).

Beyond fucoids, the size of the holdfast is positively correlated with wave exposure in *Laminaria hyperborea* (Sjøtun *et al*., 1998) and *L. japonica* (Kawanata, 2001); growth rate (quantified by blade and stipe elongation) of *L. digitata* varies as a function of wave exposure (Kregting *et al*., 2016b). On the other hand, studies of the kelp *Ecklonia radiata* in high-wave energy environments were not able to demonstrate morphology as a reliable hydrodynamic indicator (Wernberg and Thomsen, 2005). Perhaps, in certain species, response to wave exposure may simply take the form of pruning and tattering of fronds

(Blanchette, 1997; Jonsson *et al*., 2006). Size in the fucoid *Pelvetiopsis limitata* correlated well with seasonal wave exposure (Wolcott, 2007). High-energy fucoid variants in Orkney, in particular *F. distichus anceps*, possess many of the morphological adaptations associated with survival in extreme exposed conditions; growth observations might result in similar patterns of regress following seasonal increases in wave exposure.

The zones on the shore below *F. distichus anceps* typically feature the plants *Mastocarpus stellatus*, *Corallina officinalis*, and, further below bordering on sublittoral, *Alaria esculentus*. These species may help create the lower boundary of the *F. distichus anceps* zone through competitive exclusion (Connell, 1961b; Lubchenco, 1980; Schonbeck and Norton, 1980; Hawkins and Hartnoll, 1985); abiotic factors, such as desiccation (Schonbeck and Norton, 1978; Lubchenco, 1980), as well as competition (Lubchenco, 1980; Hawkins and Hartnoll, 1985) from the aforementioned *F. spiralis* f. *nanus* may help form the upper boundary. Additional factors in determining fucoid zones, especially upper limits, include grazing pressure (Lubchenco, 1983); patellid limpets being the principal grazers on the more exposed rocky mid shore (Hawkins and Hartnoll, 1985). In Orkney, patellid limpets are represented by *Patella vulgata* and *P. ulyssiponensis* – the latter reaching its cold-water distribution limits in the UK on the high wave-energy shores of northern Scotland.

The fucoid research described in this chapter has focussed primarily on responses to wave exposure and climatic change in *F. distichus anceps*. Methodological development as described earlier (see Chapter 2), has included paired evaluation of long-term environmental drivers with *F. vesiculosus* f. *linearis* (L.). Like *F. distichus anceps*, the morphology of *F. vesiculosus* f. *linearis* is characterised by strength-increasing and drag-reducing adaptations (such as absence of bladders), common features of macroalgae on extreme exposed shorelines (Wernberg and Thomas, 2005). This form differs, however, in its tendency to form perennating holdfast complexes; to what degree these complexes are comprised of multiple stipes of the same ‘individual’ or are a collection of genetically different individuals is not known (Ruuskanen and Nappu, 2005). In addition, several other fucoids, most notably, *F. spiralis* f. *nanus*, have been surveyed along WMO and east to Eynhallow Sound – community-scale fucoid research is described within Chapter 3.

4.1.1 Objectives:

In Chapter 3, current studies were described which identify a narrow set of topographic factors strongly correlating with the presence of *F. distichus anceps* on WMO, especially steep slopes and low substrate complexity. As discussed earlier, the association between exposed shores and the geographic distribution of *F. distichus anceps* on the northern and western extremes of the British Isles suggest that this plant may be a suitable candidate for studying ecological responses following wave energy extraction or climatic change. The main objectives of this study were to determine whether evidence exists to support the role of *F. distichus anceps* as an indicator species and to suggest methods which might be most useful for quantifying responses to long-term environmental factors. Methods capable of ‘capturing’ acute effects on population dynamics following short-term meteorological events might help inform predictions of long-term community change.

4.1.2 Hypotheses:

Research was conducted on WMO designed to address the following hypotheses:

-Seasonal growth patterns: on high wave-exposed shores, percentage cover and individual length of *F. distichus anceps* and *F. vesiculosus* f. *linearis* will vary seasonally owing to balance shifts between expansion and contraction driven largely by seasonal growth and exposure-driven tattering.

-Individual stability of *F. distichus anceps*: on high wave-exposed shores, *F. distichus anceps* is highly susceptible to dislodgement and therefore unstable at an individual scale.

-Population stability of *F. distichus anceps*: in contrast to individual instability, the overall population of *F. distichus anceps* is stable on a decadal scale.

-Wave exposure: acute changes in wave exposure such as seasonal storm events have short-term detectable consequences on populations of *F. distichus anceps* and *F. vesiculosus* f. *linearis*.

-Temperature: acute changes in temperature have short-term detectable consequences on populations of *F. distichus anceps* and *F. vesiculosus* f. *linearis*.

4.2 Methods:

To investigate these hypotheses, a monitoring approach has been devised primarily focussed on *F. distichus anceps* and *F. vesiculosus* f. *linearis*. A methodological approach has been developed with additional components based on well-established field methods for assessing species responses to environmental factors, such as percentage cover determination using quadrats, individual plant measurements, fixed-view point broad-scale imagery, and the use of SACFOR abundance scale. Comparison of different field methods may reveal a preferred strategy for long-term monitoring of fucoids in Orkney. The following list includes a brief description of methodology utilised:

- Quarterly percentage cover rate determination using quadrat photography to examine seasonal and long-term responses to wave and climatic factors;
- Quarterly growth rate determination of individual plants using maximum frond length to examine seasonal and long-term responses to wave and climatic factors;
- Quarterly zonation measurements using fixed point photography of extensive stands to examine seasonal and long-term responses to wave and climatic factors;
- Topographic measurements and abundance monitoring of nine fucoid forms/species (as part of larger survey of 45 littoral species) along the rocky shores of WMO (see Section 3.2.1 Littoral site survey) to examine the relationship between topography, wave exposure and the littoral community.

4.2.1 Percentage cover determination using quadrat imagery:

4.2.1.1 Image capture:

Photography of fixed quadrats provides a relatively simple and repeatable method for long-term monitoring (Glanville, 2001) and has been employed previously in population studies of *F. distichus* (Ang, 1999) and other fucoids (e.g. Schonbeck and Norton, 1980; Wolcott, 2007). Density of cover was determined using photographic images of triplicate 1m^2 quadrats for *F. distichus anceps* (at Marwick) and *F. vesiculosus* f. *linearis* (at Billia

Croo) recorded quarterly. Additionally, *F. distichus anceps* density was also measured at Northside in Birsay, located over 8 km along the coast from Marwick. Birsay was chosen as a complementary site of even more extreme exposure and orientated to the NW where substantial stands of *F. distichus anceps* can also be imaged for fixed view point monitoring (see 4.2.3.1). The location of the population of *F. distichus anceps* on the steeply sloped mid shore at such high exposure created access difficulties limiting quadrat measurements to a single repeat location in Birsay. At all locations, quadrat placements were selected at representative locations within the species zone, distanced from one another at a scale of <10 metres. Site location was recorded using GPS at the centre of each quadrat and markers for two opposing corners were chiselled into the bedrock and painted bright yellow to aid in repositioning during subsequent sampling. Paint was reapplied, as necessary. Images were recorded using dSLR (Canon) with 18-135 mm lens.

4.2.1.2 Analysis of percentage cover using quadrat imagery:

Quadrat images were electronically labelled and converted to bitmap files. Percentage cover was determined using 'Barnacle Bell': software developed at Heriot-Watt University in Orkney. This allows the operator to construct polygons overlaying the mapped image which can be assigned to any number of specific 'biotopes' (Figure 4.2.1.2.). In these applications, the only 'biotope' quantified was either *F. distichus anceps* or *F. vesiculosus* f. *linearis*, depending on the source location. A correction factor was applied to each image to eliminate the contribution of data out with the boundaries of the quadrat. In total, the following images were analysed for percentage cover:

- Billia Croo: *F. vesiculosus* f. *linearis* (3 quadrats over 19 quarters)
- Marwick: *F. distichus anceps* (3 quadrats over 16 quarters)
- Birsay: *F. distichus anceps* (1 quadrat over 15 quarters)

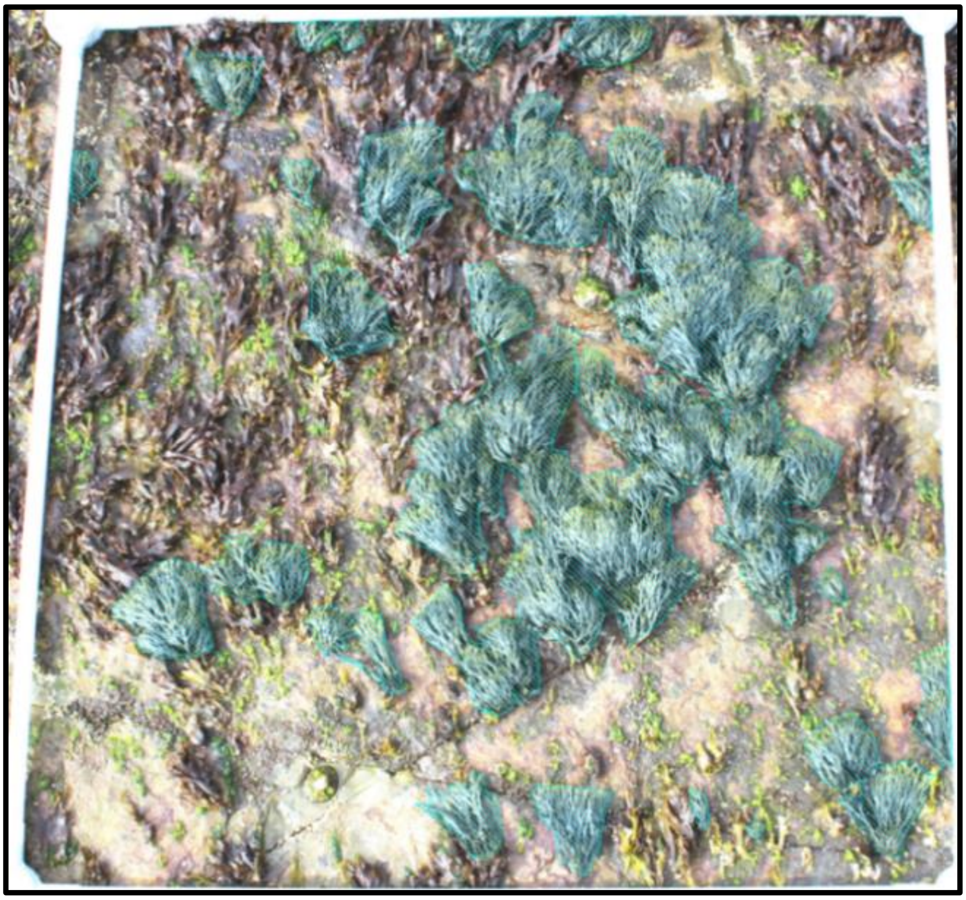


Figure: 4.2.1.2. *F. distichus anceps* quadrat from Northside in Birsay quantified using ‘Barnacle Bell’ software.

Plots were created to investigate whether percentage cover of fucoids follows cyclical patterns of growth and regress. An additional approach to examining percentage cover data is to determine and plot rate of percentage cover change over time. Data from consecutive quarters were compared to determine rate of change. Percentage cover from the previous quarter was subtracted from each quadrat: positive values indicate growth; negative values indicate regress. Total percentage difference between consecutive quarters was divided by number of days in sampling period to determine percentage cover change per day. Each data point (representing a period of growth/regress) was assigned the median calendar date between each quarter. Overall percentage cover and rate of change in percentage cover were plotted against time.

4.2.2 Individual growth:

4.2.2.1 Individual growth determination:

Individual *F. distichus anceps* plants were identified and measured quarterly in triplicate at Northside in Birsay and *F. vesiculosus* f. *linearis* at Billia Croo using maximum frond height to monitor growth cycling (Edelstein and McLachlan, 1975). Subsequent relocation of selected individuals was made using detailed laminated photographs including adjacent plants and stable, easily recognisable rock features to aid as accurate and persistent visual cues. This approach has been successful for *F. vesiculosus* f. *linearis* holdfast complexes. Trials were made using cable ties with stamped metal washers (Figure: 4.2.2.1) as aids in identifying individuals. However, this tagging procedure was abandoned quite early on as the ties were found to be unreliable in surviving storm events and ultimately were proved unnecessary because photographic records were entirely satisfactory for relocating plants.

Figure: 4.2.2.1. *F. vesiculosus* f. *linearis* marked with cable tie at Billia Croo.

4.2.2.2 Analysis of individual growth determination:

Plots were created to demonstrate whether maximum frond length of fucoids follows cyclical patterns of growth and regress. Data from consecutive quarters were compared to determine rate of change. Maximum frond length from the previous quarter was subtracted from each quarterly measurement. Positive values indicated growth; negative values indicated regress. Total maximum frond length difference between consecutive quarters was divided by number of days in sampling period to determine frond length change per day. Each data point (representing a period of growth/regress) was reassigned the median calendar date between each quarter. Overall maximum frond length growth rate was plotted against time.

4.2.3 Fixed viewpoint imagery:

4.2.3.1 Image capture:

A population study of *F. distichus anceps* was conducted on an extensive platform at Northside in Birsay using fixed viewpoint photography. This technique is a recognised and valued tool in long-term monitoring and lends itself well to broader scale characterising of rocky shores (Moore, 2001). Population characterisation at a larger scale, and in hard to access areas, is possible providing the study organisms are sufficiently large and distinct to allow reliable analysis of images. This population of *F. distichus anceps* has been imaged quarterly since September 2010. A site reference screw was placed in the rocky shore overlooking this population (Ordnance Survey Grid Reference [OSGB36]: 102877N; 325281E). Images were captured by dSLR (Canon 50D) using a lens set to 35mm focal length; ISO adjusted according to light conditions; and attached to a monopod fixed at 1 metre vertical height and placed on the reference screw. Prominent rock features, easily identifiable in fixed-view point imagery, were georeferenced using dGPS (Leica – accurate to <2 cm vertical height) (Figure 4.2.3.1; Table 4.2.3.1). At this opportunity, coordinates were also taken for other fucoid study sites, i.e. quadrat locations (see Table 4.3.3). Height measurements were recorded in metres relative to Mean Sea Level.

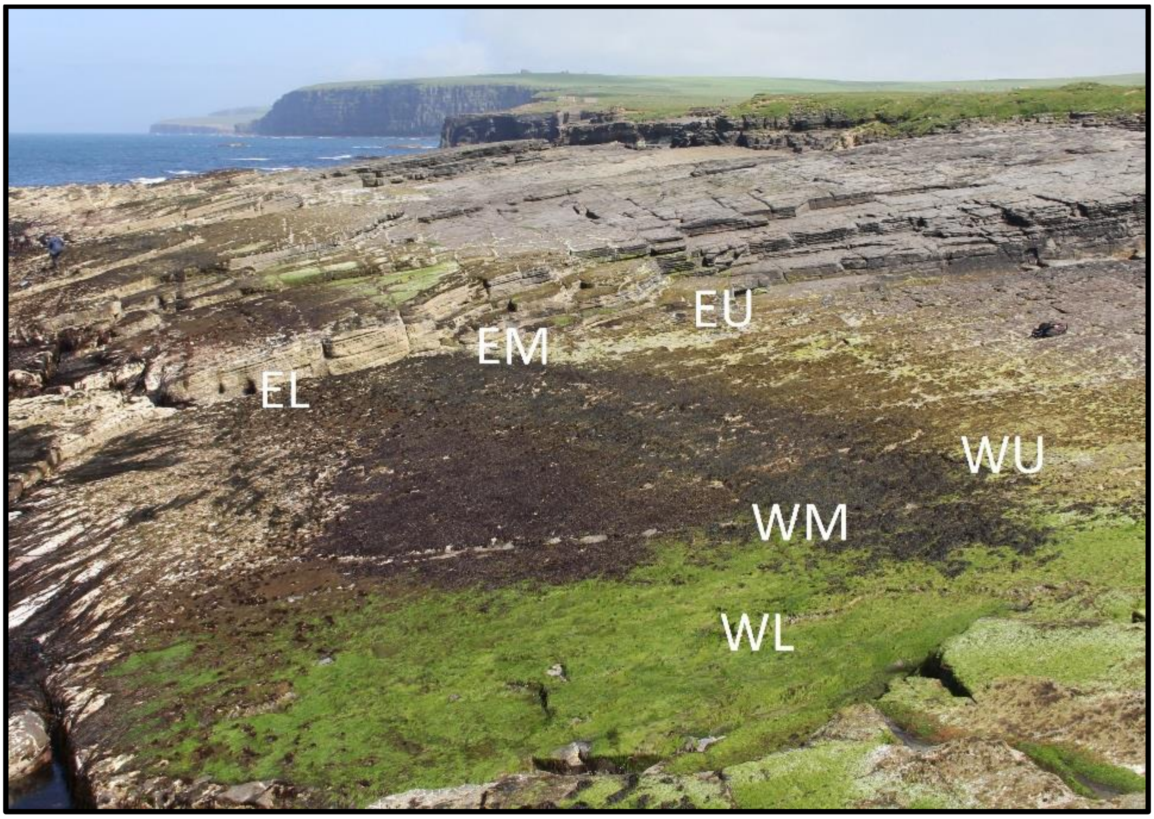


Figure 4.2.3.1: Fixed-View Point image of extensive *F. distichus anceps* population at Birsay (12 June, 2014). E = east; W = west; L = lower; M = mid; U = upper.

Table 4.2.3.1: Georeferenced coordinates (Northing; Easting; and Orthometric Height [Orth. Hgt.]) using OSGB36 at Birsay including standard deviations (SD).

Fixed-View Point ID	**Northing (m)**	**Easting (m)**	**Orth. Hgt. (m)**	**SD North**	**SD East**	**SD Hgt.**
East Low	1028782.352	325288.8843	0.9347	0.0019	0.0015	0.0042
East Middle	1028777.071	325290.3334	2.0673	0.0028	0.0023	0.0064
East Upper	1028771.052	325289.7348	3.0648	0.0032	0.0026	0.0073
West Low	1028770.965	325270.8897	0.8495	0.0010	0.0008	0.0021
West Middle	1028770.542	325274.9638	1.4259	0.0013	0.0011	0.0029
West Upper	1028767.013	325276.1223	2.2265	0.0019	0.0015	0.0042

4.2.3.2 Image analysis for quantifying fucoid cover from fixed viewpoint imagery:

Essential to the fucoid monitoring programme is the capability to make quantitative measures of baseline percentage cover. Quadrat imagery has been complemented by including analysis of photographic images using ‘Barnacle Bell’ (see 4.2.1.2) with the following amendments:

(a) an area of the image was selected using georeferenced landmarks (see Figure 4.2.3.1) within which the biotopes are to be quantified;

(b) the image was transformed to a ‘bird’s-eye view’ (See Figure 4.4.2), whereby the location of each pixel in the image is mapped and scaled to actual shore coordinates using a transformation matrix estimated from known reference points within the image.

4.2.3.3 Statistical analysis of fixed view-point image data:

Maximum and minimum heights of *F. distichus anceps* zone boundaries were determined from quarterly images. Georeferenced rock features were used to quantify zonal height (z-axis value) at points towards the eastern and western peripheries of the zone. Zonal heights, range of zone, and percentage cover rate of change of *F. distichus anceps* were plotted from Aug. 2010 – Sept. 2015.

4.2.4 Fucoid distribution:

4.2.4.1 Surveying fucoid distribution:

Abundance determination of 45 littoral species, and recording of several topographic features that might play roles in determining the distribution of intertidal organisms, were recorded on WMO and Lewis as part of an extensive cliff and shore survey programme (Chapter 3). This survey included the distribution of several fucoid species and forms: *Ascophyllum nodosum*, *F. distichus anceps*, *F. serratus*, *F. spiralis*, *F. spiralis* f. *nanus*, *F. vesiculosus*, *F. vesiculosus* f. *linearis*, *Halidrys siliquosa* and *Pelvetia canaliculata*. Specific attention was made to sites previously described by Powell (1963) to assess the stability of *F. distichus anceps* populations half a century later. Details of the methods used in this programme are found in Section 3.2.1.

4.2.4.2 Analysis of surveys of fucoid distribution:

Presence and absence of *F. distichus anceps* at 14 sites on WMO, described by Powell (1963), are presented in Table 4.3.4 and Figure 4.3.4.1. The locations of additional rocky shore survey sites conducted as part of this research work are also presented in Figure 4.3.4.1.

4.2.5 Analysis of wave and climate data:

Meteorological data from WMO kindly provided by EMEC included: Sea Surface Temperature (SST), Significant Wave Height (H_S), Wave Period (W_P), and Atmospheric Temperature (AT). More energy reaches the shore as waves increase in amplitude or period; seasonal changes in both H_S and T_P might be expected to impact organisms in the surf-zone. Fucoid ecological data were compared with wave indices: H_S and W_P were examined separately and as the combined metric of power density. Power density (P_W) of a wave (expressed as kW/m) was determined using the following formula (Scottish Executive, 2006):

$$P_W = \frac{\rho\, g^2}{4\pi}\, H_{rms}^2\, T_e$$

In this formula, H_{rms} is equivalent to standard deviation of water height above mean level; T_e is energy period. In oceanography, H_S and W_P can be substituted for H_{rms} and T_e, respectively. In addition, ρ is the density of water (1,025 kg/m^3) and g is acceleration due to gravity (9.81 m/s^2). For each of the fucoid quadrat sample intervals, the mean and upper (95 percentile) metrics were determined for: SST, H_S, W_P, P_W, and AT. Additionally, lower (5 percentile) SST and AT were determined. Wave and climate data were compared with fucoid seasonal percentage cover rate of change using linear regression to determine correlation coefficients and confidence values. The potential of lagged ecological responses to wave and climate cycling was also considered. Effects of wave impacts on fucoid cover would be expected to occur at the event, not as a lagged response, and so lags were not considered for these indices. For temperature and photoperiod data, correlation coefficients were calculated daily for each quadrat sampling period lagged back to 90 days prior and plotted to determine if lagging climate data might improve correlation.

4.3 Results:

4.3.1 Percentage cover determination using quadrat imagery:

Fucoid populations studied in Orkney revealed seasonal patterns where percentage cover increased during the late spring to late summer, reaching a peak typically in September, before decreasing through the late autumn and winter (see Figure 4.3.1.1). This is consistent with the expectation that: percentage cover of fucoids will increase as nutrients and energy are utilised to develop reproductive structures, i.e. apical receptacles, leading to gamete release in late summer (Hawkins and Hartnoll, 1983); followed by reduction in percentage cover as reproductive season passes and increasing storm events tatter fronds and remove apical structures (Blanchette *et al.*, 2000). In *F. vesiculosus* f. *linearis*, gamete production can occur throughout the year but apical receptacles peak from March to May (Twigg, 2011).

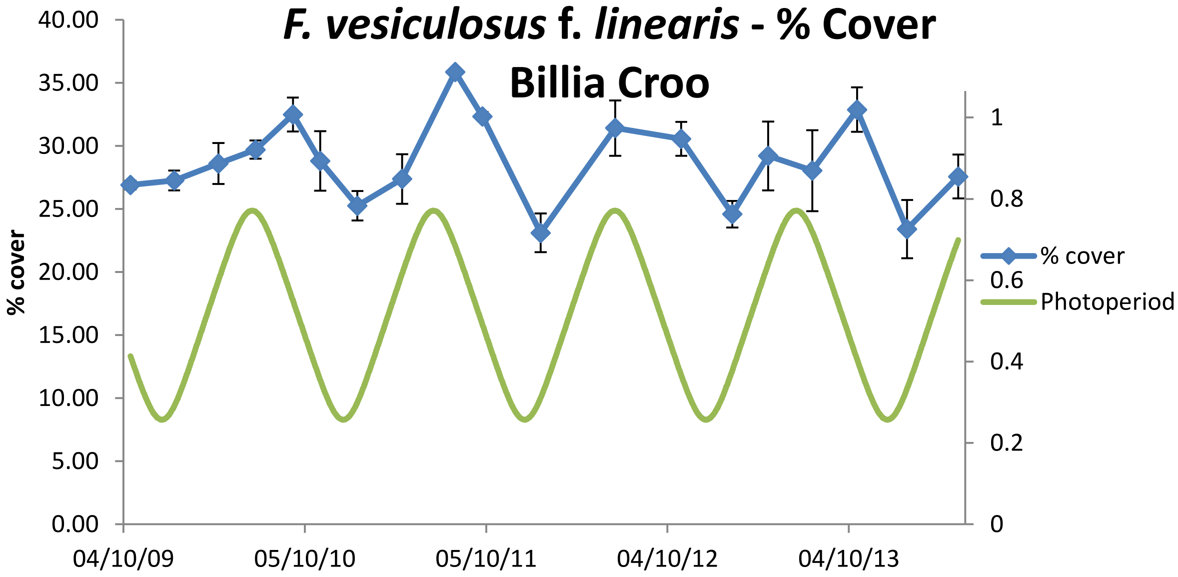


Figure 4.3.1.1: *F. vesiculosus* f. *linearis* at Billia Croo over 19 quarters (approx. 3 mth intervals). Mean of triplicate quadrats with standard error plotted with photoperiod from Orkney. Photoperiod is provided as an indicator of seasonality.

Mean percentage cover change per day was plotted using the midpoint of the sampling interval. In the population of *F. vesiculosus* f. *linearis* at Billia Croo this closely resembles Figure 4.3.1.1 with seasonal patterns of growth and regress evident. In spring, percentage cover and rate of change in percentage cover increase reaching peaks in late summer. Typically, percentage cover decreases and rate of change becomes negative in the autumn and winter seasons (see Figure 4.3.1.2).

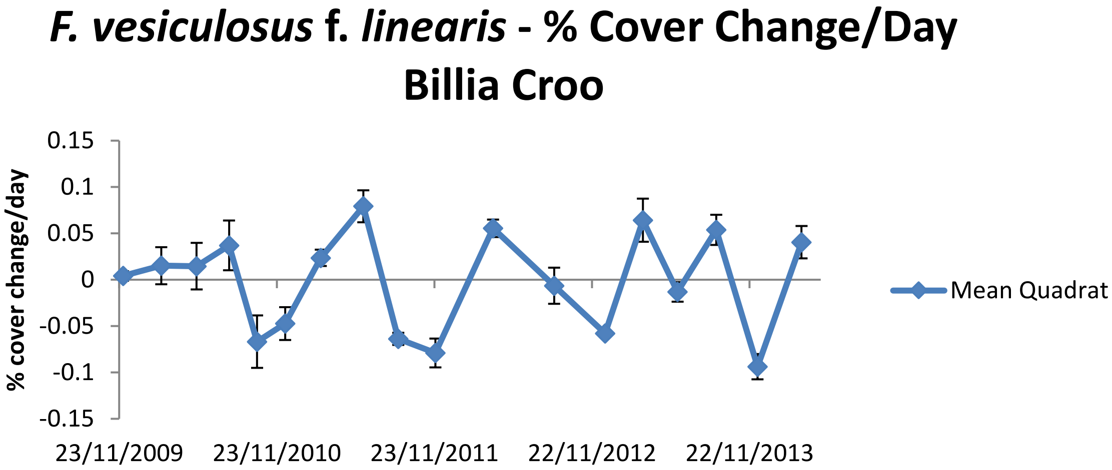


Figure 4.3.1.2: Quadrat imagery of *F. vesiculosus* f. *linearis* at Billia Croo expressed as growth rate (percentage cover change per day). Mean of triplicate quadrats with standard error.

Reproductive cycling of *F. distichus anceps* was expected to result in a similar pattern of seasonal percentage cover observed in *F. vesiculosus* f. *linearis*. In *F. distichus anceps*, receptacle development starts in January and ceases in August. Peak 'fruiting' of *F. distichus anceps* appears to vary according to location: April – August in Orkney; March – August in Ireland (Powell, 1957a). Data for 4 years of monitoring are presented in Figure 4.3.1.3. In addition to mean percentage cover, the plot contains the data series for each of the three individual quadrats at Marwick. This illustrates the dramatic growth observed in percentage cover of Quadrat 3 from February to September, 2011. During this growth period the percentage cover increased from 13.2 to 37.8%. Quadrat 3 was located higher on the shore than other Marwick quadrats (see Table: 4.3.3) and therefore may represent important processes affecting zonation dynamics rather than a stochastic event (see 4.4 Discussion – Short-term response).

Compared to Figure 4.3.1.1, a signal of seasonal pulsing associated with growth during reproductive activity in *F. distichus anceps* is not so apparent. However, when expressed as the rate of percentage cover change per day (see Figure 4.3.1.4), seasonal changes in growth can more clearly be seen. Seasonal patterns in percentage cover are similar to those observed in *F. vesiculosus* f. *linearis*, i.e. increased percentage cover in spring, peaking in late summer, and reducing in autumn and winter. The large increase in percentage cover within Quadrat 3 at Marwick is reflected in the fastest growth rate observation assigned to 17 August, 2011.

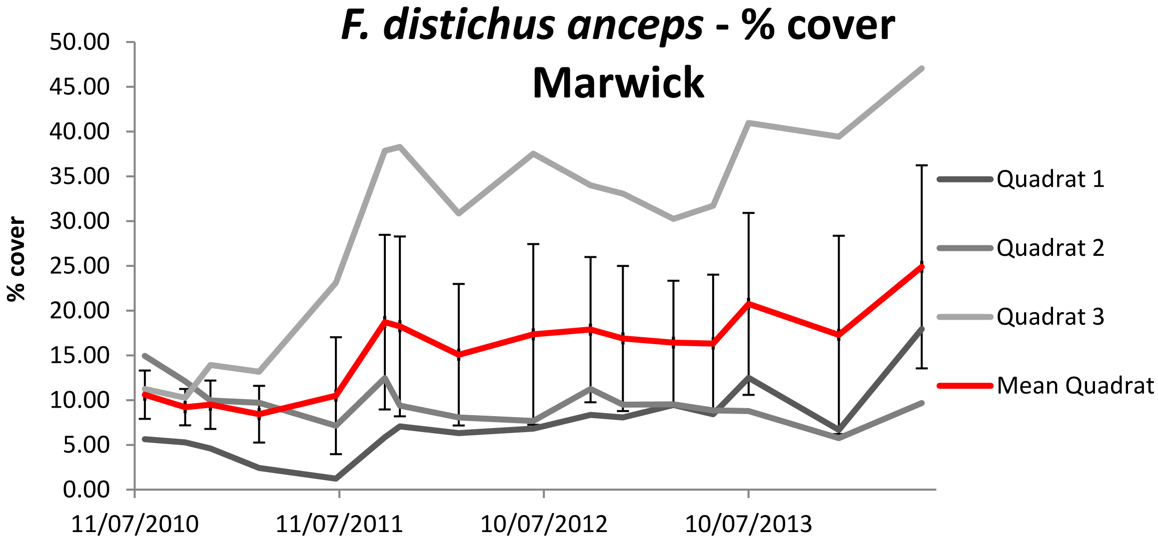


Figure 4.3.1.3: *F. distichus anceps* at Marwick over 16 quarters (approx. 3 mth intervals). Mean of triplicate quadrats with standard error. Note: the dramatic change in percentage cover within Quadrat 3 in summer 2011.

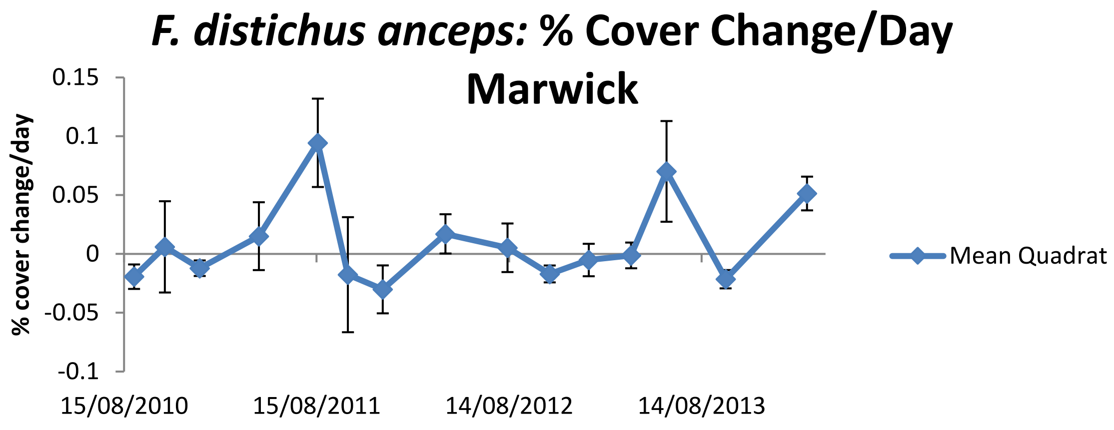


Figure 4.3.1.4: Quadrat imagery of *F. distichus anceps* from Marwick expressed as growth rate (percentage cover change per day). Mean of triplicate quadrats with standard error.

As mentioned earlier, practical constraints limited imagery to a single quadrat (plus the broader-scale fixed-view point images) at the more exposed site in Birsay. Similar to Quadrat 3 at Marwick, at Birsay the percentage cover of *F. distichus anceps* underwent sizeable growth in spring-early summer 2011. The Birsay quadrat is also relatively high on the shore (see Table 4.3.3) and may provide further evidence of acute zonation change witnessed at Marwick (see 4.4 Discussion – Short-term response).

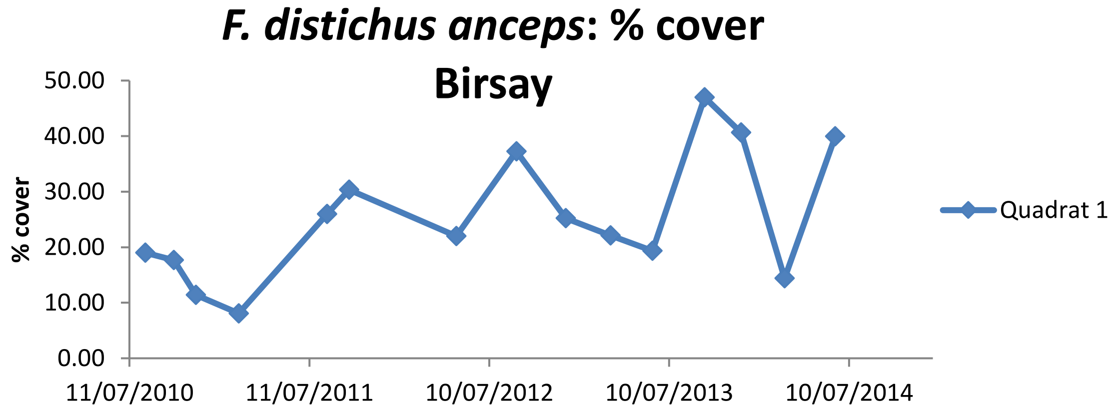


Figure 4.3.1.5: Percentage cover of *F. distichus anceps* from a single fixed quadrat at Northside in Birsay over 15 quarters (approximately 3 month intervals). Note: the percentage cover of this seaweed was <20% until the growth phase leading to the summer 2011, after which it generally remained above 20%.

Similarly to data obtained from quadrats at Marwick, seasonal patterns of percentage cover in *F. distichus anceps* at Birsay were more easily visualised when represented as rate of change (see Figure 4.3.1.6). While only one quadrat was recorded for this higher energy site, it should be noted that percentage cover rate of change was more pronounced in this quadrat compared with this species at Marwick or *F. vesiculosus* f. *linearis* at Billia Croo.

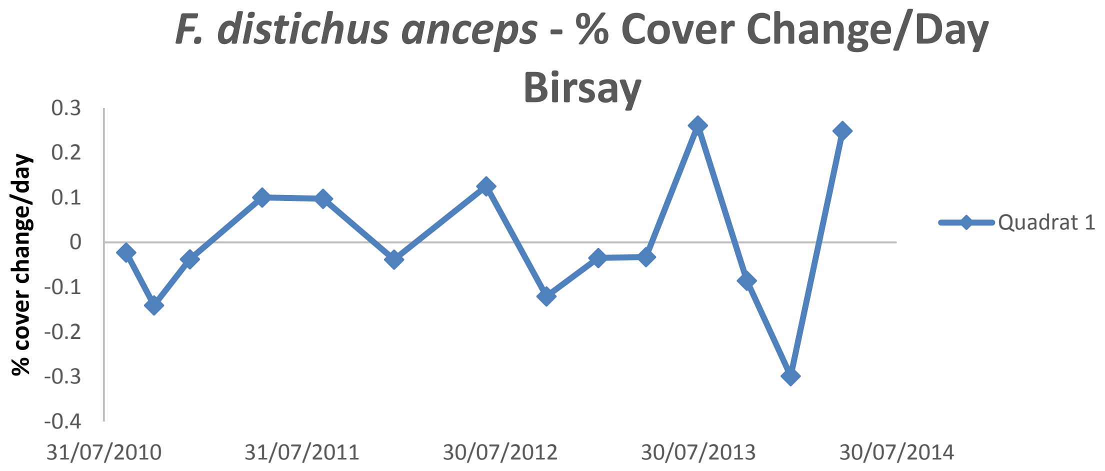


Figure 4.3.1.6: Quadrat imagery of *F. distichus anceps* from Birsay expressed as growth rate (percentage cover change per day). Note: the pronounced rate expressed in 2013-2014.

4.3.2. Individual growth determination:

Several attempts to record growth patterns using individual frond length measurements in *F. distichus anceps* at Birsay have proven problematic. Return visits to measure *F. distichus anceps* plants have recorded frequent losses of selected specimens resulting in an inability to sustain monitoring of individual plants (Figures 4.3.2.1 and 4.3.2.2). A clear pattern of seasonal growth or loss of individuals is not apparent in this limited data set.

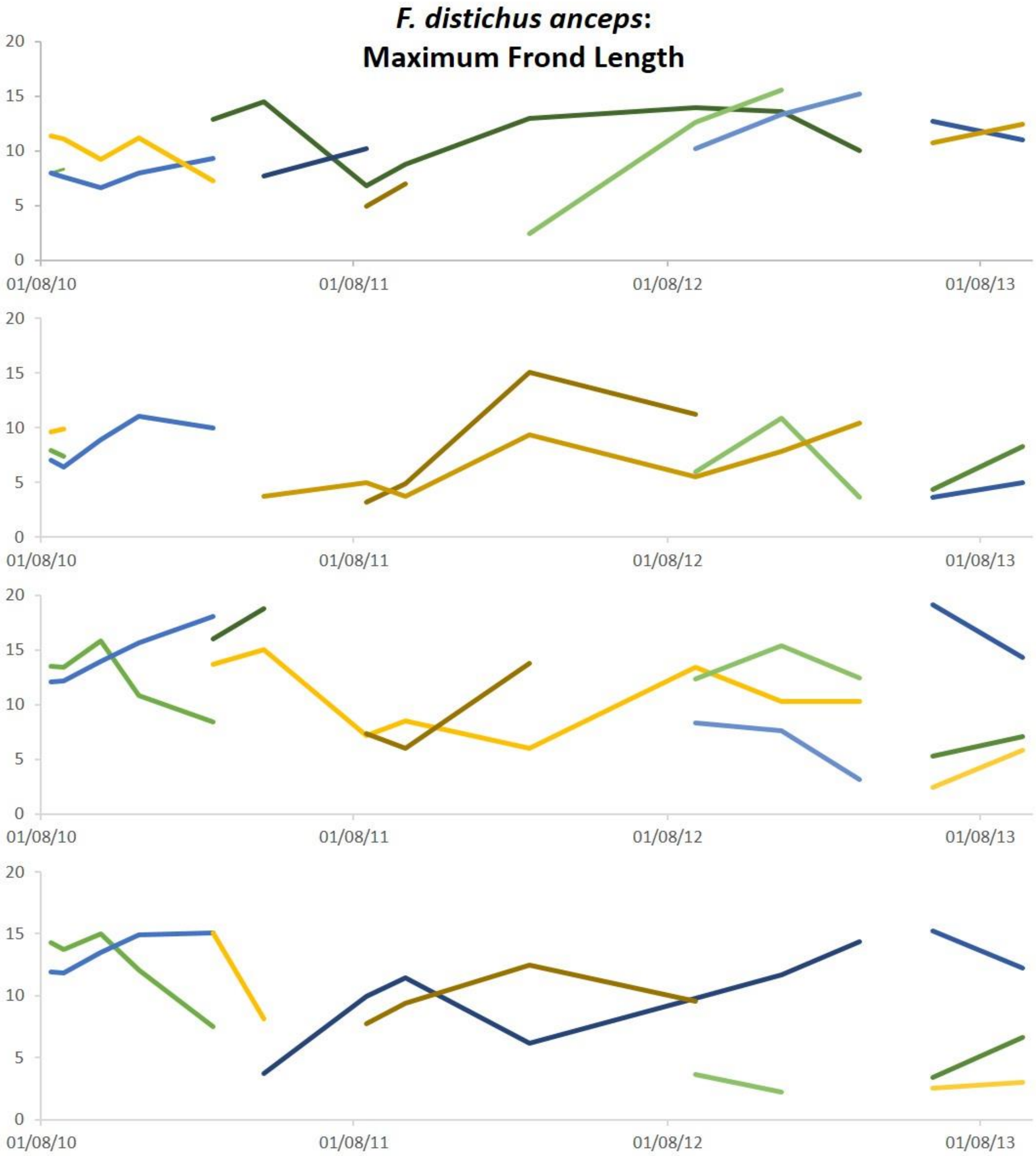


Figure 4.3.2.1: Maximum frond length (cm) from individual *F. distichus anceps* at Birsay - illustrating the rapid loss of individual plants. Each point is the mean of triplicate measurements. Growth trajectories of individual plants have been divided among four panels. Individual plants are indicated by different colours.

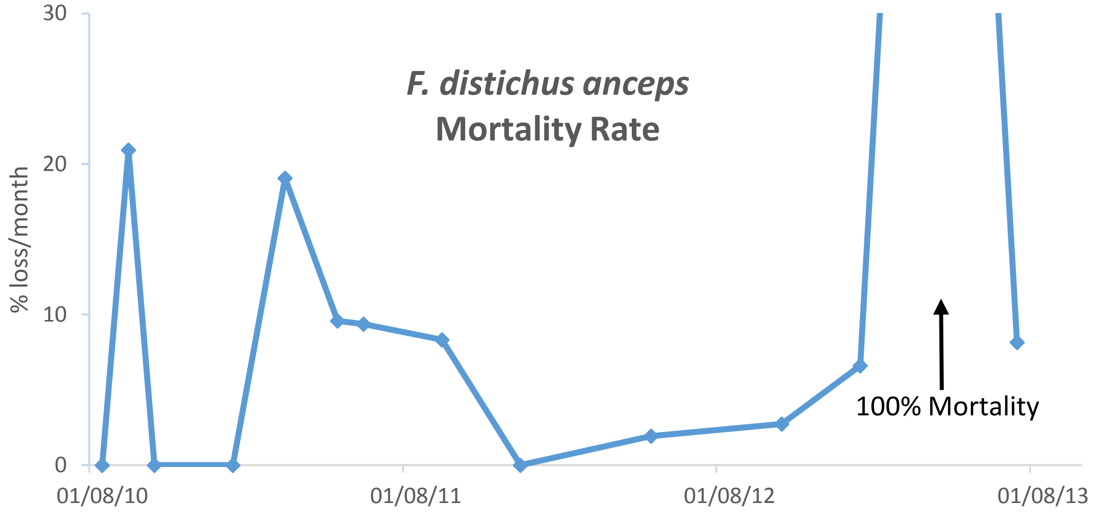


Figure 4.3.2.2: Mortality rate (percent loss per 30-day month) of individual *F. distichus anceps* selected for growth monitoring at Birsay - illustrating the rapid loss of individual plants.

In contrast, the problems experienced with loss of *F. distichus anceps* plants were not encountered in individual growth measurements of *F. vesiculosus* f. *linearis*. These progressed without event beginning in September 2009 and continuing through the PhD Studentship until May 2014. In studies of *Hesperophycus* and *Pelvetia*, Blanchette *et al.* (2000) only recorded plants as missing when the entire holdfast was lost. During the 5 years of study of *F. vesiculosus* f. *linearis*, no ‘individuals’ were lost – in the current studies, all perennating holdfasts of *F. vesiculosus* f. *linearis* at Billia Croo remained throughout. As mentioned earlier, the genetic relationship between fronds emanating from a common holdfast of *F. vesiculosus* f. *linearis* is not known, creating a nebulous definition of individuality associated with these complexes.

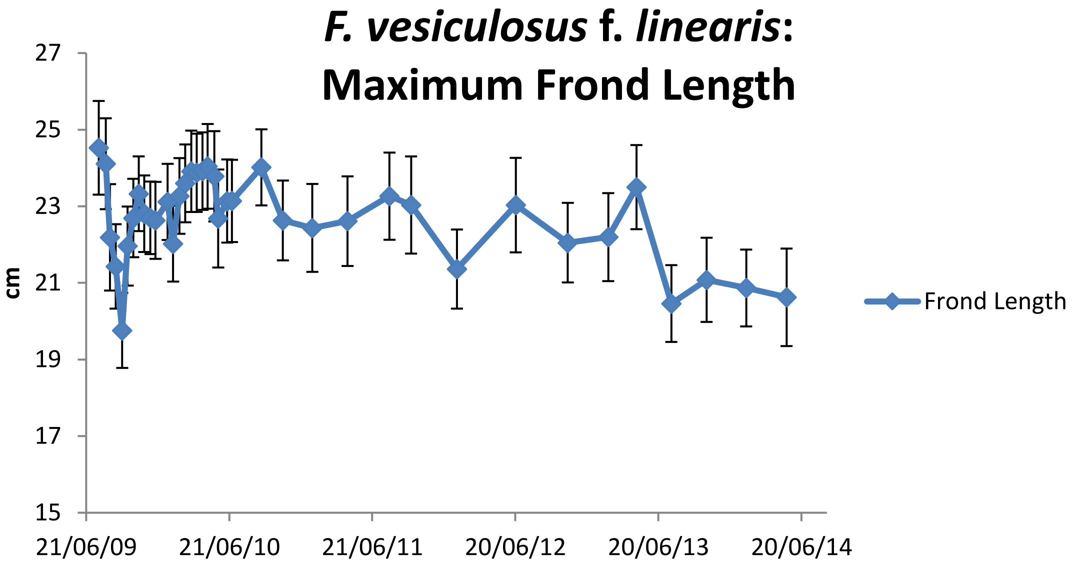


Figure 4.3.2.2: Maximum frond length (cm) from individual *F. vesiculosus* f. *linearis* at Billia Croo (n = 23). Mean of triplicate measurements with standard error.

Unlike percentage cover determined from quadrat imagery, monitoring of maximum frond length of *F. vesiculosus* f. *linearis* individuals at Billia Croo did not reveal clear evidence of expected seasonal cycling. When expressed as daily rate of change in maximum frond length, a pattern does become evident although not as clear as that expressed by percentage cover data (see Figure 4.3.2.2).

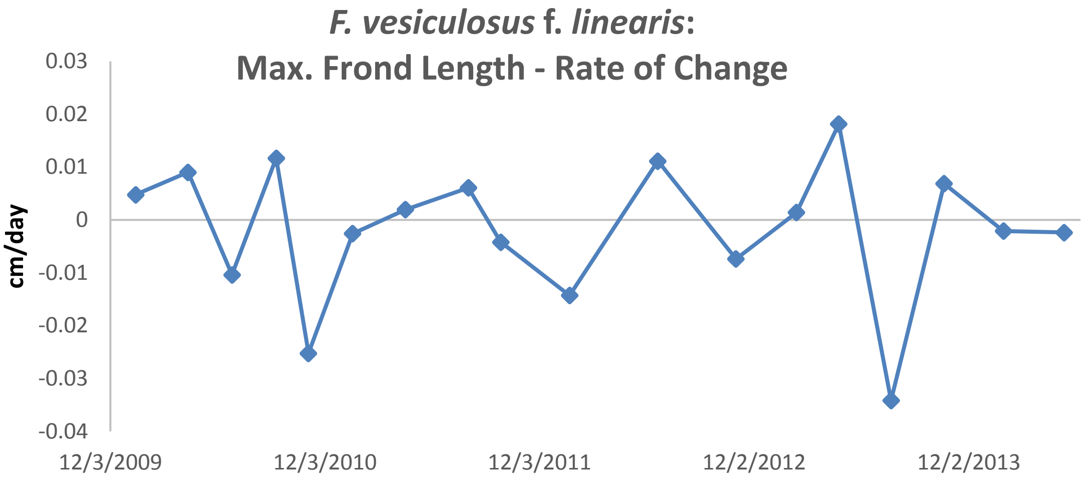


Figure 4.3.2.2: Rate of change in maximum frond length (cm/day) from mean of individual *F. vesiculosus* f. *linearis* at Billia Croo.

4.3.3 Fixed viewpoint imagery:

The upper and lower limits of an extensive population of *F. distichus anceps* at Northside in Birsay imaged quarterly over five years is presented in Figure 4.3.3.1. During these studies, the mean range of *F. distichus anceps* zonal heights varied from a minimum of less than 40 cm to a maximum of almost 80 cm. A particularly pronounced narrowing of the zone was recorded late in 2010 created by a contraction of both the upper and lower boundaries. This was shortly followed by an expansion in both boundaries between April and August of 2011. A prolonged contraction of zonal range began in autumn 2014 and continued for more than a year through the remainder of the current study. A clear seasonal pattern of zonal change is not apparent.

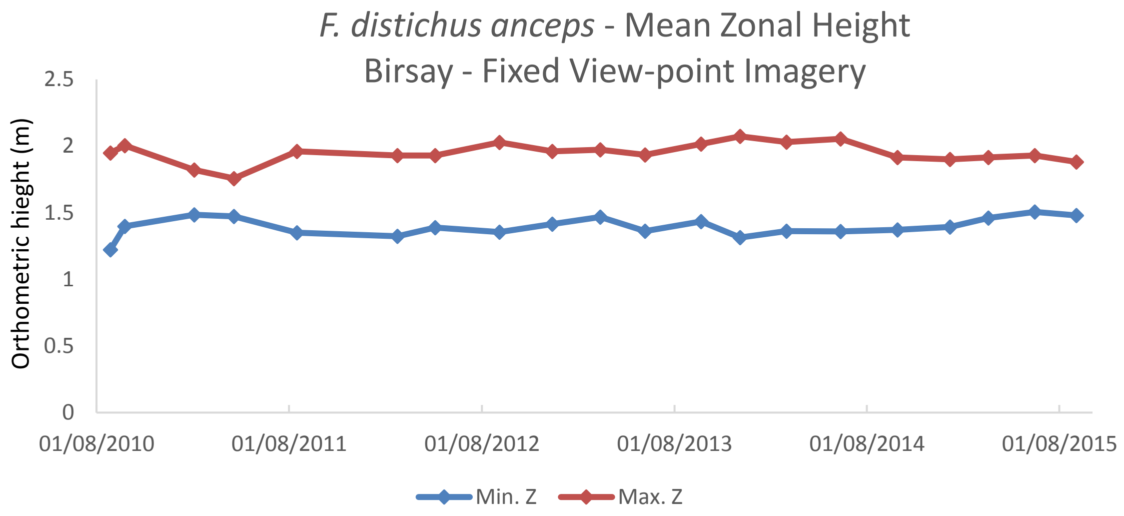


Figure 4.3.3.1: Upper and lower limits of *F. distichus anceps* population at Northside in Birsay (mean of 'east' and 'west' georeferenced points).

When rate of percentage cover change was plotted, there appears to be a cycling of the zonal range within each calendar year (Figure 4.3.3.2). Peaks of expansion and contraction, however are asynchronous with expected seasonal responses. From 2011 to 2014: periods of negative rate of percentage cover change occur predominantly in winter but include quarters in autumn and spring; periods of positive rate of percentage cover change occur predominantly in summer by also include quarters in spring and autumn. Similar to the measures of zonal height, rate of percentage cover change enters a period of prolonged contraction beginning in autumn 2014. Zonal heights relative to mean sea level are presented in Table 4.3.3 for the fixed view-point site and other fucoid study locations.

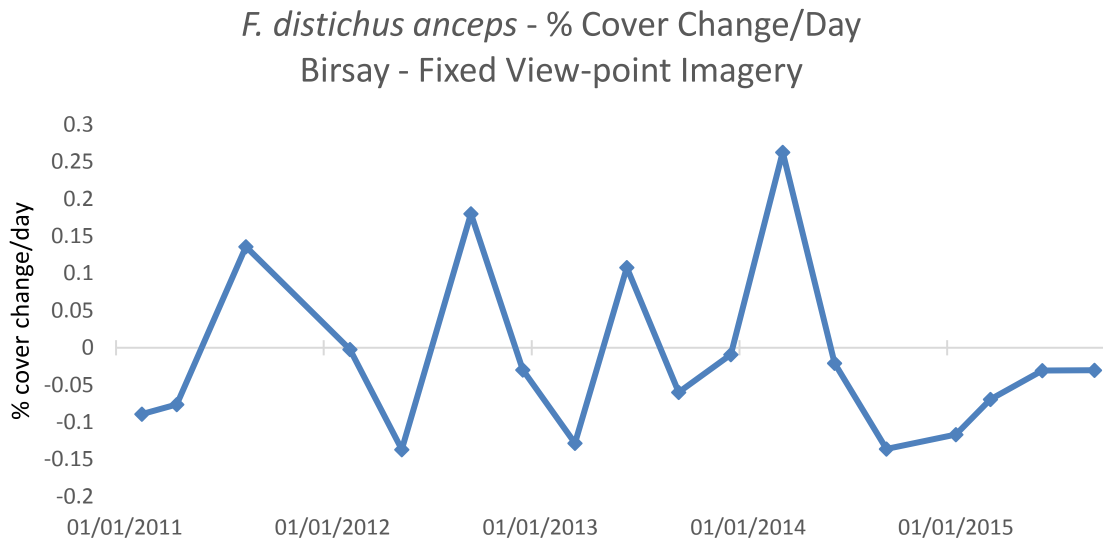


Figure 4.3.3.2: Fixed view-point imagery of *F. distichus anceps* from Birsay expressed as growth rate (percentage cover change per day).

Table 4.3.3: Height of fucoid study areas determined by dGPS.

Species	Site	Specific location	Height*
F. distichus anceps	Birsay – East	Quadrat 1	2.39
"	Birsay- West	Fixed viewpoint – upper**	1.95
"	"	Fixed viewpoint – lower**	1.37
"	Marwick	Quadrat 1	0.54
"	"	Quadrat 2	0.67
"	"	Quadrat 3	1.48
"	Axna Geo***	Upper	1.94
"	"	Lower	1.72
F. vesiculosus f. *linearis*	Billia Croo	Quadrat 1	1.29
"	"	Quadrat 2	1.30
"	"	Quadrat 3	1.03

*In metres; referenced to Mean Sea Level

**Mean of upper and lower boundaries 27/08/2010 – 02/09/2015

***Axna Geo features extensive stands of *F. distichus anceps*; dGPS was recorded at this location in anticipation of future research opportunities

4.3.4 Analysis of surveys of fucoid distribution:

In August 1962, Powell (1963) visited 14 sites in WMO where he found populations of *F. distichus anceps* at 10 of these locations. In many cases, the specific locations were described in sufficient detail to allow reassessment to discrete rock features. Half a century later, visits to these sites have found total corroboration of presence/absence of *F. distichus anceps* along WMO – this fucoid was present everywhere Powell found it and absent from all sites where he failed to locate a population (see Table 4.3.4).

Table 4.3.4: Comparison of distribution of *F. distichus anceps* between Powell (1963) and the present day (2012-2014).

Location*	Powell	Want	SACFOR	Powell Comments
Pulse Skerry 323436 1008406	-	-	N	"extremely wide… relatively sheltered, quite unsuitable"
Breckness 322012 1009434	-	-	N	As above
Billia Croo Bay 322273 1010387	+	+	R	"extremely sparse"
Hole o'Row 322594 1019009	+	+	A	"Along 20 m of reef"
Howana Geo 322706 1020237	+	+	R	No specific comment
Nebo Geo 322605 1020676	+	+	S	"maximum width of no less than 10 metres"
Below Garson 322695 1020744	+	+	C	"well developed on very extensive reefs"
Axna Geo 322820 1021134	+	+	S	As above
Outshore Point 322443 1022680	-	-	N	"reefs too wide and broken"
S. Birsay Bay 323890 1026463	+	+	S	"magnificent belts"
Brough of Birsay 323359 1028521	+	+	A	"One small patch"
Hesta Geo 325289 1028759	+	+	S	"magnificent belts"
Little Ramley Geo 328148 1029575	+	+	C	"quite good community"
Eynhallow Sound 331991 1029689	-	-	R	"altogether too sheltered"

*Using current Ordnance Survey place names; some of these names differ slightly from those used in Powell (1963); OS coordinates reported as Easting and Northing.

The scope of this survey however, extended far beyond the locations described by Powell (1963) and included detailed characterisation of the overall littoral community and several important topographic features – details are provided in Chapter 3. Beyond the 10 sites where *F. distichus anceps* was present, the current research identified an additional 20 locations of *F. distichus anceps* along WMO and extending north-west to Costa Head (see Map 4.3.4).

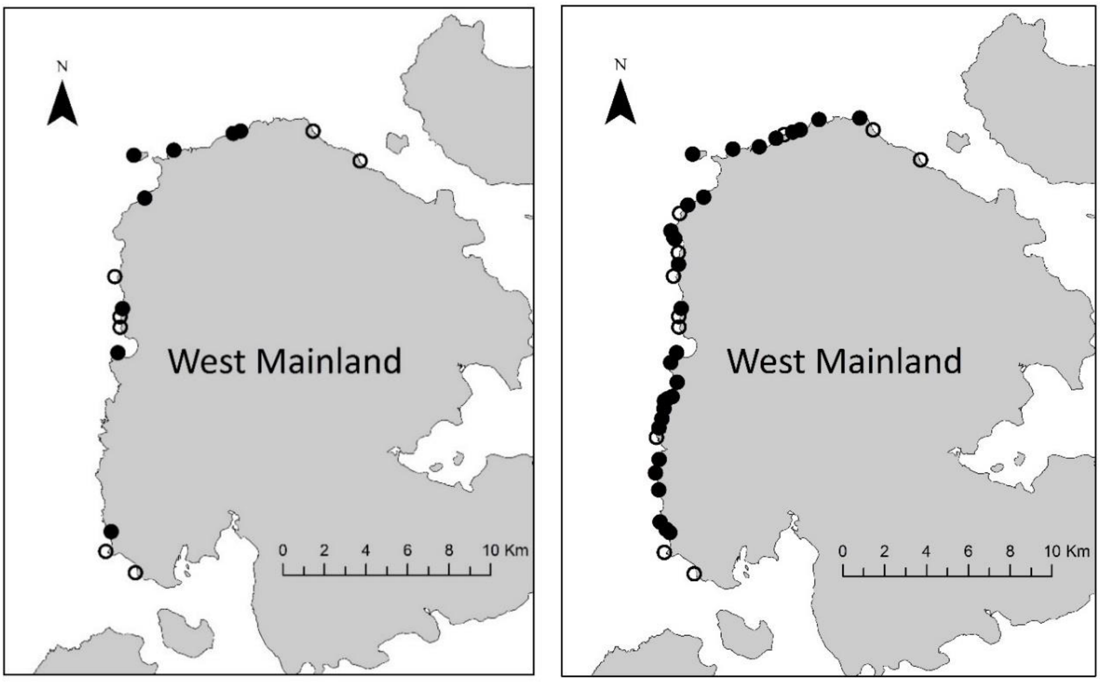


Figure 4.3.4.1: Left: survey sites examined by Powell (1963) – closed circles indicate presence of *F. distichus anceps*; open circles indicate sites where *F. distichus anceps* was not found; Right: survey sites examined during this project between April and July of 2013 – 2015.

While Powell (1963) recorded presence/absence of *F. distichus anceps* he did not use a scale by which abundances can be compared. Never-the-less, there are some interesting observations for comparison, such as: *F. distichus anceps* abundance at Billia Croo described in 1963 as “extremely sparse” and in 2012 as ‘Rare’ on the SACFOR scale; “magnificent belts occur on suitable reefs at sites 10 and 12” (South Birsay and Hesta Geo) – both ‘Superabundant’ on the SACFOR scale in 2014 and 2013, respectively. In some cases, Powell did record topographic observations but these were not rigorously quantified. For example: Powell (1963) explicitly locates the platforms below Garson in Birsay and describes the rocks as sloping at "about 25 degrees" – these have been measured in triplicate and averaged as 19.0 degrees.

4.3.5 Comparison of quadrat percentage cover and individual maximum frond length:

Practical issues with measurements of individual fucoids (i.e. loss of *F. distichus anceps* individuals; concerns over individuality of *F. vesiculosus* f. *linearis* holdfasts) and failure to capture seasonal growth and regress patterns observed through quadrat imagery, led to questions over the applicability of maximum frond length metrics on WMO. There appears to be a positive relationship between the two methods of quadrat percentage cover and individual maximum frond length but this correlation is not strong: r = 0.411; df = 17; p = 0.080 (Figure 4.3.5.).

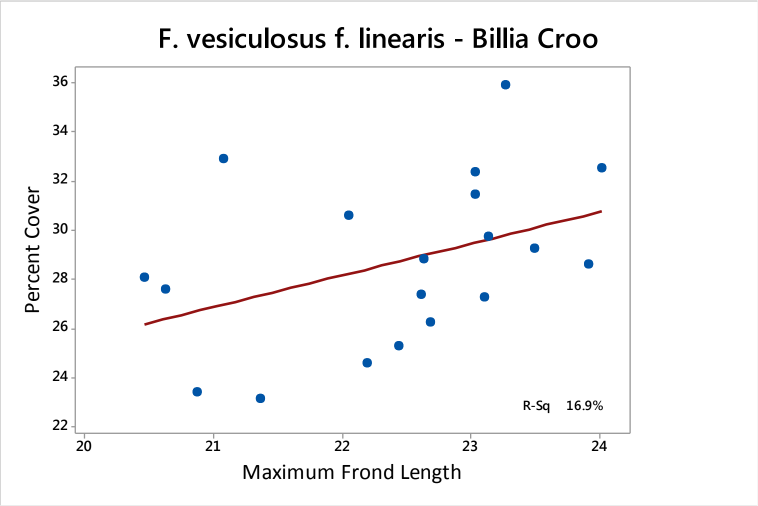


Figure 4.3.5: Linear regression of maximum frond length (mean of 23 individuals) and percentage cover (mean of 3 quadrats) of *F. vesiculosus* f. *linearis* population at Billia Croo (Oct. 2009 – May 2014).

4.3.6 Comparison of quadrat percentage cover with wave and climate data:

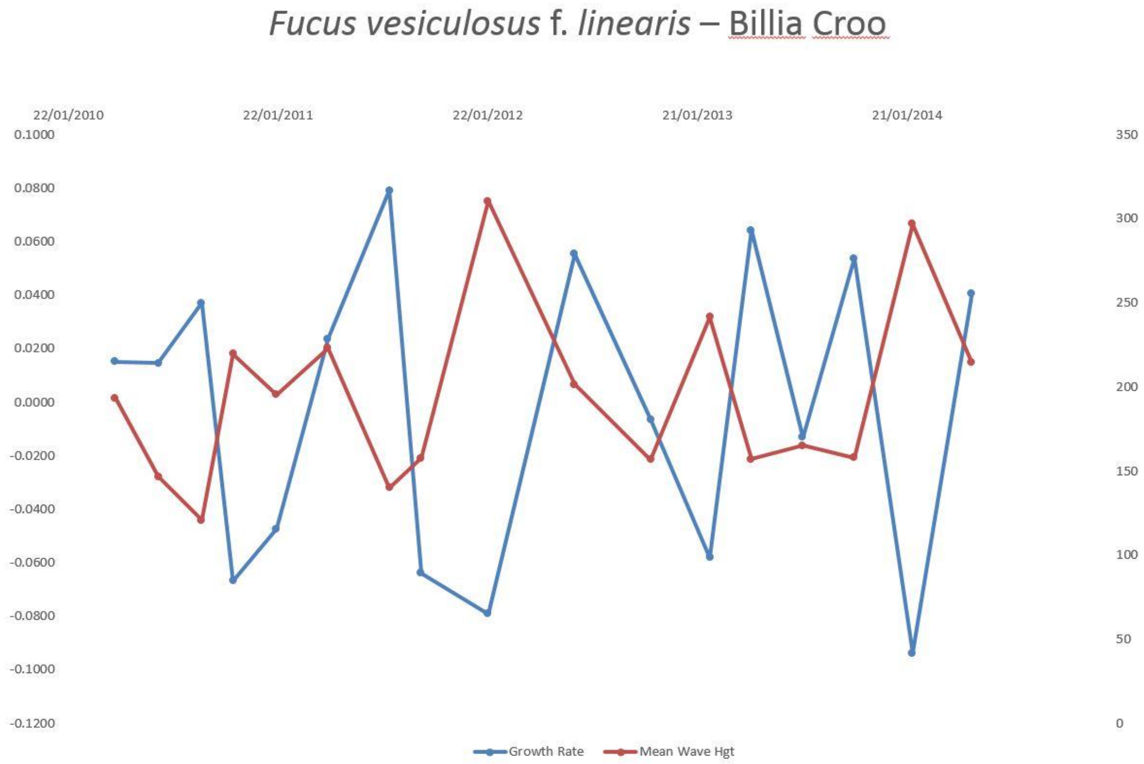
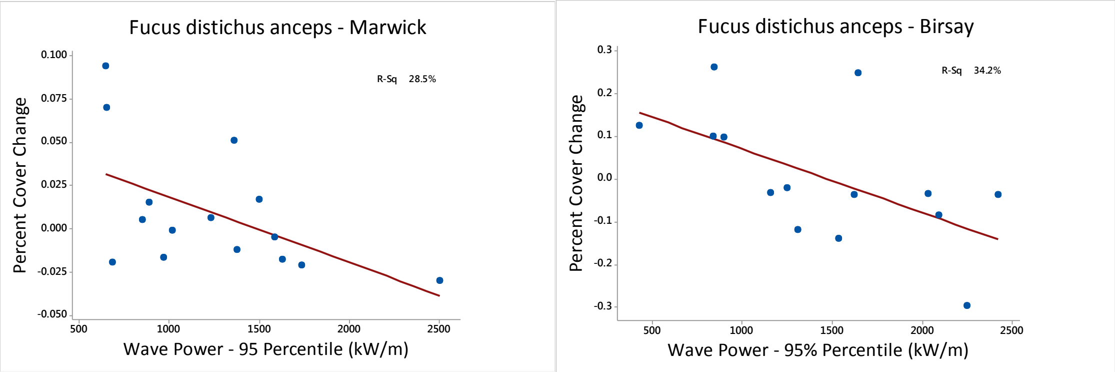


Figure 4.3.6.1 Percentage cover rate of change (blue) of *F. vesiculosus* f. *linearis* plotted with mean wave height (H_S) (red) from Billia Croo. Primary y-axis is percentage change/day; secondary y-axis is H_S (cm).

Percentage cover data from quadrat images of populations of *F. distichus anceps* at Marwick and Birsay, and *F. vesiculosus* f. *linearis* at Billia Croo were plotted against several wave and climate indices. As a general statement, fucoid percentage cover: correlated negatively with wave metrics (see Figure 4.3.6.1); correlated positively with photoperiod, and; did not correlate with temperature metrics (see summary Table 4.3.6). When compared against non-lagged data, lagged responses to photoperiod and temperature indices either did not improve correlations or simply synchronised with sinusoidal seasonal cycles. In addition to the summary table, several graphs have been selected to illustrate the relationship between quadrat percentage cover, and wave and climate data (Figures 4.3.6.2a-d).



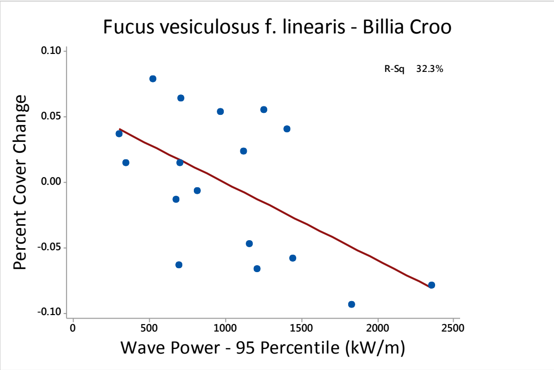
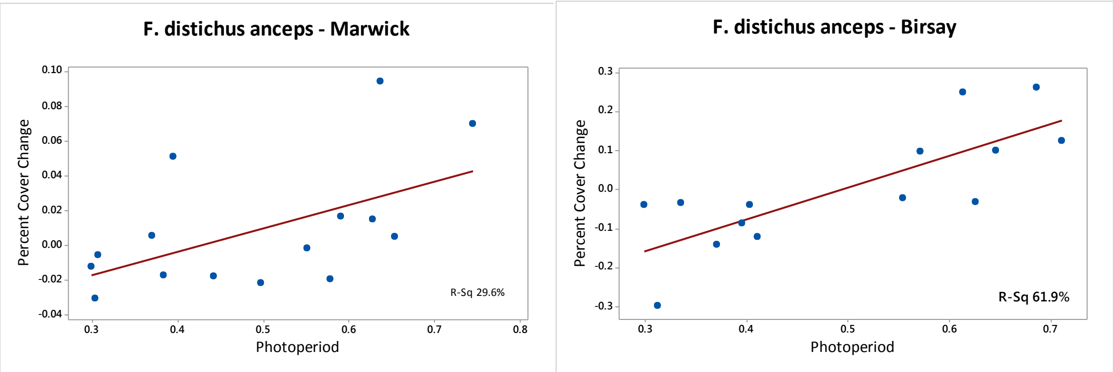


Figure 4.3.6.2a: Regression revealed significant correlation between P_w^{95} and rate of percentage cover change for *F. distichus anceps* at Marwick (R^2 = 28.5%; df = 13; p = 0.040), and Birsay (R^2 = 34.2%; df = 12; p = 0.028), and *F. vesiculosus* f. *linearis* at Billia Croo (R^2 = 32.3%; df = 15; p = 0.017).



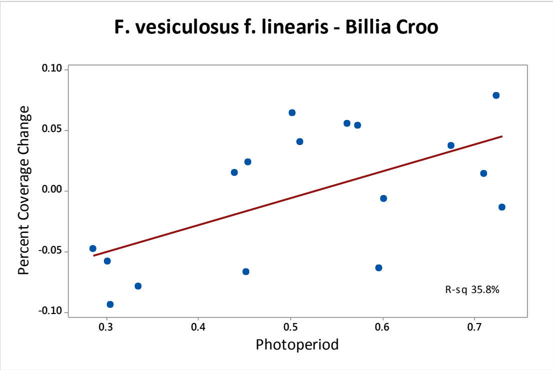
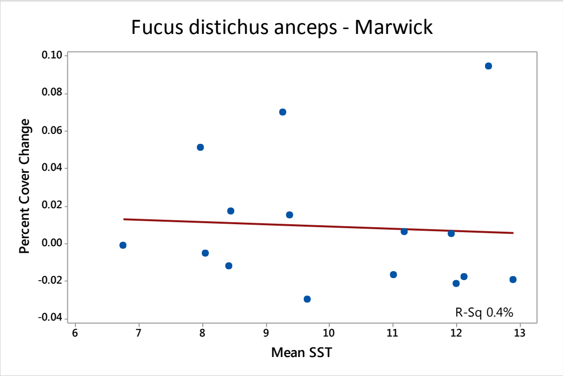
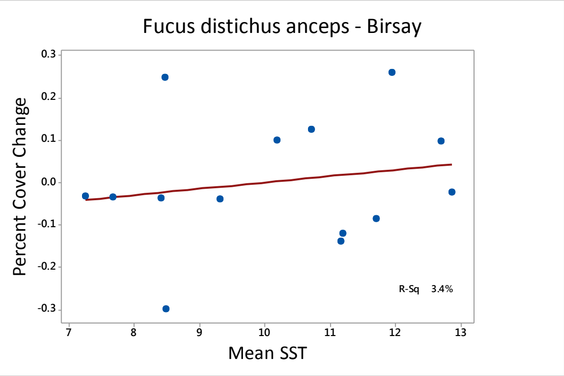


Figure 4.3.6.2b: Regression revealed significant correlation between photoperiod and rate of percentage cover change for *F. distichus anceps* at Marwick (R^2 = 29.6%; df = 13; p = 0.036), and Birsay (R^2 = 61.9%; df = 12; p = 0.001), and *F. vesiculosus* f. *linearis* at Billia Croo (R^2 = 35.8%; df = 15; p = 0.011).





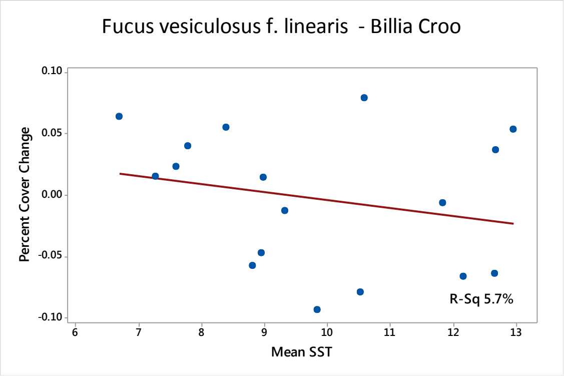
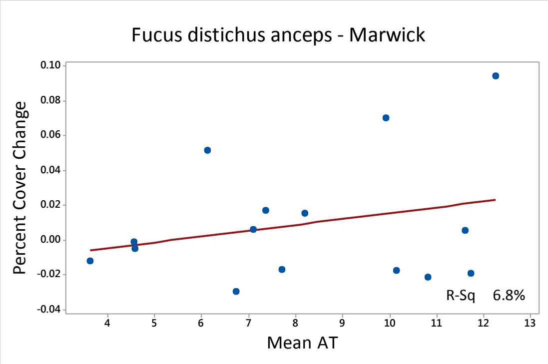
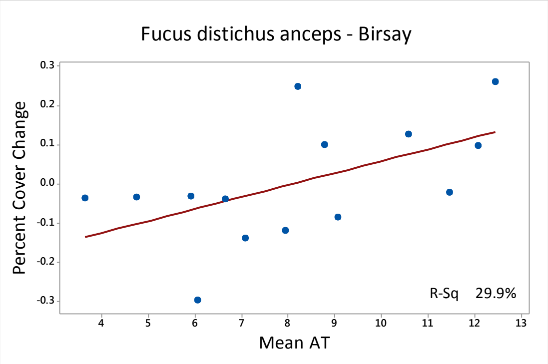


Figure 4.3.6.2c: Regression did not reveal significant correlation between mean SST and rate of percentage cover change for either *F. distichus anceps* at Marwick (R^2 = 0.4%; df = 13; p = 0.827), or Birsay (R^2 = 3.4%; df = 12; p = 0.528), or *F. vesiculosus* f. *linearis* at Billia Croo (R^2 = 5.7%; df = 15; p = 0.358).





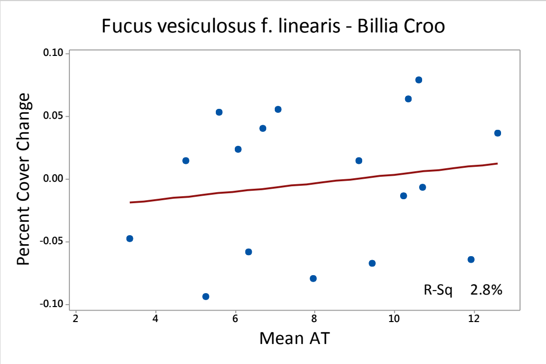


Figure 4.3.6.2d: Regression did not reveal significant correlation between mean AT and rate of percentage cover change for either *F. distichus anceps* at Marwick (R^2 = 6.8%; df = 13; p = 0.348) or *F. vesiculosus* f. *linearis* at Billia Croo (R^2 = 2.8%; df = 15; p = 0.523) but was significant at Birsay (R^2 = 29.9%; df = 12; p = 0.043).

Table 4.3.6.1: Correlation coefficient for linear regressions of fucoid percentage cover rate and photoperiod. M = Marwick (n = 14); B = Birsay (n =13); BC = Billia Croo (n = 16). Confidence symbols: $^+$<0.10; *<0.05; **<0.01; ***<0.001.

	F. distichus anceps (M)	*F. distichus anceps* (B)	*F. vesiculosus* f. *linearis* (BC)
Photoperiod	+0.544*	+0.787***	+0.599*

Table 4.3.6.2: Correlation coefficient for linear regressions of fucoid percentage cover rate and SST indices. M = Marwick (n = 14); B = Birsay (n =13); BC = Billia Croo (n = 16). Confidence symbols: $^+$<0.10; *<0.05; **<0.01; ***<0.001.

	F. distichus anceps (M)	*F. distichus anceps* (B)	*F. vesiculosus* f. *linearis* (BC)
Mean SST	-0.062	+0.184	-0.238
SST^{95}	-0.107	+0.322	-0.361
SST^{5}	+0.010	+0.071	-0.141

Table 4.3.6.3: Correlation coefficient for linear regressions of fucoid percentage cover rate and AT indices. M = Marwick (n = 14); B = Birsay (n =13); BC = Billia Croo (n = 16). Confidence symbols: $^+$<0.10; *<0.05; **<0.01; ***<0.001.

	F. distichus anceps (M)	*F. distichus anceps* (B)	*F. vesiculosus* f. *linearis* (BC)
Mean AT	+0.261	+0.547*	+0.166
AT^{95}	+0.130	+0.633*	+0.125
AT^{5}	+0.411	+0.506**	+0.252

Table 4.3.6.4: Correlation coefficient for linear regressions of fucoid percentage cover rate and wave indices. M = Marwick (n = 14); B = Birsay (n =13); BC = Billia Croo (n = 16). Confidence symbols: $^+$<0.10; *<0.05; **<0.01; ***<0.001.

	F. distichus anceps (M)	*F. distichus anceps* (B)	*F. vesiculosus* f. *linearis* (BC)
Mean H_S	-0.480$^+$	-0.663**	-0.645**
H_S^{95}	-0.605*	-0.495$^+$	-0.598*
Mean W_P	-0.212	-0.676**	-0.363
W_P^{95}	-0.221	-0.660**	-0.130
Mean P_W	-0.506$^+$	-0.696**	-0.614**
P_W^{95}	-0.534*	-0.585*	-0.568*

4.4 Discussion:

Fucoid studies reported here have focussed on several methodological approaches: abundance determination through image analysis; measuring growth rate of individuals at select monitoring sites; and surveying assemblages at a larger scale along an extensive portion of coastline. Monitoring of high-energy variant fucoids has revealed some important information on their autecology on WMO and fulfilled the research objectives. Key findings suggest that:

- a close relationship exists between exposure, topography, and the presence of *F. distichus anceps* relative to other fucoids;
- growth patterns and abundance of certain species may be of value in long-term assessment of ecological consequences following extraction of wave energy, and;
- the remarkable stability of *F. distichus anceps* populations over decades does not support its use as an indicator of changes associated with SST.

Certain methods appear to be better able to capture ecological processes; practical constraints limit the successful application of other techniques. Looking more closely at the data, the hypotheses identified in section 4.1.2 can be addressed.

Seasonal growth patterns:

Wave exposure varies seasonally with storm frequency and intensity increasing through the autumn and winter (see Figures 2.3.3 and 2.3.4). During spring and summer, seasonal reduction in wave exposure allows the balance between morphological modifications and hydrodynamic forces to shift in favour of plant growth and reproductive development. Increasing size and development of reproductive structures places individual plants at greater risk of partial or complete dislodgement from wave activity (Blanchette, 2000). Field studies of fucoids have confirmed that individual size varies seasonally with smaller specimens observed in winter (Wolcott, 2007). Data from the current studies suggests that, on WMO, the relative reduction in wave exposure through spring and summer coincides with increased growth in *F. distichus anceps* and *F. vesiculosus* f. *linearis*, best shown through quadrat imagery (see Figures 4.3.1.2 and 4.3.1.4).

Regression analyses of meteorological data and fucoid percentage cover rate of change are summarised in Tables 4.3.6.1-4. Not surprisingly, the rate of percentage cover change for *F. distichus anceps* and *F. vesiculosus* f. *linearis* in Orkney are positively correlated with photoperiod. Increased photic energy allows greater resource capture by photosynthetic organisms which may be utilised for growth and reproductive development. Also, as expected, rate of percentage cover change and exposure (as expressed through P_W) are negatively correlated. In terms of exposure, the population of *F. distichus anceps* at Marwick, responds more strongly to extremes in wave climate; *F. vesiculosus* f. *linearis* at Billia Croo responds more strongly to average exposure. With increased hydrodynamic forces placed on littoral algae during storm events, it would be expected that seasonal periods of greatest wave exposure would be most associated with reductions in percentage cover and least associated during seasonal periods of relative calm. Increased growth rate observed through quadrat imagery may result from growth of individual plants and/or settlement of new plants. Similarly, observed reductions in growth rate may result from partial loss of plants (i.e. thinning or pruning) and/or whole plant dislodgement. This is addressed in greater detail below in the review of individual stability hypothesis.

Along WMO, *F. distichus anceps* appears to survive only on rocky shores sufficiently exposed to wave energy that the survival of any potentially competing mid shore fucoids is prevented (Powell, 1963). Studies of germling rhizoids from several fucoid species found the fastest growth rate in *F. distichus anceps* (Twigg, 2011). Rapid rhizoid growth may help establish young plants and allow survival against challenging hydrodynamic forces. High-energy variants *F. vesiculosus* f. *linearis* and *F. spiralis* f. *nanus* can often be found in close proximity, if there is sufficient local complexity in topography to produce ‘micro-habitats’ of lesser and greater wave action. The balance between growth and regress might be expected to alter in response to changes in exposure following extraction of energy by WECs. A shoreline where wave energy had been reduced might tend to favour larger seaweed or those less tolerant to exposure. Species more susceptible to dislodgement or tattering of reproductive structures might be expected to be less vulnerable and become more abundant. Species such as *F. distichus anceps* might be expected to respond less favourably to wave energy extraction owing to increased competition for mid shore space with lower exposure macroalgae such as *F. vesiculosus*.

In contrast to measurement taken from quadrat photographs, maximum frond length recording and fixed view-point imagery did not clearly capture seasonal patterns of growth and regress. At the relatively less energetic site at Billia Croo, expected seasonal changes in the population of *F. vesiculosus* f. *linearis* were not captured using maximum frond length. Comparison of these two methods found that change in percentage cover is poorly explained by maximum frond length (see Fig. 4.3.5); there is not sufficient evidence to support the suggestion that these methods are describing the same process. Maximum frond length does not appear to be the key driver in observed seasonal changes in percentage cover of *F. vesiculosus* f. *linearis* at Billia Croo. Change in percentage cover also depends on additional factors including number of individuals and branching of thalli (Blanchette *et al*., 2000). In *F. vesiculosus* f. *linearis,* the stable holdfast complexes may make seasonal patterns of growth and regress less observable using maximal frond length; perhaps maximum frond length is not as good a representative of the growth profile of individuals and a different metric might better capture change in this plant (see Section 6.4: Methodological improvements in fucoid studies). In addition, another disadvantage of focussing on repeat measurements of selected individuals is that this may result in omission of new cohorts which are contributing to overall population cover. While this situation was not observed for *F. vesiculosus* f. *linearis* at Billia Croo, artificial age structuring of sampling might be created by this method (Ruuskanen and Nappu, 2005).

Clear patterns of seasonal growth and regress were also less apparent from fixed view-point image analysis (Figure 4.3.3.2). While rate of change in zonal range generally increased through the summer and decreased during winter, the onset and cessation of these periods did not coincide as precisely with seasons as results from quadrat imagery indicated. This may be because only a single population was studied using fixed view-point imagery and quarterly recording may lack temporal resolution to accurately identify transition periods. It may be that the distance from the fixed view-point to the population was too far for sufficient detail necessary to identify smaller individuals and germlings. However, it may also be that asynchronous factors at the upper and lower boundaries of this zone are contributing to observable shifts in the zone. While quadrat percentage cover may seasonally fluctuate in response to photoperiod and wave activity, settlement of *F. distichus anceps* germlings might extend the upper and lower boundaries of the adult zone, as well as occupying open patches following removal of plants. Propagule settlement outside the optimal littoral height would be expected to result in higher mortality (Schonbeck and Norton, 1978, 1980; Power *et al*., 2006), and therefore, generally seasonal changes in zonal range of *F. distichus anceps* might be expected to be temporary and subject to asynchronous stressors, beyond those affecting the adult population. For example: an upper extension of *F. distichus anceps* zone might be subject to increased desiccation and foraging activity from grazers, processes which in turn may be dependent on temperature (Hawkins *et al*., 1992), and not necessarily synchronised to stressors dominating adult growth patterns. Additional studies are necessary to further explore these suggestions.

Individual stability of *F. distichus anceps*:

Studies of *F. gardneri* on high-energy Californian shores have shown that continuing plant growth results in increasing vulnerability to dislodgement from wave action (Blanchette, 1997). While the overall population of *F. distichus anceps* at Birsay can be considered stable at a scale of 10s of metres, individual plants have a high ‘turn-over’ rate. The current studies have revealed a stark difference between *F. distichus anceps* and *F. vesiculosus* f. *linearis* in terms of long-term survivability of individual plants (Figures 4.3.2.1 and 4.3.2.2). Maximum frond length studies of *F. distichus anceps* found that the ability to monitor growth of individual plants was impaired by frequent loss of selected subjects. In contrast, in *F. vesiculosus* f. *linearis* all individuals (as defined by holdfast complex and associated thalli) remained throughout the study period.

In comparable wave conditions, studies of the Pacific fucoid *Pelvetiopsis limitata* suggest a mechanical size limit may be reached where individuals of sufficient size are increasingly vulnerable to dislodgement (Wolcott, 2007). While these same studies have not been conducted on *F. distichus anceps,* field observations on WMO indicate that similar results would be anticipated, where individual plants large enough to allow reliable maximum frond measurement and relocation in long-term studies are vulnerable to removal (Figure 4.3.2.1), especially during extreme storm events. These studies of patterns in individual growth and percentage cover changes in WMO fucoids suggest that seasonal regress may be due to contrasting processes: in *F. distichus anceps,* whole individual loss is more common and may account for reduction in percentage cover; in *F. vesiculosus* f. *linearis* individual holdfast complexes persist but tattering or pruning of thalli results in percentage cover reduction.

Seasonal tattering of macroalgal thalli associated with increased wave exposure is commonly observed and may be a necessary process in size reduction, allowing survival of the whole organism (Jenkins *et al*., 1999; Blanchette *et al*., 2000; Jonsson *et al*., 2006). The current studies confirm this process occurring in *F. vesiculosus* f. *linearis* at Billia Croo, evident through seasonal thinning of the thalli emanating from holdfast complexes and reduction in percentage cover but no loss of individual plants. At higher exposure sites such as Birsay, individually-monitored *F. distichus anceps* plants did not show signs of tattering. Instead the whole plant would become absent with no persisting holdfast or remnant stipe; vegetative propagation is not seen in *F. distichus* (Ang, 1991). Frequent loss of *F. distichus anceps* individuals at higher exposure sites might be an important driver in observed changes in percentage cover (Figure 4.3.1.6). Rate of change in percentage cover of *F. distichus anceps* were greater at Birsay than Marwick or for *F. vesiculosus* f. *linearis* at Billia Croo and might be indicative of a more dynamic population. While detailed observations of individual plants were not conducted at Marwick (a high wave energy site of intermediate exposure between Billia Croo and Birsay) larger *F. distichus anceps* individuals persist. It is plausible that tattering of the thallus may occur in larger individuals of *F. distichus anceps* and this, at least partially, accounts for seasonal reduction observed through percentage cover monitoring.

Population stability of *F. distichus anceps*:

In Orkney, the population of *F. distichus anceps* appears stable over many decades. In the early 1960s, Powell (1963) searched for *F. distichus anceps* along WMO and successfully identified it at 10 out of 14 potential sites. Approximately 50 years later, all of these sites have been revisited and the absence/presence of *F. distichus anceps* was unchanged. Additionally, these studies accessed a further 27 sites, of which *F. distichus* *anceps* was present at 20. The ability to assess many more sites owed to year-round residence in Orkney and access to a RIB necessary for detailed characterisation of large sections of previously undescribed cliff-base platforms (see Section 3.2.1). Despite the increased number of described sites with *F. distichus anceps*, there is no evidence that the population on WMO has changed in the decades following Powell's research. Interestingly, in 1953 Powell found *F. distichus anceps* when visiting the precise location where the species had been originally described 90 years earlier at Duggerna Rock, County Clare (Powell, 1957b). Additional sites visited by Powell in Clare were successfully utilised in 2006 for sample collection (Twigg, 2011). These provide further examples of the long-term stability of *F. distichus anceps* at specific locations in the British Isles.

The combination of relatively short life-cycle and narrow niche of suitable topographic conditions lends support to the suggestion that acute events can be observed with rapid turn-over of individual plants, especially at sites towards the extreme limit of *F. distichus anceps* energy tolerance. On such shores, removal or thinning of *F. distichus anceps* does not result in replacement by other macroalgae because there are no other species capable of survival in the mid shore at these exposure levels. As such, *F. distichus anceps* populations may experience high turn-over of individuals, and acute losses may occur during storm events, potentially followed by marked rebounds in response to subsequent favourable recruitment seasons. Indeed, experimentation on *F. distichus* in Alaska suggests that canopies can rapidly recover following clearances with a return to high biomass levels within a single year (Klinger and Fukuyama, 2011). On WMO it appears that the essentially unchanging topography maintains hydrodynamic conditions that allow a remarkably stable population to survive on discrete rock platforms over a decadal time scale.

During the time-frame of the current research, the population of *F. vesiculosus* f. *linearis* at Billia Croo appeared highly stable at 'individual' level and percentage cover 'pulsed' seasonally, as expected. On relatively lower energy rocky shores, fucoid presence is increasingly dependent on cyclical grazing pressures (Hawkins, 1981a, b; Hawkins and Hartnoll, 1983; Hawkins *et al*., 1992). The fucoid-barnacle-limpet mosaic (see Section 1.4) is most apparent on shores with relatively lower exposure than most of WMO. As such, studies of sites such as Billia Croo might expect to see long-term cyclical changes with *F. vesiculosus* f. *linearis* as the fucoid component owing to these biotic 'control and release' processes. However, the pressure on fucoid growth from limpet grazing changes with latitude along the wave-exposure gradient (Ballantine, 1961). While detailed monitoring of limpets and barnacles was not conducted, rocky shore surveying of this site in April 2013 found: patellid limpets were 'frequent' on the SACFOR scale (13/m^2); from a sample of 20 limpets all were identified as *P. vulgata*; barnacles (predominantly *Chthamalus stellatus* and *Semibalanus balanoides*) were evaluated as 'frequent'; and *F. vesiculosus* f. *linearis* was evaluated as 'abundant'. While Jonsson *et al.* (2006) demonstrated that limpet densities above 5-20/m^2 may be sufficient to modify local fucoid cover, grazing appears less effective in more northern latitudes (Hawkins *et al*., 1992; Jenkins *et al*., 2005).

Observations of *F. distichus anceps* length were made as part of the wider assessment of WMO rocky shore communities (see Section 3.2.1), although more detailed measurements beyond abundance scoring were not practical owing to the large amount of data gathering necessary in a short period of time. On the most extreme exposed shores with a population of *F. distichus anceps*, individuals were typically homogeneous in length and very small. This homogeneity might arise because the population is a cohort of opportunistic juveniles destined for removal in late year storms. Alternatively, perhaps the hydrodynamic forces in these precise locations select for a specific morphology. On the less exposed shores, but within the narrow gradient of wave energy where *F. distichus anceps* is found, plants were typically larger, more heterogeneous in length, and presumably more likely to either withstand winter storms or sacrifice part of the thallus during this period. Similarly, Powell (1963) described *F. distichus anceps* individuals as particularly long at two locations (Hole o' Row and the Oyce) of 'slight local shelter'.

Impacts of wave energy:

F. distichus anceps appears to survive in a narrow niche towards the extreme end of the wave energy gradient. On the relatively uncomplicated, planar rocky shores of WMO, differences in substrate topography appear to be among the main factors establishing this energy gradient. Discounting exceptions of reduced fetch on WMO caused by the proximity of neighbouring islands to the SW and NE orientated shores, and the few embayments, the presence of *F. distichus anceps* relative to other mid shore fucoids on WMO appears to be chiefly associated with higher energy conditions produced by waves breaking on uncomplicated and increasingly sloped rocky shores. This type of habitat is common to populations of *F. distichus anceps* in Caithness and Ireland (Powell, 1957b) and the Butt of Lewis (A. Want, pers. obs.). Farther north in Iceland, where this species is more common, *F. distichus anceps* is similarly associated with steeper and more exposed shores (Munda, 2004). In contrast, lower slopes and broken shores result in more energy dissipation (Denny, 1995) and other fucoids (such as *F. vesiculosus* f. *linearis*) will outcompete *F. distichus anceps* for mid shore space. In fucoids, larger size is associated with an increase in reproductive receptacle number (Wolcott, 2007). If hydrodynamic forces in the surf-zone were lowered, other macroalgae might be expected to out-compete *F. distichus anceps* for space; if wave energy was increased, whether chronically or during acute events, *F. distichus anceps* plants would be increasingly susceptible to dislodgement.

The minimum energy limit of *F. distichus anceps* survival appears to be established by the biotic factor of competition for space from other high-energy variant fucoids in the mid shore, such as *F. vesiculosus* f. *linearis*. The absence of competitive species above the maximum energy limit for *F. distichus anceps* suggests that the higher tolerance is controlled by abiotic factors imposed by hydrodynamic forces. Studies of *F. vesiculosus* and *F. spiralis* have identified mechanical limits to fucoid survivability to hydrodynamic forces (Jonsson *et al*., 2006). Presumably, the morphological adaptations necessary to survive on the most exposed shores come with an increasing reproductive cost (Wernberg and Thomsen, 2005). Rapid rhizoid growth may help to establish juvenile *F. distichus anceps* plants (Twigg, 2011), but as the growing plant commits to building a robust holdfast the available resources for reproductive development will be reduced. Other typical morphological adaptations, such as dwarfism and narrowness of the thallus, may result in reduced capacity for photosynthesis leading to reproductive failure (Jackelman and Bolton, 1990; Friedland and Denny, 1995; Blanchette *et al*., 2002). Perhaps the most exposed populations of *F. distichus anceps* become less reproductively viable owing to these morphological compromises and frequent dislodgement but are repeatedly repopulated during favourable settlement periods from parent populations some distance away. With the lack of competitive macroalgae at these exposure levels, the populations may persist even following years of poor reproductive output, as long as stock remains in close enough proximity to resupply propagules. A feature of *F. distichus anceps* is for plants to have all the apices fertile at the same time. This feature may be of value for the survival of the species (Powell, 1957b) and might also explain the presence of uniformly small individuals on particularly exposed sites (see Figure 4.4.1).

Similarly, changes in meteorological conditions, such as frequency of storm events, might be expected to contribute to long-term changes on rocky shore fucoid communities. Increased storminess has been predicted as a possible outcome of increases in temperature (Young *et al*., 2011; Collins *et al*., 2013; Woolf and Wolf, 2013). However, the lack of studies which quantify the relationship between hydrodynamic energy and individual species tolerances to exposure, leads to difficulty in modelling how changes in storminess might affect rocky shore assemblages. As a broad example, in species whose exposure preferences are well established, there remains a general lack of knowledge regarding whether this relationship is owing to chronic energy levels or to acute events (Siddon and Witman, 2003). In the case of WMO, there is insufficient evidence to determine whether *F. distichus anceps* presence on exposed rocky shores where other fucoids cannot survive is because of tolerance to increased wave energy over long-term periods of time or whether this species is better able to withstand more extreme, storm events.

In a recent SNH report, *F. distichus* was considered as an indicator of three primary environmental drivers, but was not included in a short-list of recommended species for studying wave exposure (Burrows *et al*., 2014). This study did not however distinguish between *F. distichus anceps* and other forms found in British waters, and may include spurious records from several sheltered sites (see resolution in Twigg, 2011). Furthermore, fetch-based assessment of exposure used in the report did not include topographic features that would now seem significant to this species. Perhaps most importantly, in areas of the highest wave resource targeted by the MRE industry, i.e. the northern and western shores of the British Isles, *F. distichus anceps* may be one of only a small number of macroalgae suitable for use as a long-term monitoring tool. The selection of a suite of indicator species (described in Section 2.2.2) may be helpful to studies specific to this sector.

Temperature:

Over the past three decades, SST in UK waters has increased by about 0.3°C decade^{-1} (Dye *et al*., 2013). Population distribution models have predicted range expansion and contraction of species in British waters following climate change, most notably through increased SST (Hiscock *et al*., 2004) and potential indicator species have been identified (Burrows *et al*., 2014). Ground-truthing through field research has confirmed many cases of shifting ranges (see Section 1.6 - Climate change). *F. distichus anceps* is considered a boreal species – its range extends north to the Spitzbergen archipelago (Luhning, 1990) and it forms a major component of subpolar rocky shores (Munda, 2004). The southern distribution limit is reached in the British Isles where the population extends along the outer western coast of parts of Scotland and down to Ireland, persisting at several known locations extending to Kerry Head (Powell, 1957b). It is interesting that *F. distichus anceps* remains off the west of Ireland despite SST several degrees warmer than most coastal waters around Britain. Populations of boreal species are able survive at their lower latitudinal range limits for longer than might be expected provided that populations remain reproductively connected within the species life span (Svensson *et al*., 2006). How much connectivity exists between populations of *F. distichus anceps* in Ireland is unknown as the coast has not been sufficiently studied; the difficult-to-access habitats favoured by this seaweed make the collection of samples for genetic study and identification challenging.

The continuing presence of *F. distichus anceps* on Irish shores, and the observation by Powell (1957b) of the remarkably topographical similarities home to populations on Orkney, Lewis, Caithness and St Kilda, suggest that at these latitudes, the hydrodynamic profile of these shores is a more dominant factor in determining the presence of this plant than temperature or photoperiod. While temperature (and related factors such as desiccation) is a major determinant in establishing species distributions, for an organism with such a northerly range, *F. distichus anceps* appears surprisingly tolerant to warm seas. So far, it remains stable at specific sites towards its southern limits despite evidence of warming seas.

Survival of *F. distichus anceps* at its southern edge may be reflected in dynamic reproductive strategies. As discussed earlier, isolated populations at the range edge without adjacent stock might receive propagules delivered on currents possibly originating from tattering or ‘loss’ of the whole organism. Alternatively, culture experiments have shown this fucoid to be highly capable of self-fertilisation (McLachlan *et al*., 1971) – this potential shift in balance between reproductive strategies *in situ* in *F. distichus anceps* is however not known due to lack of study. Laboratory experiments on *F. distichus anceps* are not easily related to ecological processes in the wider field (Twigg, 2011).

Powell (1957b) suggested that toward the southern limits of this plant, mid shore survival is determined by desiccation stress, with space on the lower shore remaining unavailable owing to occupation by competitive macroalgae. Powell (1957b) also argued that the southern-most populations of *F. distichus anceps* are sufficiently isolated on restricted habitats that they may represent genetically distinct ecotypes. Inbreeding, seen in monecious species like *F. distichus anceps*, may further reduce genetic variability. If this is the case, they may not be representative of the general species and so their use as indicators of climatic change might be questionable (Twigg, 2011).

In an update to a report originally commissioned by SNH, Hiscock, *et al*. (2004) predict population shifts of many rocky shore species following climate change. *F. distichus* is identified as a potential indicator for climatic change owing to its southern distribution limits in northern British waters before being subsequently re-evaluated as unlikely to change distribution following a 2°C increase in SST. It should be noted, that this report uses the descriptor *F. distichus distichus* while distribution maps indicate *F. distichus anceps*. Ecological niche modelling using 26 environmental variables has predicted an extension of the northern distribution of *F. distichus*, during the 21st and 22nd centuries into areas currently under seasonal and permanent ice cover; these models suggest little impact at the southern distribution limit (Jueterbock *et al*., 2016). Importantly, this study excludes *F. distichus anceps* and does not include any exposure-related indices in modelling. The conclusion of relative insensitivity to changes in SST is supported by laboratory and field studies demonstrating tolerance of *F. distichus* to temperatures of 15°C and above (Bird and McLachlan, 1976) and laboratory studies of *F. distichus anceps* at 15°C (Twigg, 2011). Temperature insensitivity might help explain the lack of seasonal correlation between *F. distichus anceps* and temperature indices (see Table 4.3.6.2-3). Improving models to predict changes in fucoid distribution with increasing SST may require more detailed knowledge of physiological processes, such as photosynthesis (e.g. Colvard *et al*., 2014). The suggestion that this species is not a suitable indicator species for responses to changes in SST is further supported by the observation here of decadal-scale stability on WMO.

Exposure limits and vertical surfaces:

As mentioned earlier, the steepest platforms on WMO are slightly greater than 20° - *F. distichus anceps* thrives on these slopes. Large portions of westerly-orientated WMO (from Black Craig to the Brough of Birsay) also feature sheer vertical cliffs (essentially 90°) where *F. distichus anceps* is not present. This suggests that there may be a point along the hydrodynamic gradient created by increasing slopes from approximately 20° to 90° where there is a mechanical limit above which *F. distichus anceps* cannot survive[2]. Alternatively, the absence of this plant on vertical cliff faces of WMO might result from other factors, such as competition, increased grazing, or desiccation.

Vertical cliff faces are less practical for detailed survey work. Nevertheless, observations in the present study of these habitats concluded that while kelp (especially *Alaria esculentus*) are abundant in the lower intertidal zone, higher, on the mid and upper shores, there are few macroalgae besides a band of *Mastocarpus stellatus* in the lower mid shore to compete for space with *F. distichus anceps*. Varying slopes might result in differing grazing pressures; on WMO, the predominant littoral grazers are patellid limpets. While limpets were not studied on vertical surfaces of WMO, it seems highly unlikely considering the negative correlation between extreme wave energy and patellid abundance, as well as observed decreases in grazing pressure on northern coasts (Hawkins *et al*., 1992), that limpets on vertical cliff faces would be responsible for the absence of fucoids. Upper limits of fucoids are largely established by abiotic factors (Schonbeck and Norton, 1980) and desiccation can be a dominant factor in many locations. Benedetti-

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[2] Note: there are few examples on the non-vertical rocky shores of WMO which suggest that excessive hydrodynamic forces are preventing the distribution of *F. distichus anceps*; certain clefts and surge gulleys appear to be scoured by mobile sediment effectively stripping away all macro-scale organic material.

Cecchi *et al*., (2000) found that macroalgae grow and persist better on more horizontal surfaces owing to reduced desiccation stress. Perhaps, increased drainage and desiccation stress contribute to the absence of *F. distichus anceps* on vertical surfaces on westerly-facing WMO.

To contrast with the westerly-facing coast of WMO, rocky shore surveys continued along the NW facing coasts (from Northside in Birsay to Costa Head). Along these cliffs, a few locations were identified where *F. distichus anceps* populations persisted on vertical surfaces (see Fig. 4.4.1.). In all such locations, individuals on vertical surfaces were found to be considerably smaller, regardless of reproductive maturity. Powell (1957b) makes brief reference to a single population of *F. distichus anceps* located on a vertical surface on Lewis. Upon returning to Orkney to study the distribution of *F. distichus anceps* in far greater detail, an additional example of a vertical population is described from the NW orientated cliffs near the Oyce (Powell, 1963). Similarly to my findings, this population is characterised as amongst the smallest mature *F. distichus anceps* recorded and found in mostly shaded conditions. The presence of populations of *F. distichus anceps* featuring individuals of extreme uniformity in size, shape and colour suggests that they may be all cohorts of a recent successful recruitment season (A. Want, pers. obs.).

The presence of *F. distichus anceps* on vertical surfaces on only this portion of WMO suggests that orientation of the shore may play an important role. Looking once again at potential effects of desiccation, competition, and grazing, it seems unlikely that grazing pressure would be directly affected by orientation, and the absence of competitive macroalgae in the upper mid-shore remains. Notable exceptions are an increased presence of the ‘dwarf’ fucoid, *F. spiralis* f. *nanus*, typically found above the *F. distichus anceps* zone, and an often present population of small *Palmaria palmata* on sites with extremely small individual *F. distichus anceps* (on sloped or vertical surfaces). In this habitat, *P. palmata* occurs at an early successional stage prior to fucoid establishment (Jenkins *et al*., 2005). As such, its presence may be indicative of a disturbed environment.

F. distichus anceps persistence on these vertical faces also suggests that desiccation may not be the limiting factor in the relationship between this seaweed and slope, although NW facing cliffs do receive little direct sunlight which might mitigate against desiccation. However, owing to a combination of sea spray on exposed shores, high humidity, low angle of the sun, prevalence of summer sea fog, and the timing of low-tides late in the mid-afternoon, there should not be an appreciable difference in emersion stress through insolation between cliffs facing NW and those facing due west. Instead, the coarsely-stepped reefs typical of the cliffs of NW WMO dissipate energy less homogeneously than the uniform planar platforms on the westerly-orientated coast (see Section 3.4: Discussion – Topography and exposure). That the rocky shore assemblages on westerly and north-westerly orientated coasts on WMO are quite similar suggests that, in this case, the net effect of orientation and topographic variation is to create a similar level of wave exposure in the littoral zone; on this portion of the coast there may be sufficient dissipation of energy as approaching waves refract towards obliquely orientated shores and shoaling from the stepped reefs, that certain vertical surfaces receive similar hydrodynamic forces as the sloped platforms that characterise westerly-facing shores of WMO. This is not to suggest that desiccation does not remain an important factor in limiting upper shore distribution of *F. distichus anceps* and sea spray created by stepped reefs may play an important role in reducing desiccation (Lewis, 1964). Increased susceptibility to wave-induced dislodgement following desiccation (Haring *et al*., 2002) might help explain the presence of smaller plants on Irish shores and on vertical surfaces on NW WMO. Twigg (2011) suggested that smaller plants in Ireland might result from growing in more

Figure 4.4.1: Imyala Helliar (West) - one of the few sites in Orkney featuring *F. distichus anceps* on vertical surfaces. This suggests that desiccation is not the dominant factor relating to slope. Note: the small size (mean maximum frond length approx. 8 cm) and uniformity.

marginal areas requiring greater reproductive effort; without explicit topographical descriptions or quantification of exposure, it remains unknown whether small size of *F. distichus anceps* in Ireland is a response to stresses produced from lower latitudes, wave exposure, or other factors.

Short-term responses in *F. distichus anceps* populations:

In August 2011, an upwards shift in the zone of *F. distichus anceps* was first observed at Birsay (Figure 4.2.3.1). Subsequent analysis of fixed view-point images suggests that the upper boundary of the population moved upshore by over 20 cm between April and August 2011 (Figure 4.4.2). At the nearby quadrat site in Birsay (located relatively high on the shore, about 30 metres eastwards on the opposite side of a large gully) percentage cover of *F. distichus anceps* increased from 8.1% to 30.4% over this same period. Concurrently at Marwick (approx. 8 km SW along the coast), image analysis of the uppermost quadrat (Q3) revealed a near tripling of percentage cover between February and September 2011 (see Figure 4.3.1.3). This suggests that methods used here were able to capture a simultaneous shift in zonation occurring over a large geographic area. Synchronous changes in zonation at sites distant on a km-scale suggest that, on WMO, *F. distichus anceps* may be responding to a systemic driver rather than a localised or stochastic event. In these studies, the populations with the most dynamic rates of percentage cover change were those located highest on the shore. While continuing to 'pulse' seasonally, the percentage cover of Q3 remained at the elevated amount following the dramatic increase in early 2011. A similar pattern is seen at the fixed view-point and quadrat sites in Birsay, i.e. following this period of rapid increase, the population generally remained at this higher level. This suggests that the population of *F. distichus anceps* at these upper shore locations might be returning to 'normal' shore height following a recent reduction in cover. While quadrat data collection began in September 2010 and therefore cannot be used to corroborate this suggestion, fixed view-point imagery began earlier and supports the theory that the population was 'rebounding' in early 2011 to levels from the previous year (Figure 4.3.3.1). Studies of *F. distichus* in Pacific waters showed recolonization following experimental clearance to be rapid and synchronised, on a scale of 10s of metres (Klinger and Fukuyama, 2011). In contrast, analysis of long-term abundance data from Shetland (Burrows *et al.*, 2002) found poor synchrony between *F. serratus, F. vesiculosus*, and indeterminate fucoid germlings at a scale of kilometres, suggesting that this phenomenon is not necessarily to be expected in *F. distichus anceps*.

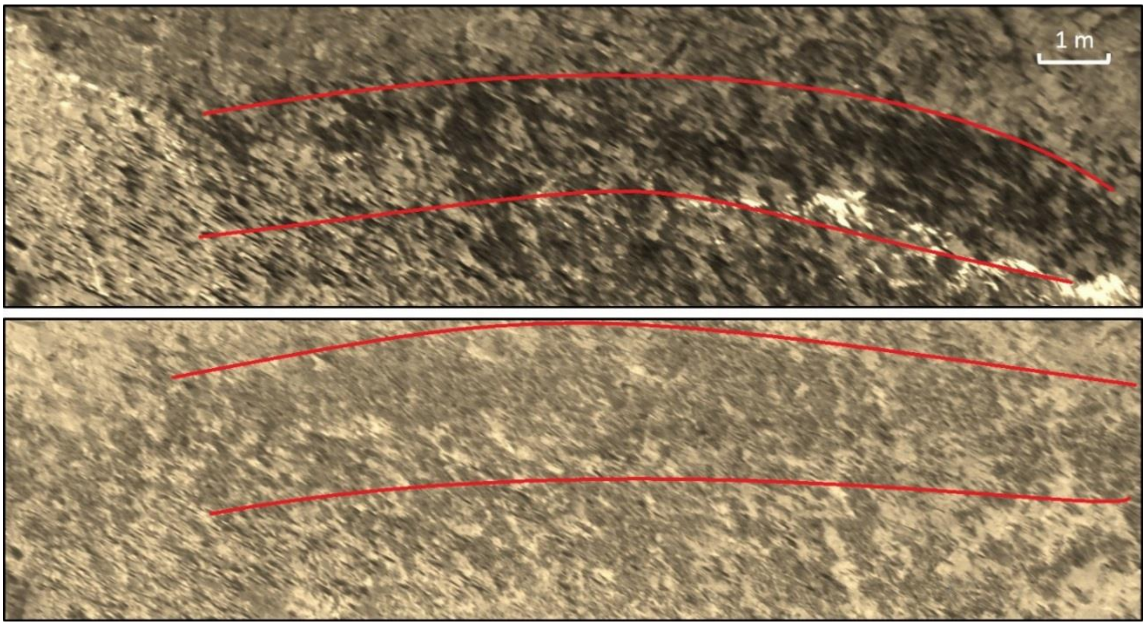

Figure 4.4.2: Fixed view-point imagery of *F. distichus anceps* population at Northside in Birsay. Images have been transformed into ‘bird’s eye’ view and cropped to precisely matching field of views using georeferenced rock features. Top: 2 February, 2011; bottom: 22 February, 2012. Red marks indicate the approximate upper and lower boundaries of the population.

Observations of abundance change in *F. distichus anceps* at the upper margin of its zone most obviously lead to questions regarding abiotic factors (Schonbeck and Norton, 1978), although seasonal or long-term cycling of biotic factors cannot be discounted (Hawkins and Hartnoll, 1985). Rapid changes in abundance of *F. distichus anceps* in the upper shore might be explained by acute events in wave or climatic factors. On high wave energy rocky shores, Thomas (1986) found a zonal difference in correlation between littoral species and exposure, with species correlating most strongly tending to occupy supralittoral rather than lower midlittoral zones; this relationship was enhanced on more steeply sloped shores. Laboratory experiments with *F. serratus*, *F. spiralis*, *F. vesiculosus*, and *Pelvetia canaliculata* showed germination temperatures related to shore zonation and seasonal timings of gamete release (Terry and Moss, 1981). Experiments by Twigg (2011) found that rhizoid growth rate was fastest for *F. distichus anceps* at temperatures higher than those seen *in situ*. Favourable temperatures during settlement may promote temporary extension of the upper zone but subsequent desiccation stress may lead to increased wave-induced removal (Haring et al., 2012) especially as storm intensity and frequency increase after the summer.

Alternatively, grazing by patellid limpets would be expected to target juvenile fucoids (Jonsson *et al*., 2006) and may play an important role in maintaining upper zonal boundaries (Lubchenco, 1983; Hawkins and Hartnoll, 1985; Boaventura *et al*., 2002). In the current studies, patellid data are limited to abundance and species proportions recorded as part of a broader survey of rocky shore assemblages (see 3.2.1 Littoral site survey). At the three main study sites, abundance of *Patella* spp. and proportion of *P. ulyssiponensis* were recorded in the lower mid shore: Birsay (6 June, 2013) - 15/m^2; 35% *P. ulyssiponensis*; Marwick (8 May, 2013) - 30/m^2; 50% *P. ulyssiponensis*; and, Billia Croo (28 April, 2013) - 13/m^2; 0% *P. ulyssiponensis*. In studies on the south coast of England, limpet densities of 5-20/m^2 prevented fucoid establishment (Jonsson *et al*., 2006). These studies, however, were on less exposed shores grazed by *P. vulgata*. The current studies would benefit from additional patellid data exploring seasonal abundances and impacts from grazing, especially at higher zones. Lastly, competition from other macroalgae at the upper height limit of *F. distichus anceps* is not expected; zones of *F. spiralis* f. *nanus* and *Porphyra umbilicalis* are typically located sufficiently far above *F. distichus anceps* for this interaction to be unlikely.

Data from quadrat analysis of *F. distichus anceps* at Marwick and Birsay and *F. vesiculosus* f. *linearis* from Billia Croo were re-examined in terms of relative shore height (see Table 4.3.3). Quadrat 3 at Marwick was 94 and 81 cm higher than Quadrats 1 and 2, respectively; the Birsay quadrat was similarly located higher on the shore relative to most of the population. At Billia Croo, Quadrat 3 was nominally lower (<30 cm) than Quadrats

1 and 2. Correlations between fucoid growth rate and several climatic indices were determined following separation into subsets based on relative shore height.

Table 4.4.1: Correlation coefficient for linear regressions of fucoid percentage cover rate and several climate indices separated into subgroups based on relative shore height within each survey area. *F. distichus anceps* (*F. dis. anc.*); *F. vesiculosus* f. *linearis* (*F. ves. lin.*). SST = Sea surface temperature; AT = Atmospheric temperature; P_W = Wave power. Confidence symbols: $^{+}$<0.10; *<0.05; **<0.01; ***<0.001.

	Marwick Upper (*F. dis. anc.*)	Marwick Lower (*F. dis. anc.*)	Birsay Upper (*F. dis. anc.*)	Billia Croo Upper (*F. ves. lin.*)	Billia Croo Lower (*F. ves. lin.*)
Mean SST	-0.037	-0.158	+0.184	-0.279	-0.120
Mean AT	+0.282	+0.159	+0.547*	+0.206	+0.061
Mean P_W	-0.567*	-0.287	-0.696**	-0.574*	-0.606**
P_W^{95}	-0.570*	-0.335	-0.585*	-0.545*	-0.533*

In Table 4.4.1, *F. distichus anceps* rate of change in percentage cover and wave energy correlated significantly with upper but not lower shore quadrats. At Billia Croo, *F. vesiculosus* f. *linearis* growth rate in the lower quadrats correlated marginally more significantly with mean P_W. That all wave indices tested against percentage cover change rate at Billia Croo at upper and lower shore heights were mostly similar is expected owing to the minimal difference in actual height. In *F. distichus anceps* and *F. vesiculosus* f. *linearis* upper quadrats are more strongly correlated with mean AT, although only the site at Birsay showed statistical significance. Quadrat subsets did not show significant correlation with mean SST and no obvious trend was shown in the relationship between species response to SST and shore height.

Collectively, these data suggest that individual *F. distichus anceps* plants in the uppermost zone respond more strongly to increased wave exposure and higher AT; Jueterbock *et al*., (2016) has described the upper zonal limit of *F. distichus* shifting geographically in response to AT. These individuals may be more susceptible to periodic removal followed by rapid recolonization during the next settlement season. The frequency of acute changes in *F. distichus anceps* zonation is unknown but it is possible that the upper zone, especially on the most extreme exposed shores might be considered ephemeral. While more data are necessary to support this assertion, the presence of uniform populations of small *F. distichus anceps* found on some vertical surfaces on NW WMO (Figure 4.4.1) and shores that appear to be newly disturbed (A. Want, pers. obs.) might provide evidence of recent recolonization.

Close examination of seasonal meteorological data associated with retraction and expansion of the upper zonal limit of *F. distichus anceps* at Birsay and Marwick, during autumn 2010 and spring 2011, respectively, however, did not reveal evidence of any unusual climatic events that might explain population fluctuations. Wave metrics recorded during the loss in the upper zone showed less stormy conditions than the seasonal average in the years 2009-2015. Similarly, during both zonal retraction and expansion, AT and SST records do not indicate any obvious links. While AT in winter 2011 was colder than average (recorded from 2009-2016), retraction of the zone had already occurred; during summer 2010, AT was close to the average and lower 5% SST was below average; and, upper 5% SST was warmer than average in winter 2011. The observation of synchronous changes in the upper zonal limit of *F. distichus anceps* on differently orientated shores separated by 8 km suggests that the plants were responding to a large-scale driver. There is however, insufficient evidence to assign a meteorological or biological cause underpinning this response.

Summary:

During the present studies, methods for evaluating fucoid growth have been developed and tested at individual and population scales; results indicate that these methods are capable of capturing ecological responses to short-term environmental variation and seasonal changes in fucoids. Practical problems with some of these methods have been identified, especially apparent on the more exposed rocky shores of WMO. Comparisons between fucoid percentage cover and maximum length methods suggest that percentage cover is a preferred method of capturing seasonal changes in growth and regress. However, methodological problems associated with high loss of individual *F. distichus anceps* plants may reveal clues to important contrasts in ecological processes between this species and *F. vesiculosus* f. *linearis*. While seasonal regress in *F. vesiculosus* f. *linearis* appears to primarily result from tattering or pruning of thalli, in *F. distichus anceps* regress is more associated with loss of whole organisms, at least on higher energy shores. Similarly, while fixed view-point imagery of an extensive population of *F. distichus anceps* may not perform as well as quadrat images in capturing seasonal changes, this broader scale method may more successfully identify important fluctuations in zonal boundaries.

The presence of *F. distichus anceps* on WMO appears to be strongly linked to a narrow ‘window’ at the upper-end of the hydrodynamic gradient. Topographically, shore slope and substrate complexity appear to play important roles in creating an optimal level of exposure favoured by *F. distichus anceps*. This specific set of topographic variables might explain the limited geographic distribution of this plant, including its infrequent presence on the west coast of Shetland (Powell, 1963; Russell, 1974) and restriction to the NE orientated corner of the island of Lewis. Reduction in wave energy might be expected to favour competing high-energy variant fucoids, such as *F. vesiculosus* f. *linearis*, at the expense of *F. distichus anceps*. At the other end of the exposure gradient, surge gullies and vertical cliff faces on westerly-orientated WMO, may be too energetic for survival of *F. distichus anceps*. Comparing presence and abundances of rocky shore species between sites with varying slope and complexity may provide examples of expected responses following extraction of wave energy. The selection of *F. distichus anceps* as an indicator species for changes in exposure is supported by these studies. On the other hand, decadal-scale stability of *F. distichus anceps* and persistence of southern populations in Ireland suggest that this species is not particularly sensitive to changes in SST and its role as an indicator species for climatic change is not supported.

Chapter 5 - Long-term monitoring of littoral barnacle recruitment at the northern distribution limit of *Chthamalus* spp.:

5.1 Introduction:

The dominant barnacles on the rocky shores of the British Isles belong to the genera *Semibalanus* and *Chthamalus* (Southward, 1976, 2008) (Figure 5.1.1). The former is represented by *S. balanoides* (L.) widely found on both sides of the North Atlantic, as well as the North Pacific; the latter by *C. stellatus* (Poli) and *C. montagui* (Southward), two organisms superficially similar enough to have received separate species status only relatively recently (Southward, 1976).

Figure 5.1.1: *Chthamalus stellatus* at Billia Croo; *Semibalanus balanoides* at Bay of Sandoyne.

In northern Scotland, the two genera of barnacles are typically found in close proximity, with chthamaloids occupying an upper zone, relative to the *S. balanoides*, which dominate closer to the sublittoral zone (Lewis, 1986). In the lower zone, *S. balanoides* out-compete *C. montagui* by occupying settlement spaces and growing atop the more slowly growing *C. montagui* (Connell, 1961a)[3]. Examination of the internal structure of shell plates reveal tubiferous shell components in balanoids, in contrast to solid walls in chthamaloids (Bourget, 1977). This may produce an evolutionary advantage for *S. balanoides* to outcompete for space by more rapid growth in overall size allowed by lower density of shell components. The upper boundary of *Chthamalus* spp. is determined largely by abiotic factors such as desiccation and temperature stress which increase mortality (Connell, 1961a; Foster, 1971; Wethey, 1984; Power *et al*., 2011). In northern Europe, chthamaloids appear to be refugees on the upper shore (Wethey, 1984), surviving through necessary adaptations (Anderson, 1994) including tightly closing opercular plates (Foster, 1971) and solid wall plates (O'Riordan *et al*., 2010). Uppermost barnacle zones are dominated by *C. montagui,* while *C. stellatus* typically dominates in the mid shore (Power *et al*., 2006), although this pattern can vary locally, presumably owing to hydrographic differences associated with wave exposure (Pannaciuli and Relini, 2000).

For intertidal barnacles, the physiological challenges presented by highly fluctuating temperatures and desiccation stress during emersion (Power *et al*., 2011) may be less of an issue on the cool, wet, exposed shores of Orkney (Baxter *et al*., 1985). Local meteorological conditions may explain the extension of barnacle zones higher on the shore in Scotland than in the south of England (Kendall *et al*., 1982). Species occupying higher shore zones have to be more tolerant of high temperature especially in warmer southern areas (Southward, 1965). Processes contributing to vertical zone establishment have garnered considerable interest (e.g. Connell, 1961a; Wethey, 1984; Burrows *et al.*, 1992; Svensson *et al*., 2006) with many factors beyond temperature identified. Establishment of zones of *S. balanoides* and *Chthamalus* spp. might occur during larval

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[3] Much of the important groundwork in barnacles in northern European waters was conducted prior to the recognition of *C. montagui* as a separate species. As such, in many cases pioneering research was conducted on *C. montagui* but assigned to *C. stellatus*.

settlement or through post-settlement mortality: research in SW England suggests that larval settlement of *C. stellatus* and *C. montagui* follows existing adult distribution patterns (Jenkins, 2005); while studies of these same species in southern Ireland suggest zonation patterns are not established at settlement but through subsequent mortality (Power *et al*., 2006). Processes affecting settlement and recruitment between *S. balanoides* and *Chthamalus* spp. are dynamic with reproductive output occurring at different seasons. *S. balanoides* produces one brood which typically settle in spring; *Chthamalus* spp. produce multiple broods released over an extended period from summer into early autumn, although this becomes increasingly constricted at higher latitudes (Kendall and Bedford, 1987)[4]. Therefore, short-term climatic changes may preferentially affect one competitor more than the other, depending on timing relative to critical processes. Furthermore, through behaviour-mediated settlement processes such as gregariousness (Knight-Jones and Crisp, 1953) and competition for limited space resource (Roughgarden *et al*., 1985), recruitment may vary based on prior success or failure of the competitor species.

Semibalanus balanoides is found on rocky shores across a wide range of exposure levels. Within chthamaloid zones, *C. stellatus* tends to be more dominant on headlands and open, wave exposed shores (2-3 Ballantine scale; Ballantine, 1961), while embayments (3-6 Ballantine scale) tend to feature more *C. montagui* (Crisp *et al*., 1981). This relationship between chthamaloid species is seen on the coast of WMO where most sites are dominated by *C. stellatus* (1-2 Ballantine scale) with *C. montagui* found on the upper shores and on relatively lower energy sites (3-4 Ballantine scale) (see Chapter 3). High exposure and positioning relatively lower on the shore appears to favour reproductive

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[4] In Orkney, settlement of *S. balanoides* typically occurs in April; chthamaloid settlement is typically restricted to August and September (A. Want, pers. obs.).

success (in both brooding output and larval supply) of *C. stellatus* over *C. montagui* (Burrows *et al*., 1992). These differences may result from larger size and longer planktonic life which favours more oceanic distribution in *C. stellatus* (Burrows *et al*., 1999). It is anticipated that long-term changes in environmental forcing agents, such as wave exposure and temperature, will affect the abundance and vertical distribution pattern of barnacles on WMO. For organisms most associated with high energy environments, such as *C. stellatus*, extraction of wave energy will reduce abundance indicated by observable changes in recruitment, growth rates, and zonation. While overall density within the barnacle zone might remain constant (Power *et al*., 2011), with reduced exposure the barnacle zone would be expected to narrow and move down shore in the area immediately 'downstream' of WECs. The role played by *C. montagui* on wave-exposed WMO and how this might change with removal of wave energy is discussed later in this chapter (see 5.4.5 Energy extraction – *Chthamalus montagui*).

Temperature is the overriding factor controlling the latitudinal distribution of intertidal barnacles, mediated through competition and creating the observed geographic boundaries (O'Riordan *et al*., 2010; Jones, et al. 2012). *C. stellatus* and *C. montagui* are warm-water barnacles with similar distribution ranges as one another: south from the west coast of Africa to their poleward limit at the Northern Isles of Scotland (Southward, 2008). Moving northward along the Atlantic coast, several studies have identified delayed onset and reduced period of recruitment with higher latitudes (see O'Riordan *et al*., 1995, for review). In contrast, *S. balanoides* is a boreal, cold-water species with a range extending from Spitzbergen in the north towards a southern distribution across the English Channel to large parts of the Brittany coast before forming more isolated pockets on the Spanish Bay of Biscay (Southward, 2008). Orkney is very much in the 'middle' of latitudinal and temperature range of this species.

It is well established that a relationship exists between temperature events or trends and subsequent gains or losses in competitive barnacle species in the North Atlantic (Southward, 1967; Southward and Crisp, 1954a, 1956; Southward *et al*., 1991, 1995; Wethey *et al*., 2011). These studies support the general conclusion that cooler temperatures favour successes in *S. balanoides* at the expense of *Chthamalus* spp., while warmer temperatures favour successes in *Chthamalus* spp. at the expense of *S. balanoides*. There is not, however, a consensus on which seasonal temperature event is the greater driver in shifts in this competitive relationship. For example, regarding chthamaloids: Burrows *et al*. (1992) found that increased summer atmospheric temperature (AT) in SW England is associated with increased reproductive output (through prolonged release period and additional broods); while O'Riordan *et al*. (2012) reported that changes in reproductive output in Ireland were associated with failures owing to cold winters. Furthermore, recruitment success in *Chthamalus* may be largely driven by space availability following spring recruitment of *S. balanoides* (Poloczanska *et al*., 2008) (Figure 5.1.2). New recruits typically require two years to mature and begin contributing to the reproductive output of the population (Southward *et al*., 1991, 1995; Wethey *et al*., 2011). As such, the correlation between temperature and changes in barnacle population is strongest after including a phase lag (Southward *et al*., 1995), especially with chthamaloids (Poloczanska *et al*., 2008). In Orkney, at the northern distribution of *Chthamalus*, the relationship between temperature and barnacle zonation has not been studied in detail.

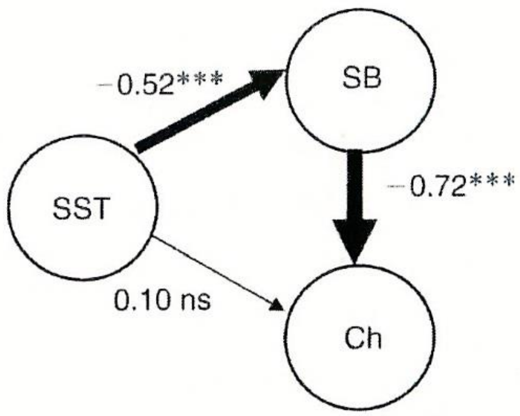

Figure 5.1.2: Path analysis used to reveal causal relationships between littoral barnacle abundances. ***, P<0.001; ns, not significant. From: Poloczanska *et al*. (2008).

Owing to sensitivity to changes in temperature, chthamaloid barnacles have been identified as potential indicators of climate change, (Southward *et al*., 1995; Hiscock *et al*. 2001, 2004; Poloczanska *et al*., 2008; Wethey *et al*., 2011). Extreme climatic events, such as the severe winter of 1962-1963 may have profound effects on the range and abundance of certain littoral rocky shore organisms (Crisp, 1964) and recent changes in geographic distribution of barnacles are associated with similar temperature fluctuations (Jones *et al*., 2012). Following analysis of rocky shore community data from Shetland, Burrows *et al*. (2002) described *S. balanoides* as a particularly valuable indicator of large scale environmental changes and additional studies of intertidal barnacles suggest associations with long-term oceanic cycling, such as the AMO (Mieszkowska *et al*., 2014).

5.1.1 Objectives:

While responses of littoral barnacle populations to changes in temperature are recognised, detailed studies have not been conducted in Orkney. The aim of this study is to explore recruitment towards the northern distribution limit of *Chthamalus* where population dynamics might be more readily observed. At range margins, populations may be more sensitive to changes in environmental factors which establish distribution. Furthermore, the interface between these two species may be a valuable indicator of environmental changes as the location of strongest competition (Connell 1961a; Foster, 1971). In this study, the term ‘recruits’ is used to describe juveniles in their first year, observed at a minimum of 4 months post-settlement. On the rocky shores of Orkney, the competitive zone between *S. balanoides* and *Chthamalus* spp. may provide a useful example of expected community change in response to wave energy extraction against a background of climatic change. With extraction of wave energy we might expect barnacle zones to become narrower and lower on the shore, as well as possible changes in species composition; there may be an increase in the proportion of *C. montagui* in the upper zone. Increases or decreases in temperature would be expected to favour reproductive success in *Chthamalus* spp. and *S. balanoides*, respectively, while the overall ‘guild’ of barnacles might remain constant. Methods developed here aim to capture changes in littoral zonation and provide a possible ‘short-cut’ to response detection through experiments involving removal of intact barnacle cover. Previous studies using clearance methods have been used to study settlement patterns in these barnacle species (Kendall and Bedford, 1987; Pannacciulli and Relini, 2000; Kent *et al.*, 2003; Jenkins, 2005). Observations of post-clearance recruitment might allow population dynamics to be followed more readily or earlier than studying only intact surfaces. In the present study, clearance occurred semi-annually giving each barnacle species the opportunity to settle with and without interspecies competition for space resource. To the best of my knowledge there have been no previous studies performing semi-annual clearance experiments specifically intended to allow observation of seasonal recruitment and the effects of resource competition between species, although modelling of a similar scenario has been simulated using recruitment data from *C. montagui* and *S. balanoides*, collected in Portugal and the Isle of Man, respectively (Svensson *et al.*, 2006). Comparisons between cleared and intact sites may illustrate the role of behaviour-mediated processes, such as gregariousness, during barnacle settlement.

5.1.2 Hypotheses:

The following hypotheses were tested which examine the role of environmental factors and interspecies competition in determining barnacle recruitment at the northern distribution limit of *Chthamalus* spp.:

-Temperature: changes in the zonal relationship between *Chthamalus* spp. and *S. balanoides* following acute fluctuations in temperature may be more readily observed at the northern distribution limit of *Chthamalus* spp. Previous studies suggest that observable responses are lagged by one or two years following the temperature event (Southward *et al*., 1995; Poloczanska et al., 2008; Wethey *et al*., 2011). The present study of littoral barnacles on exposed rocky shores (where wave energy may be extracted at an industrial-scale) aimed to explore recruitment responses following acute temperature events using a modified model of geographic distribution, based on temperature zonation (Hutchins, 1947). In this model, the following scenarios in barnacle populations are examined:

1. Cold winter: will result in decreased *Chthamalus* spp. and increased *S. balanoides*.
2. Warm winter: will result in decreased *S. balanoides* and increased *Chthamalus* spp.
3. Cold summer: will result in decreased *Chthamalus* spp. and increased *S. balanoides.*
4. Warm summer: will result in decreased *S. balanoides* and increased *Chthamalus* spp.

-Response detection: responses of barnacle populations to environmental change will be apparent on cleared surfaces before intact surfaces. Creation of additional free space will reduce resource competition allowing recruitment responses to be manifest more rapidly when compared with non-manipulated surfaces with less free space.

-Semi-annual clearances: recruitment of *Chthamalus* spp. onto cleared surfaces is dependent upon the timing of clearances relative to settlement of *S. balanoides*, and vice versa. Space availability for settlement is an obvious consideration when studying population dynamics in sessile marine organisms (Roughgarden *et al*., 1985). Clearing barnacle shores at semi-annual intervals, ahead of species-specific settlement periods, will provide each year cohort with the opportunity to settle onto surfaces with and without interspecific competition for space resource. Prior settlement by one barnacle species will reduce recruitment in the other species; while recruitment on to sites without prior settlement by the competitive species will be higher.

-Gregariousness: recruitment densities of juvenile barnacles will be affected by species-specific gregariousness at settlement. Contrasting recruitment between intact surfaces and those cleared (with and without interspecific competition for space resource) will provide evidence of settlement behaviour at the northern limit of chthamaloid distribution.

5.2 Methods:

As part of the background studies (Chapter 2: Site selection), Marwick Head was chosen as the primary site for barnacle studies. This site was considered most suitable for barnacle monitoring based on the following criteria:

- Occurrence of both major species (*C. stellatus* and *S. balanoides*) on the shore with a zone of overlap in their vertical distribution
- Few complex rock features: which might otherwise create small-scale deviations from typical zonation patterns
- Relative absence of other encrusting organisms
- Accessibility of the shore on foot

This shoreline features a lower zone dominated by *S. balanoides*, with lower to mid-level mixing with *C. stellatus*, and the latter species dominating from mid to higher portions of the shore. Within the barnacle-dominated zone are: frequent patellid limpets, patches of small *Mytilus edulis* (especially in clefts, depressions and empty barnacle shells), small tufts of *Corallina officinalis*, and, occasional juvenile fucoids. The barnacle predator *Nucella lapillus* is occasionally present on the open rock study areas during low-tide, but typically located on adjacent lee-ward faces and clefts. Within the barnacle zone, abundant *Melarhaphe neritoides* are typically found in empty barnacle shells and crevices. In addition to the mosaic of biological components, the barnacle zone also features frequent small patches of bare surface created by wave-driven impacts or removal by predators/grazers. This site is in close proximity to the proposed deployment of a large WEC array.

Identification of barnacle species is made by close observation of several features including the shape of the operculum and the ontogeny of the rostrum. Many of these features become less distinct in older individuals, as the shell plates tend to fuse, and in more ‘crowded’ populations where competition for space leads to modification in shell shape. However, the shape and sutures of the opercular plates are relatively conserved in crowded areas thereby remaining as a reliable identifier. Quadrats measuring 10 x 10 cm

(Minchinton and Scheibling, 1993; Pannacciulli and Relini, 2000) were photographed along vertical transects; a distinct reversal of dominant barnacle species was observed over a linear distance of about 120 cm – on the steep shore at Marwick (~13°) this translates to around 27 cm vertical height. This transition region is hypothesised to be of greatest potential value for paired species monitoring, as predicted population shifts between these organisms will be expected to be most observable here. This procedure was repeated at three rocky platforms at Marwick and served as the original focus for baseline and clearance studies.

5.2.1 Preliminary imagery and clearances:

Barnacle studies focused on photographic monitoring of triplicate intact and cleared columns on the rocky shore at Marwick. The procedure included:

- Placement of two reference screws representing higher and lower borders of the transition zone of dominance from balanoid to chthamaloid barnacles – approx. 120 cm in length (vertical interval of ~27 cm);
- Demarcating the column into 10 cm intervals using a scored string attached between reference screws;
- Photographic imagery (Canon EOS 50D with 50 mm lens) of the intact rock surface using 10 x 10 cm quadrats deployed at 20 cm intervals;
- Clearance of the imaged column (approx. 15 cm wide x 120 cm length) between the reference screws using a paint scraper and wire brush (Figure 5.2.1);
- Observation and semi-annual photographic imaging of subsequent barnacle recruitment.

Figure 5.2.1: Clearance at Marwick prior to *S. balanoides* settlement. 26 Feb. 2013.

This procedure was first trialled in March 2010 (before *S. balanoides* propagule settlement), under the SuperGen project prior to the current studentship. In March 2011, images were recorded for intact precleared surfaces and for strips cleared 12 months previous. Photographing cleared surfaces in March allows for approximately 7 months post-settlement growth of chthamaloids. This aids in image analysis because chthamaloids are much smaller at settlement than *S. balanoides* and typically grow much slower (Southward, 2008).

5.2.2 Field method improvements:

Under the PhD Studentship, the barnacle studies were continued but significant alterations were made following analysis of the images and advice from colleagues (see acknowledgements). Most significant was the addition of a second study shore at Northside in Birsay located about 8 km farther north and east, and orientated to the north-west (contrasting with the westerly orientated shore at Marwick) (Figure 2.1). Together, these sites were selected as representative of wave exposed northern rocky shore habitat (Lewis, 1964). Inclusion of an additional shore (with three subsites) allows two scaled hierarchical studies: between shores and sites within shores (Power *et al*., 2006). However, the time consuming nature of image analysis (see Section 5.2.3) has meant that with prioritisation of time resources under this PhD Studentship only data from Marwick have been fully explored. The archive of images from Birsay represents a resource for future work; comparisons of barnacles between shores will be completed when possible depending on available time and resources.

Additionally, clearance and photographic studies were expanded to include semi-annual assessment with removal of intact cover occurring prior to settlement period for both species, i.e. one clearance occurred in late winter prior to *S. balanoides* settlement, followed in mid-summer by another clearance prior to chthamaloid settlement. Georeferenced coordinates were obtained at high precision (<2 cm for z-axis) (Leica dGPSS) for the six study sites (Table 5.2.2).

C. montagui is present at Marwick but these were under-recognised in the earlier stages of the research. Subsequently, a more complete appreciation of this species has resulted in the observation that *C. montagui* contributes up to 9% of total barnacles within imaged parts of the Marwick research area. *C. stellatus* is clearly the most abundant mid-littoral chthamaloid but the presence of adult *C. montagui* and the difficulty in identification of juvenile chthamaloids from photographic images requires a broader identification label to be applied. Furthermore, because a large amount of highly labour-intensive image analysis had already been completed, a decision was made to describe all the intertidal barnacles in the research areas as either *S. balanoides* or *Chthamalus* spp.

Table 5.2.2: Georeferenced coordinates using OSGB36 at Marwick and Birsay including standard deviations (SD) referenced to Mean Sea Level. Note: consistent with greater wave exposure at Birsay, the competitive zone between barnacles is located considerably lower on the more sheltered shore at Marwick.

Barnacle Site	**Northing (m)**	**Easting (m)**	**Orthometric Height (m)**	**S.D. North**	**S.D. East**	**S.D. Height**
Marwick North – Upper	1024491.087	322508.2866	0.3537	0.0014	0.0017	0.0008
Marwick North - Lower	1024490.937	322506.9383	-0.0106	0.0014	0.0017	0.0008
Marwick Middle - Upper	1024479.077	322511.6978	0.2213	0.0128	0.0071	0.0211
Marwick Middle - Lower	1024478.949	322509.9309	-0.1717	0.0006	0.002	0.0007
Marwick South – Upper	1024470.981	322513.7268	0.0374	0.0009	0.0018	0.0006
Marwick South - Lower	1024471.048	322512.3962	-0.2739	0.0009	0.0019	0.0006
Birsay West – Upper	1028828.949	325413.5382	1.3759	0.0032	0.0023	0.0067
Birsay West – Lower	1028830.293	325413.2894	1.1968	0.0025	0.002	0.0054
Birsay Middle – Upper	1028847.776	325418.1241	0.8851	0.0037	0.0026	0.0076
Birsay Middle – Lower	1028848.951	325417.341	0.5585	0.004	0.0027	0.0081
Birsay East- Upper	1028839.897	325423.0311	0.6323	0.0042	0.0029	0.0084
Birsay East – Lower	1028840.781	325422.2819	0.3697	0.004	0.0028	0.0081

5.2.3 Image analysis:

Quadrat images were electronically labelled and converted to bitmap files. Percentage abundance cover was determined using ‘Barnacle Bell’. Images were analysed for *S. balanoides*, *Chthamalus* spp., and other contributing species including the animals *Mytilus edulis* and *Patella* spp., with infrequent *Nucella lapillus* and *Actinia equina*; algae included *Corallina officinalis, Fucus vesiculosus* f. *linearis*, *Himanthalia elongata* and others. Graphs of percentage cover of individual classes are presented in Figures 5.3.1.1-2. A further ‘species’ contribution was quantified as ‘unclassifiable barnacle’; owing to inevitable issues of image resolution, depth of field limits, shadowing and visual obstructions, a small percentage of individual barnacles could not be reliably assigned to either *S. balanoides* or *Chthamalus* spp. The overall contribution to percentage cover of ‘unclassifiable’ barnacles over the full suite of pre-clearance quadrat images analysed (n=48) was 0.78%. Owing to practicalities of time and research focus, abundance cover of *Melarhaphe neritoides* was not recorded. A review table of ‘other’ contributing organisms is provided below in Table 5.3.1. In addition to percentage cover, a total individual barnacle count of each species was tallied during the analysis of each quadrat image. Abundance and count allowed the determination of mean barnacle size which may serve as a convenient estimate of typical age and as a proxy for recruitment success. Proportions between barnacle species were determined for count, percentage cover and mean size data; a ‘Barnacle Index’ was determined as the proportion of *Chthamalus* spp. to all barnacles (Southward *et al*., 1995).

Field imaging is a balance between collecting sufficient data to characterise the shore and subsequent labour-intensive analysis. Data collection should be broad enough to capture stochastic patchiness owing to periodic disturbances (in the case of barnacles, presumably through predation, recruitment failure or large sediment impacts). While the analysis method developed here successfully allows quantified assessment of the biological assemblage within the study area, the amount of time necessary to process one image was discovered to be too great to allow complete analysis of all images. For example, preclearance images taken at Marwick in the summer of 2013 required identification, counting and percentage cover determination of up to 1600 barnacles/quadrat. After the initial baseline images were analysed for the entirety of the study columns at Marwick, it was decided to focus image analysis on one upper and one lower quadrat per strip. Each of the three study sites within Marwick had been positioned on discrete rock platforms delineated by edges, steps or rock pools located in close proximity (typically within a metre) above and below. Upon careful observation of the positioning it was decided to focus the image analysis on two quadrats separated linearly by 60 cm, one above the other. This still allowed sufficient vertical difference (approx. 13 cm) to demonstrate a transition in barnacle distribution between the species, while also restricting the analysis to more central portions of the site and away from potential complicating influences of changing topography towards the edges of the platforms.

Image analyses of the barnacle areas remains highly labour-intensive but with the reduced subset of quadrats, all baseline strips, i.e. preclearance, have been quantified for Marwick. This includes: annual assessment of late-winter rocky shores from 2011-2015 and semi-annual assessment each late-winter and midsummer from late-winter 2012 to late-winter 2015 at Marwick. Image collection and clearance experimentation have continued in summer 2015 and through 2016; owing to time restriction of the studentship, these data are not yet analysed. A ‘library’ has been developed for the following images of each site:

- Intact, i.e. preclearance, recorded semi-annually.

- After approximately 6 months following clearance, when only one of the competitive barnacle species has had the opportunity to settle. Semi-annually, the order of which species has the ‘clean-slate’ to settle upon is reversed.
- After approximately 12 months following clearance, when both barnacle species have had the opportunity to settle. Semi-annually, the order of which species settles first and which follows is reversed.
- After approximately 18 months following clearance, when both barnacle species have had the opportunity to settle once and one of the species has had a second settlement season (Figure 5.2.3). Semi-annually, the order of which species settles first and which follows is reversed.
- This pattern has been repeated at Marwick since February (late-winter) 2012. Therefore at the most recent sampling, images were captured on intact barnacle shore, as well as surfaces previously cleared at 6, 12, 18, 24, 30, 36, 42, and 48 month intervals.
- Priority has been placed on analysing intact and 12-month post-clearance quadrats (Section 5.2.6). Other time intervals have been captured but not yet analysed.

Figure 5.2.3: Quadrat (10 x 10 cm), Marwick: 18 months post-clearance (summer 2014: prior to *Chthamalus* settlement). This image features: two year cohorts of *Semibalanus balanoides* - larger ‘beige’ individuals (approx. 16 months post-metamorphosis) and numerous small ‘white’ individuals (approx. 4 months post-metamorphosis); and one year cohort of *Chthamalus* spp. – less numerous small ‘tan’ individuals (approx. 11 months post-metamorphosis).

5.2.4 Image analysis alternatives:

Additional labour-saving approaches have been considered which attempt to minimise analysis time by creating subsets of image data. In all cases, these were tested using images of known barnacle abundance percentages and individual counts. Assigning random sample points for analysis was considered. In this approach, any number of random sample points on the image can be generated followed by classification of the sample into different ‘species’ (Table 5.3.1.2). This approach is based on previously described methods which have been effectively used to determine percentage cover

(Minchington and Scheibling, 1993; Menge, 2000). However, because individuals differ in size, the probability of being 'hit' by a random point is not consistent, and thus it does not allow for tallying individual counts. Therefore, neither count nor average size can be determined without returning to the original method. While time is saved by providing an estimate for percentage cover, the reliance on onerous counting necessary to compare populations of juvenile and adult barnacles meant that this approach was trialled but ultimately dismissed.

A second strategy was considered and software created to allow the user to subdivide images into any number of grid squares and for the random selection of a subsample of grid squares to be analysed for both percentage cover and individual counts. Tests were performed on previously analysed images divided into 16 grid subsamples (Figure 5.2.4). All subsamples were analysed using the original method; subsequent 'pooling' of the 16 subsamples produced results similar to the original whole analysis. Boot-strapping was performed on this data set using 3, 4, 6 and 8 subsamples (run 1000 times for each subsample size) to examine the extent to which different levels of subsampling were able to give results that were representative of the image as a whole. While the results were encouraging (Table 5.3.1.3), this method was ultimately not used; after further analysis of intact barnacles, preferential labour saving strategies were implemented (see Section 5.2.5).

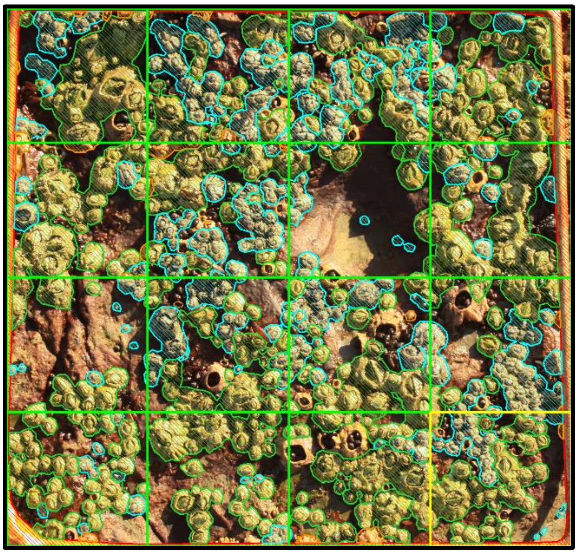

Figure 5.2.4: Tests were performed to determine if labour-saving alternatives could produce sufficiently accurate estimates of count and percentage cover. Estimates were determined by analysing varying subsets of quadrat images.

5.2.5 Analysis of intact barnacle population using quadrat images:

Count data would be expected to display Poisson or lognormal rather than normal distribution (Townend, 2002). Log-transformed count data, percentage cover data, and mean size data from upper and lower shore quadrats of intact barnacles sites at Marwick were plotted from winter 2012 until summer 2015 (winter 2015 for count data) and tested using analysis of variance (ANOVA) for three factors: year, season and shore height, as well as first order interactions between factors. Year was defined as the combination of two semi-annual observations of the same recruitment cohorts, i.e. in *Chthamalus* spp., winter$_1$ and summer$_1$; in *S. balanoides*, summer$_1$ and winter$_2$.

ANOVA was conducted using generalised linear modelling (GLM) procedures in Minitab 17 (Minitab, 2010). Parsimonious models were generated using backward elimination of factors ($\alpha = 0.1$). To constrain values to feasible limits during analysis, all proportional data (*P*) (e.g. 'Barnacle Index') were logistically transformed prior to ANOVA using the following formula:

$$Logit(P) = \ln\left(\frac{P}{1-P}\right)$$

GLM of preliminary data on intact rocky shores showed that seasonal variance could be captured using count data as effectively as using percentage cover data. As a general statement, the same factors were identified in modelling count and percentage cover data but with lower P-values and higher coefficients of determination for each factor in count models (Tables 5.3.2.1-4 in Results). The onerous task of image analysis necessary to determine percentage cover was therefore eliminated in favour of the more efficiently-determined metric of raw count. Analysis of intact shores beyond summer 2014 and on all post-clearance images was based on count data alone.

5.2.6 Analysis of post-clearance barnacle population using quadrat images:

A decision was made to prioritise analysis of images captured 12 months post-clearance to compare against intact quadrats. This allowed the opportunity for both species to contribute one annual recruitment season. Furthermore, because data collection occurred at approximately 6-month intervals, the order of settlement between chthamaloids and *S. balanoides* is reversed at each sampling event. In other words, every 6 months each species is given the first opportunity to settle onto a cleared rock surface – almost literally, a ‘clean slate’. Intact populations were re-analysed following assignment into two age cohort groups based on size and condition of shell: juvenile (<12 months old) and adult barnacles (>12 months). Separation into cohorts allowed comparison of recently cleared quadrats (which contain only juveniles) with intact populations of juveniles and to distinguish recruitment from persistence.

5.2.7 Analysis of barnacle and meteorological data:

Examination of several years AT cycles revealed average summer highs and winter lows occurring in approximately the first week of August and February, respectively (Figure 2.3.2). Using daily mean values, seasonal AT indices were determined for mean, upper (95 percentile) and lower (5 percentile) from mid-June to mid-September (summer) and mid-December to mid-March (winter). Examination of several years SST cycles revealed a lag response when compared with AT with average summer highs and winter lows occurring in approximately mid-September and mid-March, respectively (Figure 2.3.1). Using daily mean values seasonal SST indices were determined for mean, upper (95 percentile) and lower (5 percentile) from August to October (summer) and February to April (winter).

The relationship between recruitment count data and lagged temperature indices was tested by modifying GLMs previously created to explore the experimental factors of year, season and height (see Section 5.2.5). Temperature indices (mean, upper and lower SST, and mean, upper and lower AT) were substituted for year factor and correlation coefficients were calculated semi-annually for each sampling period back to 3 years prior to determine if correlations with SST and AT data might improve with lagging, based on previous studies. Modified GLMs were compared with original GLMs by F-test.

5.3 Results:

5.3.1 Preliminary results of intact (pre-cleared) barnacle zones:

Percentage cover values were plotted against time from winter 2012 to summer 2014 at Marwick (Figures 5.3.1.1 and 5.3.1.2). Unclassified percentage cover is referred to on the graphs below as 'free-space'. While unclassified 'free-space' is mostly bare rock suitable for larval settlement, this component also includes empty barnacle shells, and a small, mobile contribution of unevaluated *Melarhaphe neritoides*. Temporal variation is clearly evident with seasonal fluctuations in percentage cover. On the rocky shores of southern Ireland, Power *et al* (2011) found the cover of the guild of barnacles to be typically around 70%. On the wave exposed shores of WMO, the cover of intact barnacle areas averaged 53% (n=48 analysed quadrats).

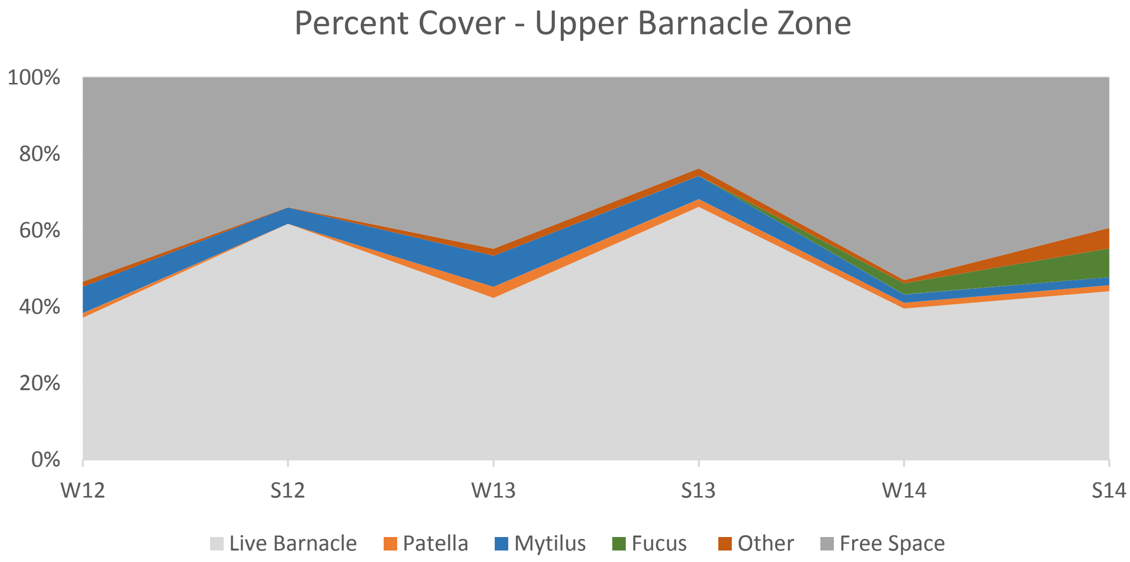

Figure 5.3.1.1: semi-annual percentage cover of intact upper barnacle transition zone of Marwick from winter 2012 (W12) - summer 2014 (S14) (mean of 3 sites). 'Other' includes additional algal and animal species.

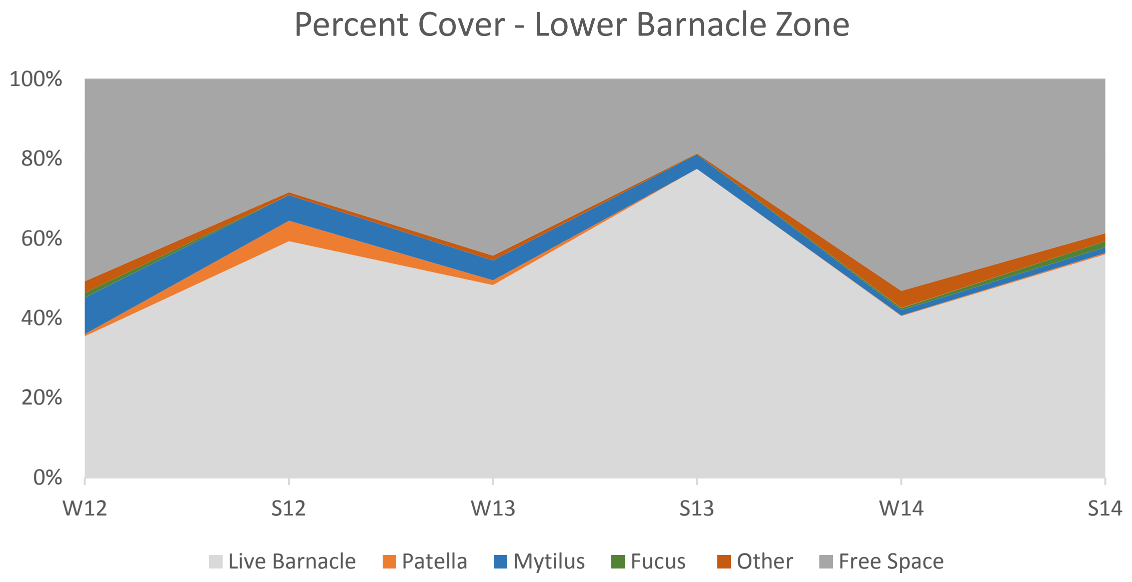

Figure 5.3.1.2: semi-annual percentage cover of intact lower barnacle transition zone of Marwick from winter 2012 (W12) - summer 2014 (S14) (mean of 3 sites). 'Other' includes additional algal and animal species.

Images of intact barnacle communities reveal a patchwork containing clusters of densely packed adults, open rock surfaces and recently settled juveniles. In addition to barnacles, the most common organism was *Mytilus edulis*, found in all but one baseline quadrat (Table 5.3.1.1). Less abundant, but still present in most quadrats were patellid limpets. Other fauna represented in analysed images in descending order of percentage cover were: *Nucella lapillus*, *Actinia equina*, and *Idotea* spp. The most common floral component were juvenile *Fucus* spp. Other flora represented in analysed images in descending order of percentage cover were: *Corallina officinalis*, 'Red Turf', *Mastocarpus stellatus*, *Osmundea* spp., *Himanthalia elongata*, *Palmaria palmata*, *Lomentaria articulata*, *Nemalion helminthoides*, and *Porphyra umbilicalis.*

Attempts to reduce labour-intensive image analysis included trialling percentage cover estimations using random sample point assignments and extrapolation from subsamples of whole images. As expected, percentage cover estimation based on identifying sample points improved with greater number of assigned points (Table 5.3.1.2). Extrapolation from subsamples of the total image resulted in little improvement in percentage cover estimation with greater subsample number. However, increasing subsample size led to more precise estimation (lower CV) (Table 5.3.1.3).

Table 5.3.1.1: major non-barnacle components in the barnacle shore at Marwick. Percentage cover is the mean contribution of each organism to baseline images (n = 48); percent presence refers to presence/absence from all baseline images.

Species	**% cover**	**% presence**
Mytilus edulis	4.66	98
Patella spp.	1.25	63
Fucus spp.	0.83	17
Nucella lapillus	0.08	29

Table 5.3.1.2: Mean percentage cover estimation using randomised sample points. Actual percentage cover of class abundances from a representative image (Marwick NE100 20130226) were compared with multiple random generations (n = 5) of varying sample points (10, 50, 100 and 200 per image).

Class	Actual %	10	50	100	200
A	4.21	0.00	1.60	4.20	3.41
B	37.88	36.22	38.00	41.60	38.94
C	0.62	2.00	0.00	0.60	0.80
D	40.09	43.32	41.20	37.00	39.04
E	17.20	18.44	19.20	16.60	17.82

Table 5.3.1.3: Mean percentage cover estimation using subsamples of quadrat image. Previously analysed image was divided into 16 grids. Actual percentage cover of full image was compared with results determined through subsamples of grids. Bootstrapping was performed on these data using 3, 4, 6 and 8 random pooling of subsamples (run 1000 times for each subsample size). SD, standard deviation; CV, coefficient of variation.

Class	Actual %	3	4	6	8
S. balanoides %	40.74	41.24	40.65	40.62	40.58
SD		7.84	6.53	5.61	4.66
% CV		19.00	16.08	13.81	11.49
Chthamalus spp. %	17.50	17.47	17.67	17.52	17.48
SD		6.87	6.06	5.07	4.28
% CV		39.34	34.28	28.94	24.48

5.3.2 Graphing preliminary results of intact (pre-cleared) barnacle zones:

Quadrat images of three intact barnacle sites on the rocky shores at Marwick and Birsay were recorded semi-annually at higher and lower locations within the zone of transition between *S. balanoides* and *Chthamalus* spp. Winter images were captured in February or March, prior to the settlement of *S. balanoides* larvae; summer images were captured in July, prior to chthamaloid larval settlement. Overall, there is clear evidence that the experimental study areas represent a transition zone between these species. In general, there was a higher count of *Chthamalus* spp. on the upper shore than the lower shore. Based on the known distribution relative to *S. balanoides*, this is an expected result. Results of individual count, percentage cover and average size are presented below with standard error bars. In addition, ANOVA is also presented below derived from GLM of three factors: year, season and shore height, as well as first order interactions between factors.

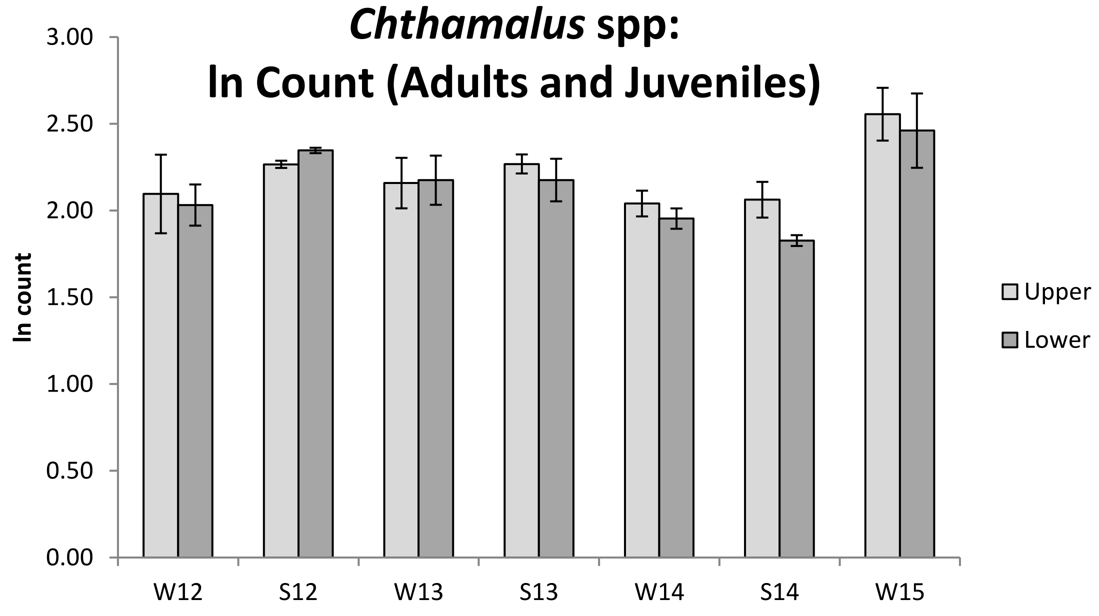

Fig. 5.3.2.1: *Chthamalus* spp. Semi-annual count data (log-transformed) of intact shores at Marwick, WMO from winter 2012 (W12) to winter 2015 (W15); summer represented by (S). Each bar represents mean of 3 sites (± S.E.).

For chthamaloid barnacles on intact shores at Marwick, there appears to be a trend towards overall decrease in count from summer 2012 until summer 2014; this trend reverses at winter 2015 (see Figure 5.3.2.1). ANOVA applied to *Chthamalus* spp. count data from W12-W15 revealed a highly significant effect between years ($R^2 = 0.505$; Table 5.3.2.1). A seasonal trend is not apparent.

Table 5.3.2.1: Final GLM for *Chthamalus* spp. (adults and juveniles) log-transformed count at Marwick from winter 2012 – winter 2015.

Source	df	SS	MS	*F*-value	*P*-value
Year	4	1.6939	0.42347	10.96	<0.001
Error	43	1.6618	0.03865		
Total	47	3.3557			

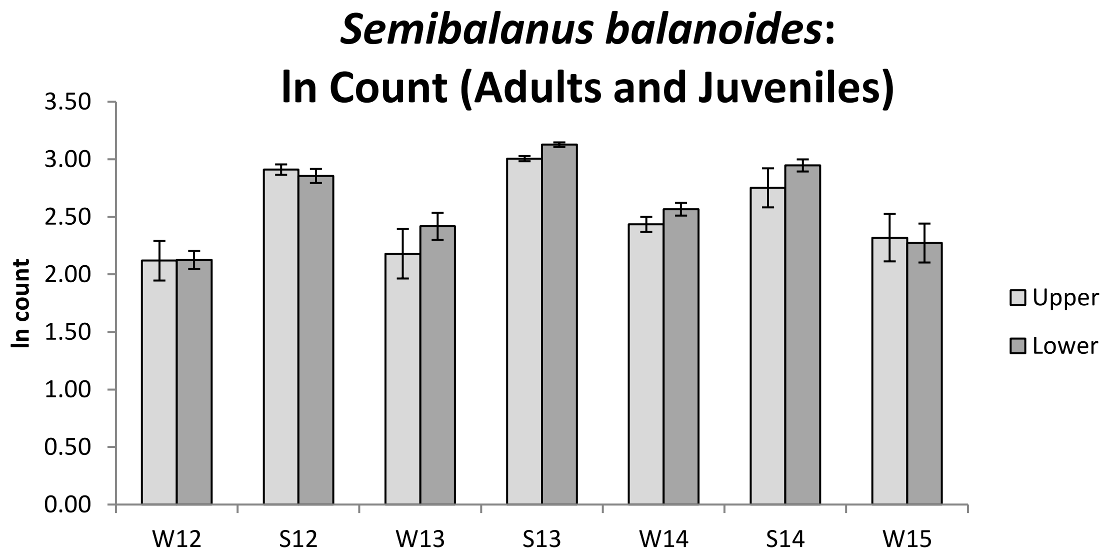

Fig. 5.3.2.2: *Semibalanus balanoides.* Semi-annual count data (log-transformed) of intact shores at Marwick, WMO from winter 2012 (W12) to winter 2015 (W15); summer represented by (S). Each bar represents mean of 3 sites (± S.E.).

For *S. balanoides* on intact shores at Marwick, a strong seasonal trend is apparent where total counts observed are much greater in the summer compared with the winter. With the settlement of *S. balanoides* in the spring, this is an expected result. There appears to be a trend towards overall increase in *S. balanoides* count from W12 until W14. The highest counts were observed on the lower shore in summer 2013. No obvious difference is apparent in trends associated with upper versus lower shore populations of *S. balanoides* (see Figure 5.3.2.2). GLM of *S. balanoides* count data from W12-W15 produced a final (most parsimonious) model using the factors of season and year ($R^2 = 0.748$). Season and year were highly significant factors (Table 5.3.2.2).

Table 5.3.2.2: Final GLM for *S. balanoides* (adults and juveniles) log-transformed count at Marwick from winter 2012 – winter 2015.

Source	df	SS	MS	*F*-value	*P*-value
Year	3	0.5070	0.16899	4.32	0.010
Season	1	2.9003	2.90033	74.07	<0.001
Error	43	1.6838	0.03916		
Total	47	6.6684			

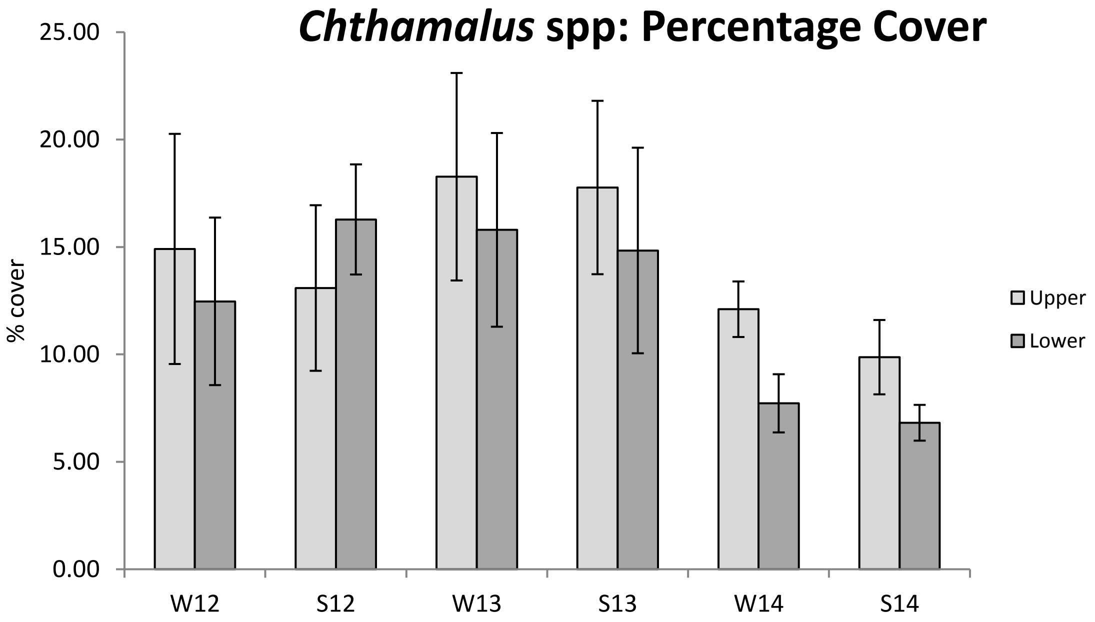

Fig. 5.3.2.3: *Chthamalus* spp. Semi-annual percentage cover on intact shores at Marwick, WMO from winter 2012 (W12) to summer 2014 (S14). Each bar represents mean of 3 sites (± S.E.).

For chthamaloid barnacles on intact shores at Marwick, there appears to be a decrease in percentage cover recorded in 2014 compared with 2013. Compared with count data, there appears to be a greater difference in percentage cover between upper versus lower populations, but this is not statistically significant (see Figure 5.3.2.3). ANOVA applied to *Chthamalus* spp. percentage cover data from W12-W15 revealed a highly significant effect between years ($R^2 = 0.319$; Table 5.3.2.3). A seasonal trend is not apparent.

Table 5.3.2.3: Final GLM for *Chthamalus* spp. (adults and juveniles) percentage cover at Marwick from winter 2012 – winter 2015.

Source	df	SS	MS	*F*-value	*P*-value
Year	3	690.1	230.02	5.92	0.002
Error	38	1475.7	38.83		
Total	41	2165.8			

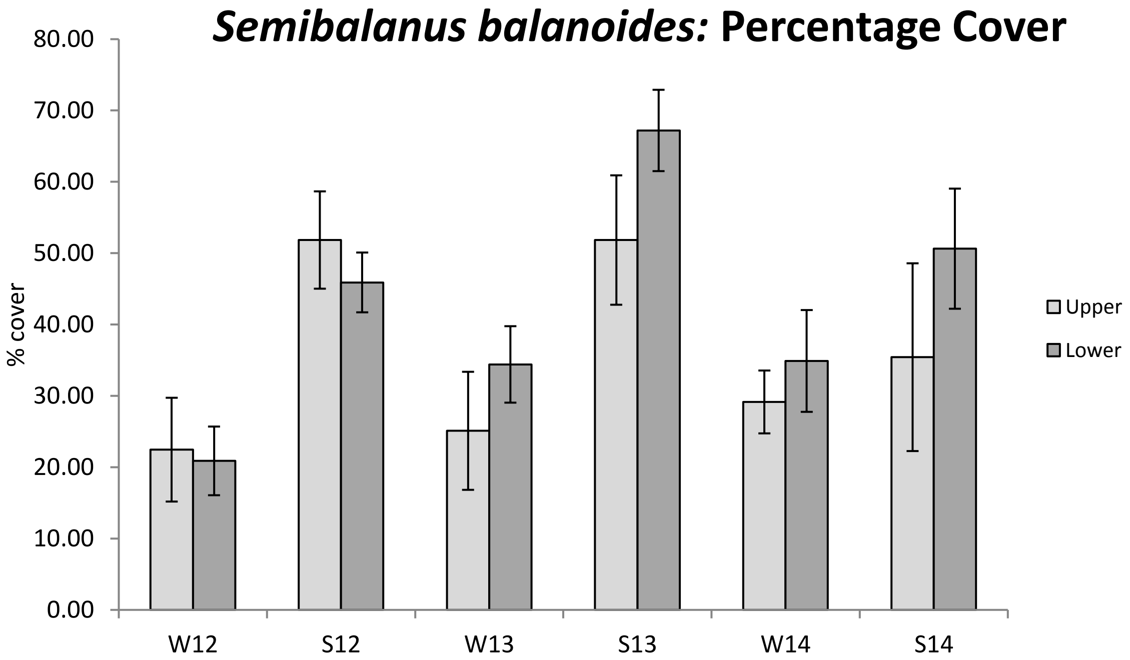

Fig. 5.3.2.4: *Semibalanus balanoides.* Semi-annual percentage cover on intact shores at Marwick, WMO from winter 2012 (W12) to summer 2014 (S14). Each bar represents mean of 3 sites (± S.E.).

For *S. balanoides* on intact shores at Marwick, a strong seasonal trend is apparent where percentage cover is much greater in the summer compared with the winter. With the settlement of *S. balanoides* in the spring, this is an expected result. There appears to be a trend towards overall increase in winter percentage cover of *S. balanoides* from 2012 to 2014; percentage cover in summer appears to 'peak' in 2013 (see Figure 5.3.2.4). ANOVA applied to *S. balanoides* percentage cover data from W12-W15 revealed a highly significant effect of seasonality ($R^2 = 0.445$; Table 5.3.2.4).

Table 5.3.2.4: Final GLM for *S. balanoides* (adults and juveniles) percentage cover at Marwick from winter 2012 – winter 2015.

Source	df	SS	MS	*F*-value	*P*-value
Season	1	5154	5153.8	32.06	<0.001
Error	40	6430	160.7		
Total	41	11584			

Generalised linear modelling of count and percentage cover data produced similar models for both barnacle species but with greater significance and confidence in count-based models. These data helped inform the decision to focus future image analysis on count only (see Section 5.2.5).

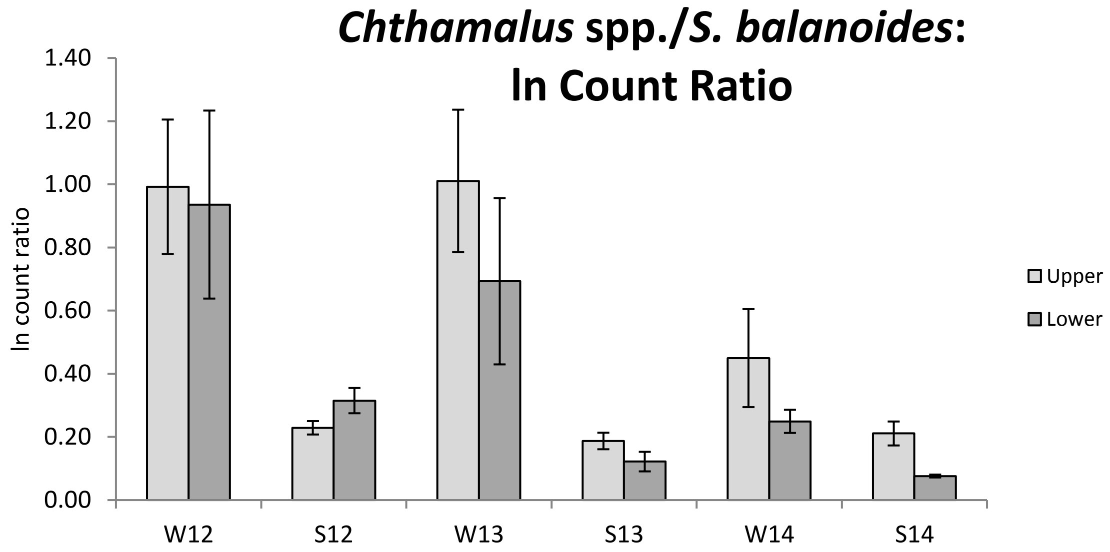

Fig. 5.3.2.5 semi-annual proportion of *Chthamalus* spp. to *S. balanoides* count data on intact shores at Marwick, WMO from winter 2012 (W12) to summer 2014 (S14). Each bar represents mean of 3 sites (± S.E.).

There is a strong seasonal relationship between relative abundance of *Chthamalus* spp. and *S. balanoides* based on count data and percentage cover (see Figures 5.3.2.5 and 5.3.2.6). This is expected owing to large recruitment of juvenile *S. balanoides* in summer followed by subsequent die-off. There appears to be an annual trend towards a lower proportion of *Chthamalus* spp. to *S. balanoides*. This is consistent with an overall decrease observed in chthamaloid population during this time-series.

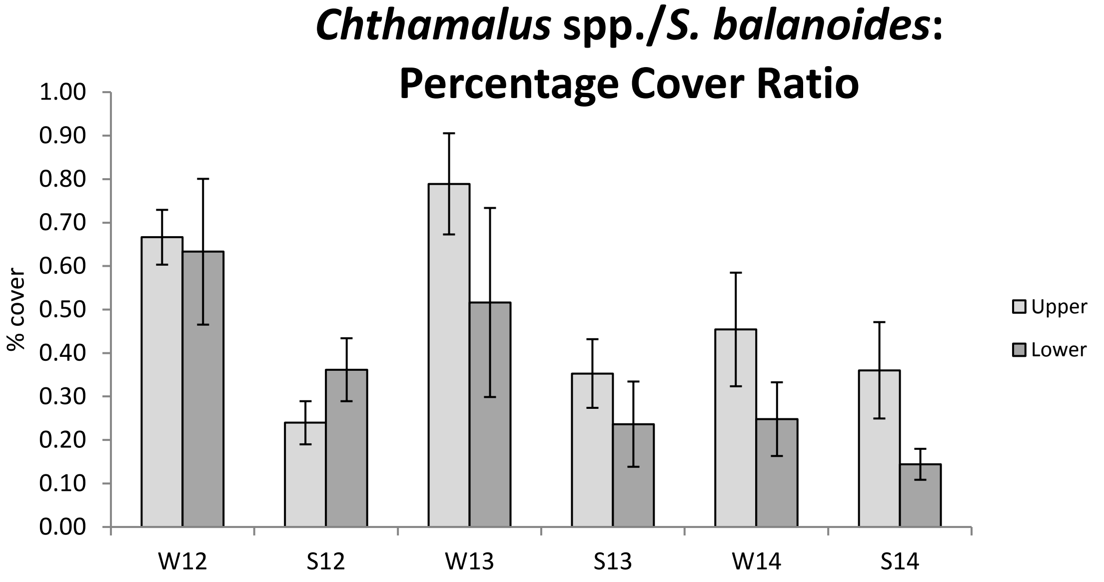

Fig. 5.3.2.6: semi-annual proportion of *Chthamalus* spp. to *S. balanoides* percentage cover on intact shores at Marwick, WMO from winter 2012 (W12) to summer 2014 (S14). Each bar represents mean of 3 sites (± S.E.).

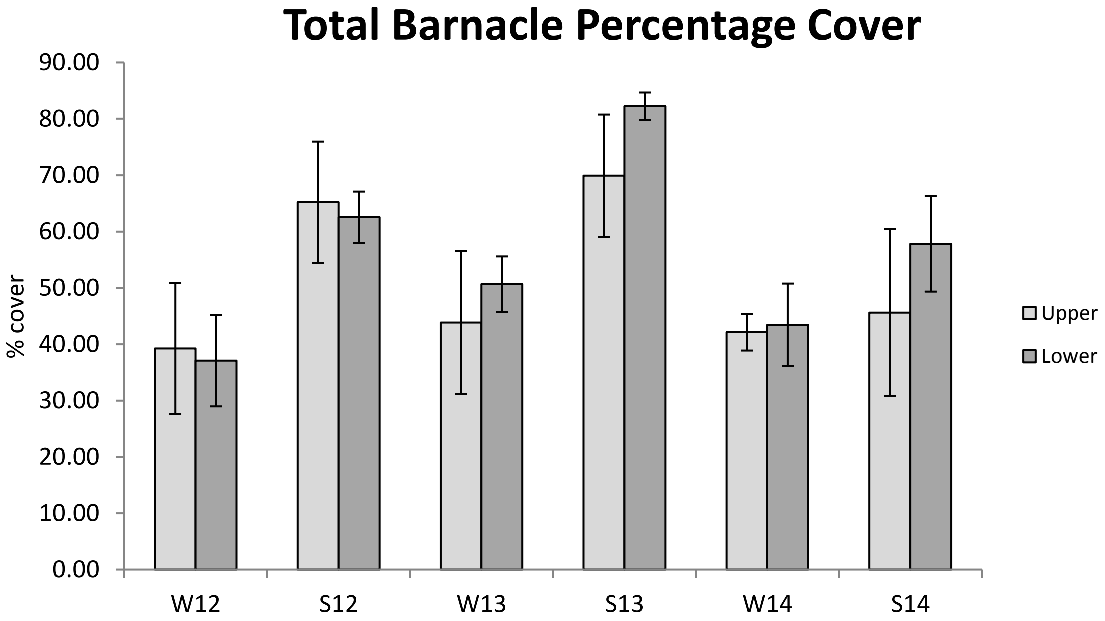

Fig. 5.3.2.7: semi-annual percentage cover of live barnacles (all species) on intact shores at Marwick, WMO from winter 2012 (W12) to summer 2014 (S14). Each bar represents mean of 3 sites (± S.E.).

As a general statement, there does not appear to be a difference in total barnacle cover in the upper versus lower shores (see Figure 5.3.2.7). A seasonal trend is apparent where total percentage cover is greater in the summer compared with the winter. With the large settlement of *S. balanoides* observed in the spring, this is an expected result. While there are the clear spikes in total percentage cover (i.e. S13) there is not an obvious annual trend in total barnacle percentage cover.

5.3.3 Results of barnacle counts separated into adult and juvenile on intact (pre-cleared) shores:

Note: the intact shore graphs plotted below are using the same data as the preliminary graphs above (Section 5.3.2) except that the population count of each barnacle species has been separated into adult and juveniles.

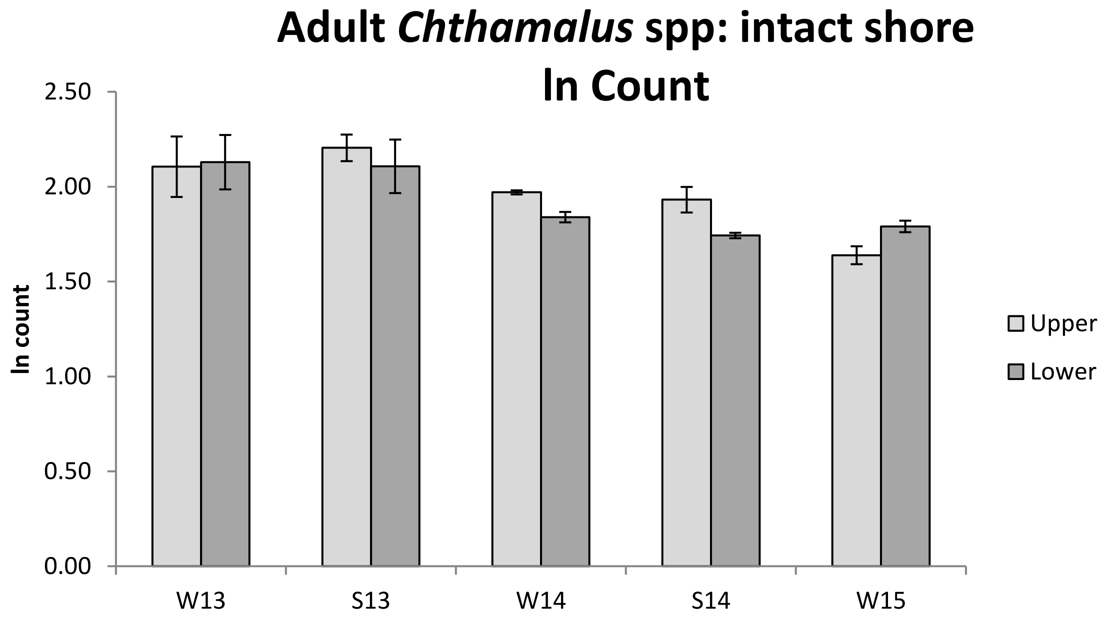

Fig. 5.3.3.1: *Chthamalus* spp. Semi-annual count data (log-transformed) of adult barnacles on intact shores at Marwick, WMO. Each bar represents mean of 3 sites (± S.E.).

For adult chthamaloid barnacles on intact shores at Marwick, there appears to be a trend towards overall decrease in count from winter 2013 to winter 2015 (see Figure 5.3.3.1). This trend does not appear to affect one shore height more than the other and a seasonal trend is not apparent. ANOVA applied to *Chthamalus* spp. adult count data from W13-W15 revealed a highly significant effect between cohort years ($R^2 = 0.569$; Table 5.3.3.1).

Table 5.3.3.1: Final GLM for adult *Chthamalus* spp. log-transformed count on intact shores at Marwick from winter 2013 – winter 2015.

Source	df	SS	MS	*F*-value	*P*-value
Year	2	0.8243	0.41215	17.84	<0.001
Error	27	0.6236	0.02310		
Total	29	1.4479			

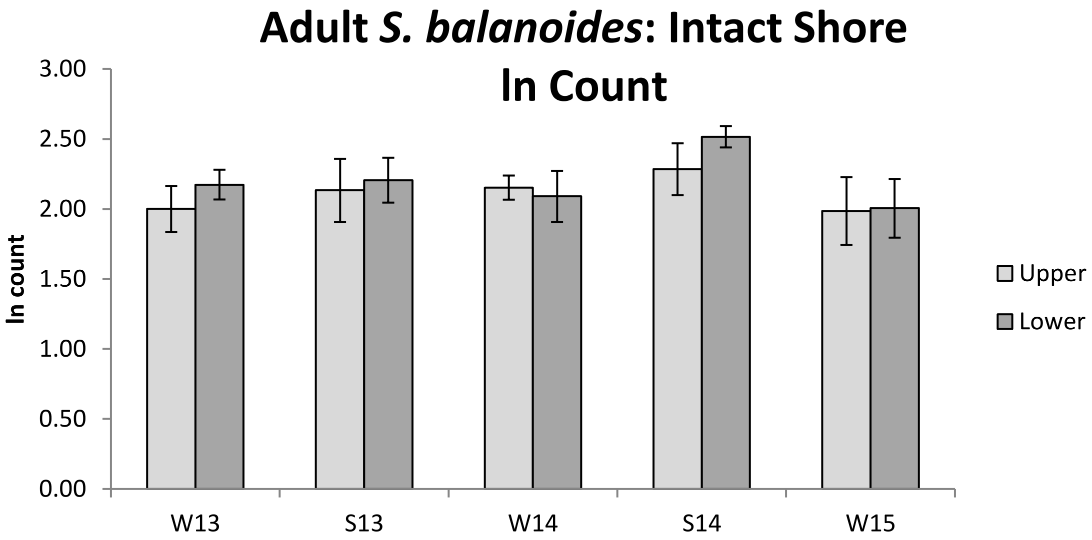

Fig. 5.3.3.2. *Semibalanus balanoides.* Semi-annual count data (log-transformed) of adult barnacles on intact shores at Marwick, WMO. Each bar represents mean of 3 sites (± S.E.).

For adult *S. balanoides* on intact shores at Marwick, there does not appear to be an annual population trend, although there is an increase in adult count in summer 2014 which is most apparent in the lower shore (see Figure 5.3.3.2). Following removal of juvenile count from the data, comparison of seasonal data for *S. balanoides* is no longer highly significant ($R^2 = 0.136$; Table 5.3.3.2).

Table 5.3.3.2: Final GLM for adult *S. balanoides* log-transformed count on intact shores at Marwick from winter 2013 – winter 2015.

Source	df	SS	MS	*F*-value	*P*-value
Season	1	0.3376	0.33763	4.43	0.045
Error	28	2.1362	0.07629		
Total	29	2.4739			

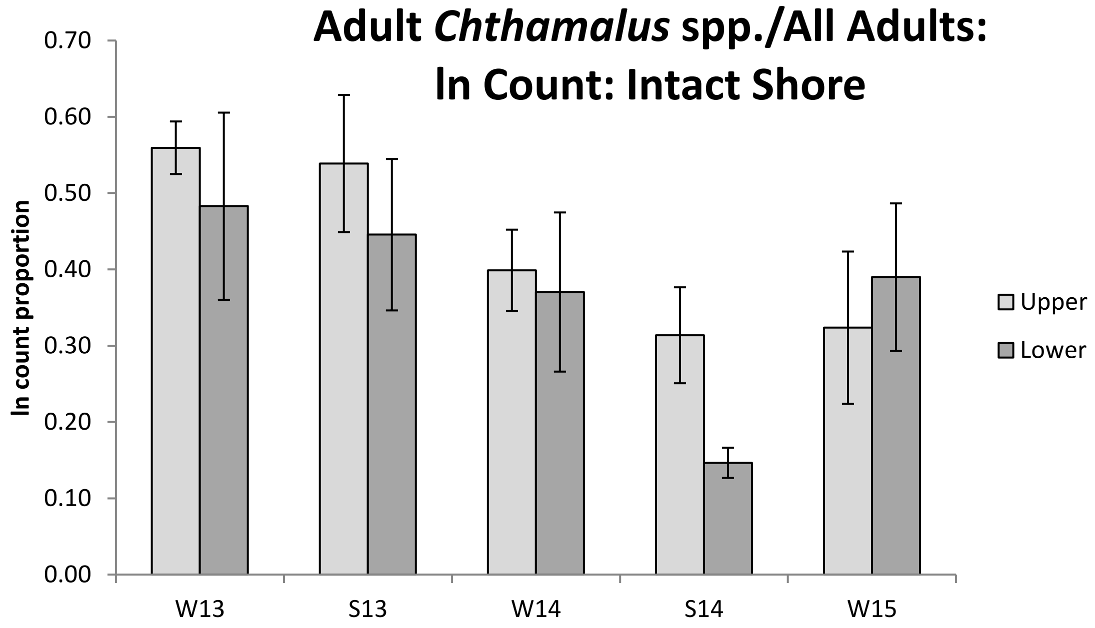

Fig. 5.3.3.3: Semi-annual proportion of adult *Chthamalus* spp. to all adult barnacle count data (i.e. Southward's Barnacle Index) on intact shores at Marwick, WMO. Each bar represents mean of 3 sites (± S.E.).

Proportion of count data between barnacle species (Barnacle Index) shows an overall decrease in adult *Chthamalus* spp. relative to *S. balanoides* from winter 2013 until summer 2014; the decreasing trend is especially evident in summer 2014. This is consistent with an overall decrease observed in chthamaloid population during this time-series. The Barnacle Index on the lower shore at winter 2015 reverses this trend (see 5.3.3.3). ANOVA applied to the Barnacle Index from W13-W15 revealed a significant effect between years ($R^2 = 0.303$; Table 5.3.3.3). A seasonal trend is not apparent.

Table 5.3.3.3: Final GLM for adult 'Barnacle Index' (*Chthamalus* spp./total barnacle) using logistically transformed proportion of counts on intact shores at Marwick from winter 2013 – winter 2015.

Source	df	SS	MS	*F*-value	*P*-value
Year	2	0.9885	0.49423	5.86	0.008
Error	27	2.2781	0.08437		
Total	29	3.2666			

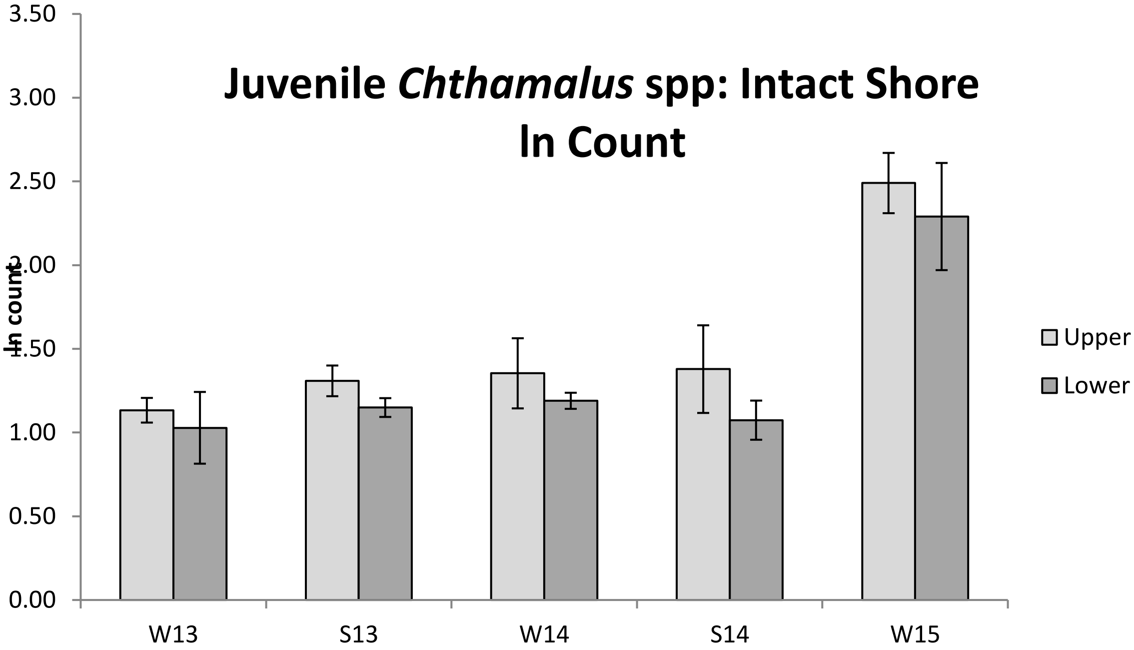

Fig. 5.3.3.4: *Chthamalus* spp. Semi-annual count data (log-transformed) of juvenile barnacles on intact shores at Marwick, WMO. Each bar represents mean of 3 sites (± S.E.).

For juvenile chthamaloid barnacles on intact shores at Marwick, there is a clear increase in counts observed in both upper and lower shore populations in winter 2015 (see Figure 5.3.3.4). Between winter 2013 and summer 2014, juvenile counts of *Chthamalus* spp. appears consistent. GLM of juvenile *Chthamalus* spp. count data from W13-W15 produced a final (most parsimonious) model using the factors of year and shore height (R^2 = 0.776). Year factor was highly significant; shore height factor was approaching significance (Table 5.3.3.4). No seasonal trend is apparent.

Table 5.3.3.4: Final GLM for juvenile *Chthamalus* spp. log-transformed count on intact shores at Marwick from winter 2013 – winter 2015.

Source	df	SS	MS	*F*-value	*P*-value
Year	2	6.8060	3.40301	43.28	<0.001
Shore height	1	0.2593	0.25934	3.30	0.081
Error	26	2.0445	0.07864		
Total	29	9.1099			

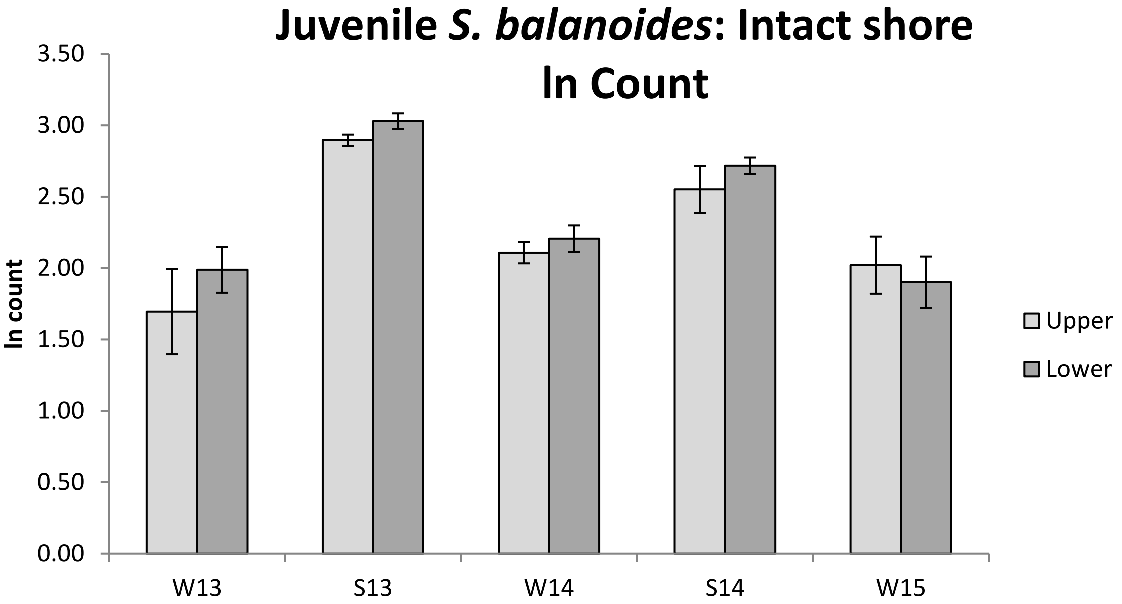

Fig. 5.3.3.5: *Semibalanus balanoides.* Semi-annual count data (log-transformed) of juvenile barnacles on intact shores at Marwick, WMO. Each bar represents mean of 3 sites (± S.E.).

For juvenile *S. balanoides* on intact shores at Marwick, there is a clear seasonal pattern of increased count in summer observations compared with winter. With the settlement of *S. balanoides* in the spring followed by mortality, this is an expected result. There appears to be a trend towards overall increase in juvenile *S. balanoides* count peaking with the summer 2013 and winter 2014 cohort, with summer 2014 and winter 2015 cohort illustrating a modest decrease in count (see Figure 5.3.3.5). GLM of juvenile *S. balanoides* count data from W13-W15 produced a final (most parsimonious) model using the factors of season and year ($R^2 = 0.761$; Table 5.3.3.5).

Table 5.3.3.5: Final GLM for juvenile *S. balanoides* log-transformed count on intact shores at Marwick from winter 2013 – winter 2015.

Source	df	SS	MS	*F*-value	*P*-value
Year	2	0.6003	0.30016	4.65	0.019
Season	1	3.2831	3.28314	50.86	<0.001
Error	26	1.6782	0.06455		
Total	29	7.0254			

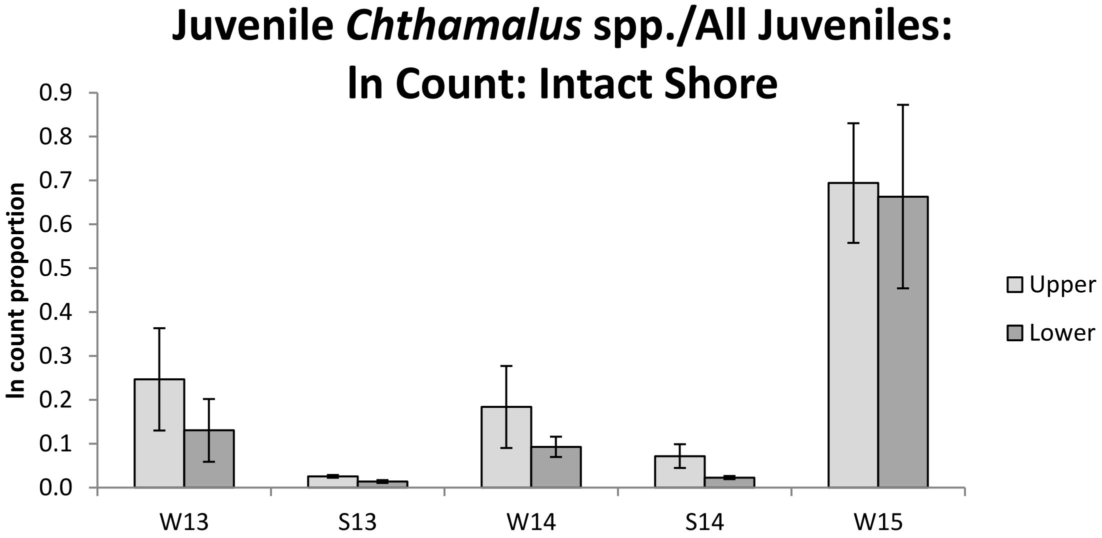

Fig. 5.3.3.6: Semi-annual proportion of juvenile *Chthamalus* spp. to all juvenile barnacle count data (i.e. Southward's Barnacle Index) on intact shores at Marwick, WMO. Each bar represents mean of 3 sites (± S.E.).

Proportion of juvenile count data between barnacle species (Barnacle Index) shows a strong seasonal trend where *Chthamalus* spp. count ratio relative to *S. balanoides* is greater in the winter compared with summer. With the recruitment of large numbers of *S. balanoides* following settlement in the spring of 2013 and 2014, this is an expected result. A dramatic increase in juvenile *Chthamalus* spp. was observed in winter 2015. GLM of juvenile Barnacle Index data from W13-W15 produced a final (most parsimonious) model using the factors of season, year and shore height (R^2 = 0.806). The factors of season and year were highly significant; shore height neared significance (Table 5.3.3.6).

Table 5.3.3.6: Final GLM for juvenile 'Barnacle Index' (*Chthamalus* spp./total barnacle) using logistically transformed proportion of counts on intact shores at Marwick from winter 2013 – winter 2015.

Source	df	SS	MS	*F*-value	*P*-value
Year	2	6.3208	3.16041	19.63	<0.001
Season	1	3.3519	3.35188	20.82	<0.001
Height	1	0.6678	0.66783	4.15	0.052
Error	23	4.0248	0.160990		
Total	29	20.7760			

5.3.4 Results of recruitment following semi-annual clearances:

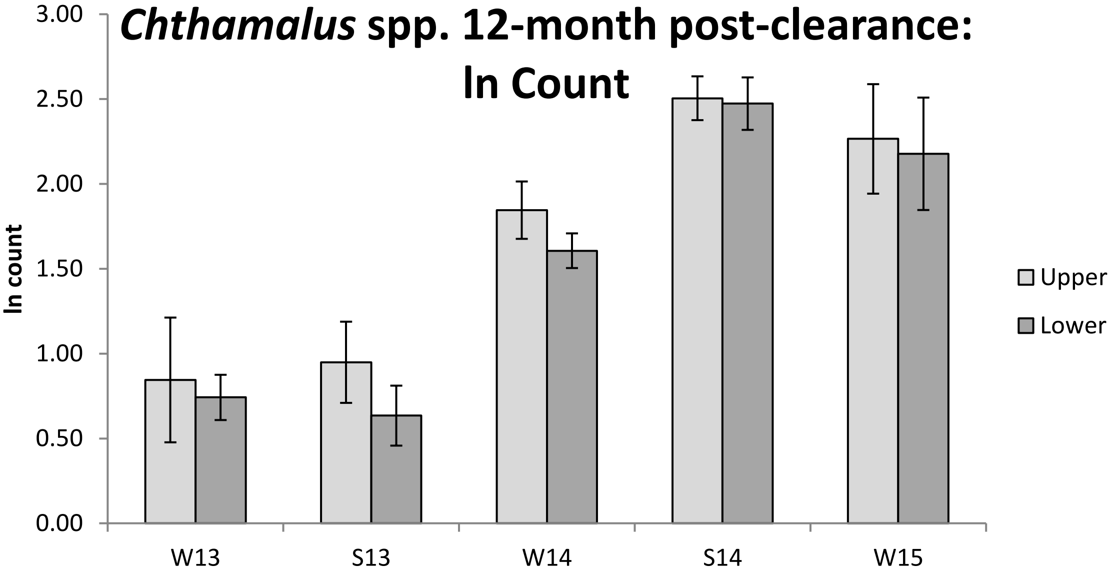

Fig. 5.3.4.1: *Chthamalus* spp. Semi-annual count data (log-transformed) of juvenile barnacles on shores cleared 12 months earlier at Marwick, WMO. Each bar represents mean of 3 sites (± S.E.).

In Figure 5.3.4.1 counts of juvenile *Chthamalus* spp. represent three consecutive year cohorts, as follows:

- W13: individuals settled in approximately August 2012 on a surface already settled by *S. balanoides* approximately 4 months earlier

- S13: individuals settled in approximately August 2012 on a recently cleared surface
- W14: individuals settled in approximately August 2013 on a surface already settled by *S. balanoides* approximately 4 months earlier
- S14: individuals settled in approximately August 2013 on a recently cleared surface
- W15: individuals settled in approximately August 2014 on a surface already settled by *S. balanoides* approximately 4 months earlier

Chthamalus spp. juveniles counted in W14 and S14 are from the same cohort (assessed at a 6 month interval), having settled in approximately August 2013. A marked difference is apparent not only between this cohort and the previous year, i.e. W13 and S13, but also within the cohort, between W14 and S14. Differences observed between winter and summer 12-month post-clearance of the same cohort of *Chthamalus* spp. will be owing to a combination of either: a) variation during settlement possibly affected by the presence/absence of *S. balanoides* juveniles, and/or; b) post-settlement mortality. In the case of presence of *S. balanoides* juveniles, this is presumably owing to reduced space availability during chthamaloid settlement; with regards to mortality differences, semi-annual assessment of the same cohort would expect to result in higher loss following 12 months post-settlement when compared with 6 months post-settlement. An increase in juvenile *Chthamalus* spp. count is first notably observed in winter 2014, following that year's recruitment. This trend continues in summer 2014. On intact shores (see Figure 5.3.3.4), there is also an increase in juvenile *Chthamalus* spp. count but this is not seen until the following year in winter 2015. GLM of juvenile Barnacle Index data from W13-W15 produced a final (most parsimonious) model using the factors of season and year ($R^2 = 0.764$) of which year was highly significant (Table 5.3.4.1).

Table 5.3.4.1: Final GLM for juvenile *Chthamalus* spp. 12-month post-clearance log-transformed count at Marwick from winter 2013 – winter 2015.

Source	df	SS	MS	*F*-value	*P*-value
Year	2	14.0755	7.0377	42.06	<0.001
Season	1	0.8699	0.8699	5.20	0.031
Error	26	4.3500	0.1673		
Total	29	18.4516			

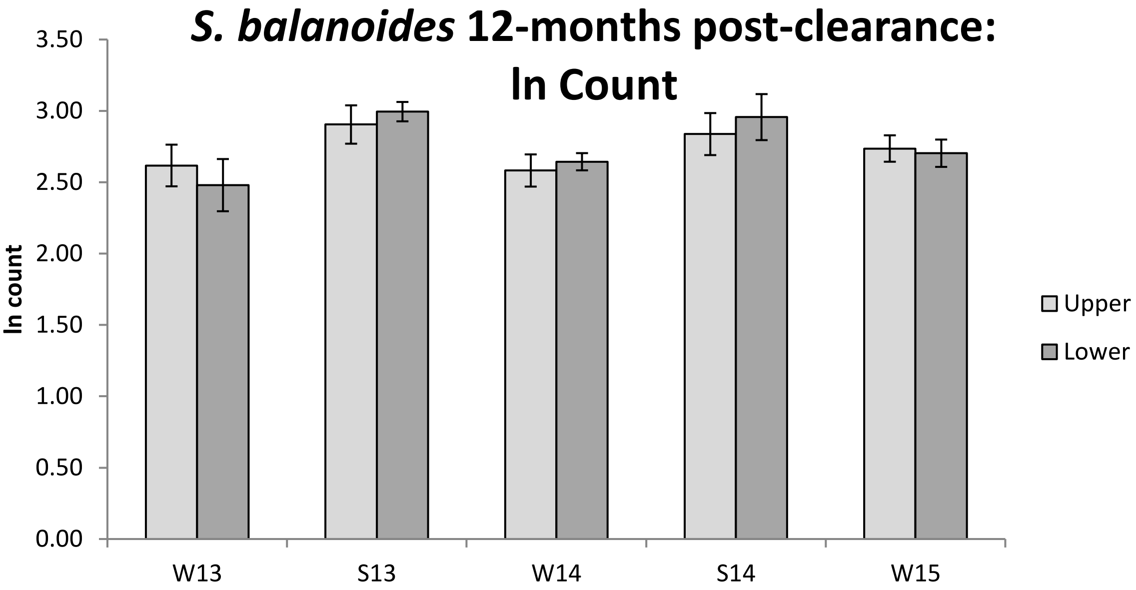

Fig. 5.3.4.2: *Semibalanus balanoides.* Semi-annual count data (log-transformed) of juvenile barnacles on shores cleared 12 months earlier at Marwick, WMO. Each bar represents mean of 3 sites (± S.E.).

In Figure 5.3.4.2 counts of juvenile *S. balanoides* represent three consecutive year cohorts, as follows:

- W13: individuals settled in approx. April 2012 on a recently cleared surface
- S13: individuals settled in approx. April 2013 on a surface already settled by *Chthamalus* approx. 8 months earlier
- W14: individuals settled in approx. April 2013 on a recently cleared surface
- S14: individuals settled in approx. April 2014 on a surface already settled by *Chthamalus* approx. 8 months earlier
- W15: individuals settled in approx. April 2014 on a recently cleared surface

S. balanoides juveniles counted in S13 and W14 are from the same cohort (assessed at a 6 month interval), having settled in approximately April 2013 (and similarly with S14 and W15, 12 months later). In both years, there is a difference between semi-annual assessments: highest count were observed in the earlier observation (summer), rather than the latter observation (winter). This contrasts with the *Chthamalus* spp. cohort which settled in August 2013 where counts were higher at the latter observation. Differences observed between summer and winter 12-month post-clearance of the same cohort of *S. balanoides* will be owing to a combination of either: a) variation during settlement possibly affected by the presence/absence of chthamaloid juveniles, and/or; b) post-settlement mortality. In the case of presence of chthamaloid juveniles, this is presumably owing to reduced space availability (or some other deterring factor) during *S. balanoides* settlement; with regards to mortality differences, semi-annual assessment of the same cohort would expect to result in higher loss following 12 months post-settlement when compared with 6 months post-settlement. ANOVA applied to *S. balanoides* juvenile count data (12-month post-clearance) from W13-W15 revealed a highly significant effect between seasons ($R^2 = 0.360$; Table 5.3.4.2).

Table 5.3.4.2: Final GLM for juvenile *S. balanoides* 12-month post-clearance log-transformed count at Marwick from winter 2013 – winter 2015.

Source	df	SS	MS	*F*-value	*P*-value
Season	1	0.6315	0.63153	15.75	<0.001
Error	28	1.1225	0.04009		
Total	29	1.7540			

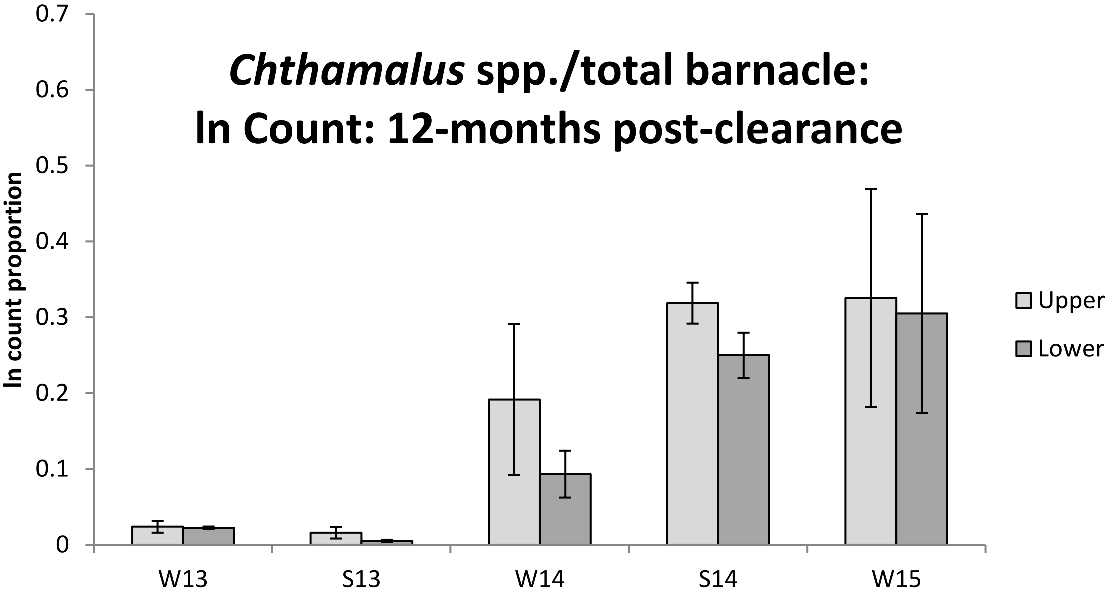

Fig. 5.3.4.3: Semi-annual ratio of juvenile *Chthamalus* spp. to all juvenile barnacle count data (i.e. Southward's Barnacle Index) on shores cleared 12 months earlier at Marwick, WMO. Each bar represents mean of 3 sites (± S.E.).

Relative to *S. balanoides* there was an almost total recruitment failure of juvenile *Chthamalus* spp. from the cohort which settled in approximately August 2012. This is in contrast to intact shores where the Barnacle Index for this cohort, while still reduced, was not as low. Barnacle Index 12-months post-clearance shows a marked increase in the following year cohort, and a suggestion of this continuing in the cohort settled in approximately August 2014. ANOVA applied to Barnacle Index 12-months post-clearance data from W13-W15 revealed a highly significant effect of years ($R^2 = 0.699$; Table 5.3.4.3).

Table 5.3.4.3: Final GLM for juvenile 'Barnacle Index' (*Chthamalus* spp./total barnacle) 12-month post-clearance using logistically transformed ratio of counts at Marwick from winter 2013 – winter 2015.

Source	df	SS	MS	*F*-value	*P*-value
Year	2	13.383	6.6917	31.40	<0.001
Error	27	5.753	0.2131		
Total	29	19.137			

5.3.5 Comparison of barnacle and temperature data:

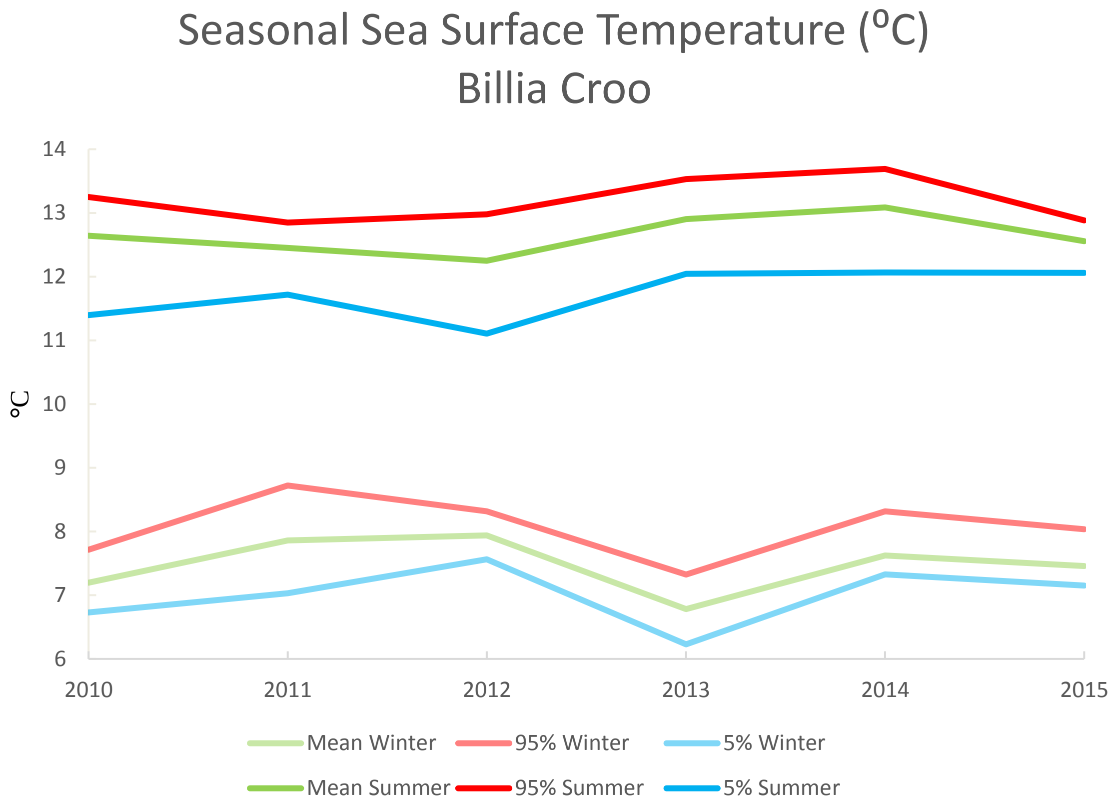

Figure 5.3.5.1: Daily mean sea surface temperature from Billia Croo, WMO presented as seasonal intervals used in modelling the relationship between climate and recruitment in littoral barnacles. Winter = February to April; summer = August to October.

During the 6-year period applied to barnacle recruitment data in this study, SST indices never fluctuated more than 0.8°C from mean records. The period of greatest deviation was recorded in winter 2013 where mean and percentiles of SST were all notably below long-term mean records; summer SST was highest in 2013 and 2014. Compared with AT, relatively little annual fluctuation in SST is not unexpected. However, even small changes in SST may be important to littoral species with particularly sensitive larval phases (Barnes, 1956a; Hiscock *et al*., 2004).

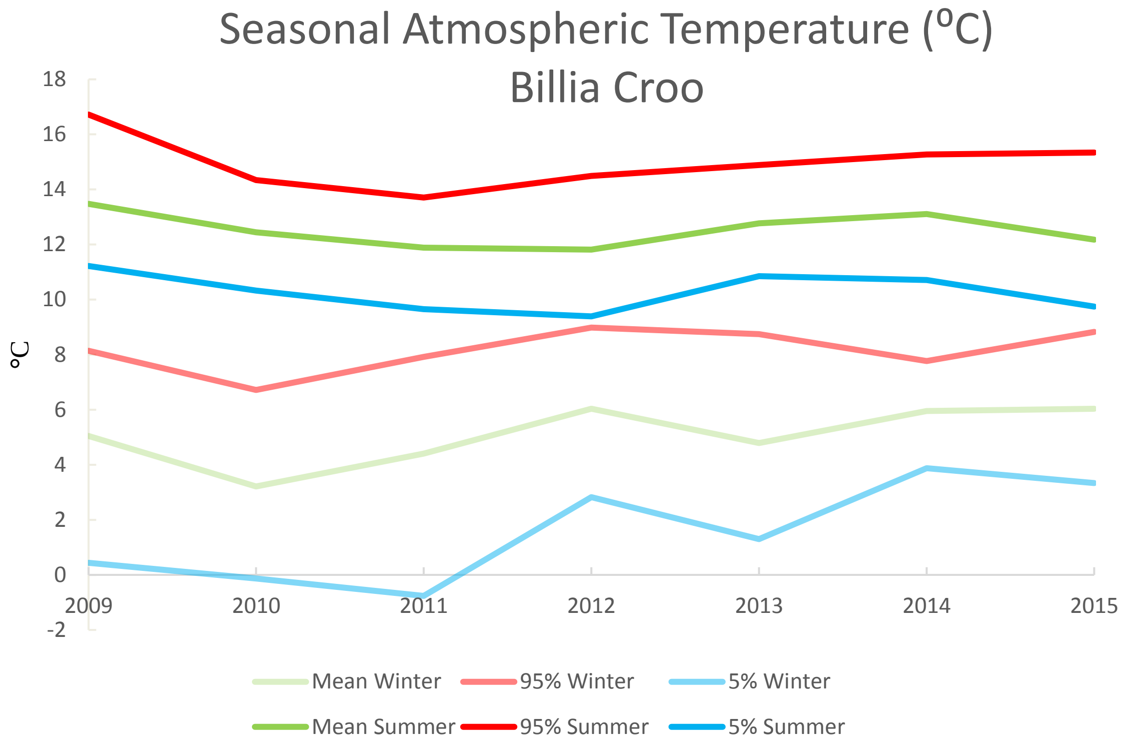

Figure 5.3.5.2: Daily mean atmospheric temperature from Billia Croo, WMO presented as seasonal intervals used in modelling the relationship between climate and recruitment in littoral barnacles. Winter = mid-Dec - mid-Mar; summer = mid-June - mid-Sept.

When compared with SST, AT fluctuated more, both annually and between seasons. Lower 5 percentile AT was particularly low immediately preceding and in the early years of this study. Cold seasonal AT was recorded for 3 consecutive winters beginning in 2008-2009. Fluctuations in AT were often accompanied by similar directional changes in SST, e.g. the winter of 2009-2010 was characterised by the lowest AT and second lowest SST of the data set; at other times AT and SST demonstrated opposing trends. For example: in winter 2010-2011, lower 5 percentile AT was >2°C below the 7-year mean for this index; during this same winter, lower 5 percentile SST was >0.5°C above the 6-year mean for this index. Beginning in 2011-2012, winter seasonal indices were generally warm, although SST in winter 2012-2013 was the coldest during the study. Summer temperatures were notably colder in 2011 and 2012 for both SST and AT; beginning in 2013 summer seasonal SST and AT were generally stable and modestly warmer than the study mean.

Generalised linear models comparing barnacle count data with year, season and shore height were generated for adult and juveniles on intact sites and juveniles on post-clearance sites for *Chthamalus* spp. and *S. balanoides* (5.3.3 and 5.3.4). The effect of lagged temperature indices on annual variation in barnacle recruitment was tested by substituting temperature data for year into the original model, or adding temperature data to models where year had not been identified. Modified GLMs with temperature substitution had one fewer degrees of freedom. F-tests were used to determine whether models including temperature were preferred to the existing final models identified above (Tables 5.3.5.1-6). In general, GLMs modified with seasonal temperature data were consistent with original models using annual recruitment data. Inferences, however, are limited by the relatively short time sequence of this study and by highly correlated temperature variables. Overall, cohort strength appears to be more closely associated with temperature in *Chthamalus* spp. than *S. balanoides*. However, with strong correlations between alternative temperature indices coupled with the short time-series of barnacle observations, it is not possible to associate these effects with specific points in barnacle life histories based on lagged correlations.

Table 5.3.5.1: Coefficient of determination (R^2) of GLMs of adult *Chthamalus* spp. log-transformed count on intact shores at Marwick from winter 2013 – winter 2015 with lagged temperature index included as co-variate (df = 1). R^2 of original model was 56.9% (df = 2). (S) = summer; (W) = winter. Figures in bold indicate temperature models that are statistically preferred to previous final models.

Temp. Index	**0 mths (S)**	**6 mths (W)**	**12 mths (S)**	**18 mths (W)**	**24 mths (S)**	**30 mths (W)**
Mean SST	**55.48**	18.10	07.81	23.26	**55.07**	**52.97**
Upper 5% SST	**55.56**	07.85	40.34	46.67	38.18	34.22
Lower 5% SST	**50.81**	13.88	00.16	03.87	00.58	**50.60**
Mean AT	**56.13**	09.93	22.74	16.47	**53.19**	**53.21**
Upper 5% AT	**55.58**	41.08	**56.83**	42.18	02.77	**56.13**
Lower 5% AT	47.10	00.02	15.61	33.10	**56.42**	16.08

Table 5.3.5.2: Coefficient of determination (R^2) of GLMs of juvenile *Chthamalus* spp. log-transformed count on intact shores at Marwick from winter 2013 – winter 2015 with lagged temperature index substituted for year as co-variate (df = 2). R^2 of original model (year and height) was 77.6% (df = 3). (S) = summer; (W) = winter. Figures in bold indicate temperature models that are statistically preferred to previous final models.

Temp. Index	**0 mths (S)**	**6 mths (W)**	**12 mths (S)**	**18 mths (W)**	**24 mths (S)**	**30 mths (W)**
Mean SST	33.86	03.77	61.56	**75.50**	58.55	26.21
Upper 5% SST	34.21	10.68	**76.10**	72.17	07.39	05.16
Lower 5% SST	21.70	05.62	30.77	53.98	42.18	67.76
Mean AT	36.91	08.53	**75.26**	04.35	26.74	63.30
Upper 5% AT	56.75	**75.79**	42.70	10.52	19.28	54.31
Lower 5% AT	15.94	36.00	70.64	04.67	38.74	71.03

Table 5.3.5.3: Coefficient of determination (R^2) of GLMs of juvenile *Chthamalus* spp. log-transformed count on cleared shores at Marwick from winter 2013 – winter 2015 with lagged temperature index substituted for year as co-variate (df = 2). R^2 of original model (year and season) was 76.4% (df = 3). (S) = summer; (W) = winter. Figures in bold indicate temperature models that are statistically preferred to previous final models.

Temp. Index	**0 mths (S)**	**6 mths (W)**	**12 mths (S)**	**18 mths (W)**	**24 mths (S)**	**30 mths (W)**
Mean SST	**76.35**	43.16	01.10	14.73	66.36	**76.04**
Upper 5% SST	**76.33**	27.85	38.49	49.15	65.32	61.53
Lower 5% SST	**75.05**	37.37	08.22	00.15	02.50	56.52
Mean AT	**76.04**	31.35	14.12	40.99	**76.11**	61.94
Upper 5% AT	67.76	39.67	**74.79**	68.85	17.46	69.45
Lower 5% AT	72.70	05.20	06.69	60.40	**75.74**	07.12

Table 5.3.5.4: Coefficient of determination (R^2) of GLMs of adult *S. balanoides* log-transformed count on intact shores at Marwick from winter 2013 – winter 2015 with lagged temperature index included as co-variate with season (df = 2). R^2 of original model (season) was 13.6% (df = 1). (S) = summer; (W) = winter. No temperate models were preferred.

Temp. Index	**2 mths (W)**	**8 mths (S)**	**14 mths (W)**	**20 mths (S)**	**26 mths W)**
Mean SST	14.41	14.21	16.07	13.68	15.12
Upper 5% SST	14.44	13.91	13.89	17.01	17.41
Lower 5% SST	14.43	14.37	18.73	19.39	13.70
Mean AT	14.44	14.07	18.95	15.09	13.65
Upper 5% AT	13.90	13.65	16.58	19.78	13.76
Lower 5% AT	14.35	14.13	17.52	14.35	16.96

Table 5.3.5.5: Coefficient of determination (R^2) of GLMs of juvenile *S. balanoides* log-transformed count on intact shores at Marwick from winter 2013 – winter 2015 with lagged temperature index substituted for year as co-variate with season (df = 2). R^2 of original model (year and season) was 76.1% (df = 3). (S) = summer; (W) = winter. Figures in bold indicate temperature models that are statistically preferred to previous final models.

Temp. Index	**2 mths (W)**	**8 mths (S)**	**14 mths (W)**	**20 mths (S)**	**26 mths W)**
Mean SST	**76.11**	72.18	67.65	67.64	67.60
Upper 5% SST	**75.76**	69.11	67.65	67.58	67.57
Lower 5% SST	**76.07**	**74.36**	67.62	67.60	67.65
Mean AT	**75.91**	70.64	67.57	67.60	67.64
Upper 5% AT	69.04	67.73	67.58	67.58	67.63
Lower 5% AT	**74.00**	71.31	67.57	67.62	67.64

Table 5.3.5.6: Coefficient of determination (R^2) of GLMs of juvenile *S. balanoides* log-transformed count on cleared shores at Marwick from winter 2013 – winter 2015 with lagged temperature index included as co-variate with season (df = 2). R^2 of original model (season) was 36.0% (df = 1). (S) = summer; (W) = winter. No temperate models were preferred.

Temp. Index	**2 mths (W)**	**8 mths (S)**	**14 mths (W)**	**20 mths (S)**	**26 mths W)**
Mean SST	36.40	36.59	40.34	38.98	37.09
Upper 5% SST	36.05	37.81	39.93	36.18	36.08
Lower 5% SST	36.22	36.08	39.02	38.30	39.60
Mean AT	36.10	37.12	36.12	37.12	39.29
Upper 5% AT	37.84	39.31	36.32	36.96	38.70
Lower 5% AT	36.14	36.87	36.06	37.77	40.08

5.4 Discussion:

Studies reported here have focussed on recruitment in the competitive zone between littoral barnacle species at the northern distribution limit of *Chthamalus*, and environmental factors which might affect this process. These data confirm the findings from previous studies in British waters further south that *S. balanoides* typically dominates lower shore levels relative to *Chthamalus* spp. and that the chthamaloid zone on high exposure shores is dominated by *C. stellatus* rather than *C. montagui*. Experimental clearances of barnacles at semi-annual intervals and comparisons with intact populations over several years have revealed dynamic populations which may be responding to important environmental forcing agents. Some general observations can be drawn for the period 2012-2015 at Marwick on WMO:

- Overall, on intact shores, the population of adult *Chthamalus* spp. decreased.
- During the period of decrease in adult *Chthamalus*, juvenile recruitment was very low.
- In winter 2015, the numbers of *Chthamalus* recruits on intact shores ‘rebounded’, increasing by an order of magnitude.
- Recruitment failure in juvenile *Chthamalus* may be linked to particularly cold seasons experienced in winter 2009-2010 and 2010-2011 and summer 2011 and 2012.
- *S. balanoides* count was dominated by seasonal recruitment events with large influx of juveniles observed in summer, followed by high seasonal mortality of juveniles before observation in winter.

- Juvenile recruitment in *S. balanoides* was highest in summer 2013 which may relate to cold temperatures experienced over the previous two summers and winters of 2009-2010 and 2010-2011.
- Adult *S. balanoides* population was stable on intact shores but with a notable increase in summer 2014, presumably owing to maturation of the successful 2013 cohort of recruits.
- Increased recruitment in *Chthamalus*, first observed on recently cleared surfaces in winter 2014, was not seen on intact shores until the following year, winter 2015.
- Competition for free space was observed in experiments where *Chthamalus* recruitment onto cleared surfaces was reduced owing to pre-settlement of *S. balanoides*; the reverse scenario, where pre-settlement by *Chthamalus* may limit *S. balanoides* recruitment by pre-empting free space might occur but could not be supported by these data.
- Juvenile *Chthamalus* count varies with space resource with higher recruitment observed at times on intact shores featuring only small patches of free-space, compared with fully-cleared surfaces, suggesting gregariousness at settlement.

GLMs of subgroups comparing factors of year, season, and shore height, and interactions between factors, infrequently identified height in final models. This was not unexpected because of the close vertical proximity of upper and lower quadrats within the monitored transition zone (approximately 13 cm in vertical height) and limited number of sites. In other words, based on the specific design parameters, the vertical zonation ‘signal’ was not strong enough to consistently display statistical significance, even if a difference existed.

Most marine organisms, including barnacles, have complex life cycles spent in larval and adult stages, often in contrasting habitats subject to varied environmental factors (Roughgarden *et al.*, 1988). It is worth noting that a much wider range of processes may influence population fluctuations than have been considered here, including processes occurring during both larval and adult phases (Underwood and Fairweather, 1989), as well as affecting local retention of propagules (Thorson, 1950; Roughgarden *et al.*, 1985). The studies described here have focussed on recruitment of juvenile barnacles and long-term change in intact adult populations. These studies do not include direct evaluation of reproductive condition or output, larval supply, settlement, or causes of post-settlement mortality. Based on previous work by other researchers, some assumptions can be considered regarding these processes. Meteorological records may support speculation on the role of temperature fluctuations on reproductive function and larval settlement patterns. Based on studies from farther south, *Chthamalus* brooding and larval supply would be expected to increase during warm conditions and decrease during cooler conditions; *S. balanoides* would be expected to respond in an opposite way to temperature changes (Southward *et al.*, 1995; Wethey *et al.*, 2011). Minchington and Scheibling (1993) argue that reduced water velocity may enhance cyprid settlement and allow greater discrimination of substrate during settlement; micro-hydrodynamic phenomena may contribute to spatial variation in spat settlement (Pineda, 1994). However, wind and wave data suggest that on ‘blue-water’ locations such as WMO, larval supply is well-mixed with a preponderance of conditions favouring maximal settlement on rocky shores (Kendall *et al.*, 1982; Burrows *et al.*, 1999). On WMO, these conditions include a largely uncomplicated linear coast following a northerly orientation with heavy swell and wave conditions arriving perpendicular to the shores, powered by winds blowing onshore from a typically westerly direction. Under these circumstances, settlement is assumed to be associated more with reproductive performance from source adults and free space resource than with local hydrographic conditions (see Bennell, 1981; Hawkins and Hartnoll, 1982). However, interpretations must be delivered with caution in light of lack of direct evidence in early life stage processes. With this in mind, the hypotheses identified in 5.1.2 can be addressed.

5.4.1 Effects of temperature on barnacle recruitment at the northern distribution limit of *Chthamalus* spp.:

Beginning with preliminary studies in 2011 and continuing until summer 2014, the abundance of adult *Chthamalus* spp. gradually declined on intact shores at Marwick on WMO. This was seen in *Chthamalus* count data (Figure 5.3.3.1) and using Southward's Barnacle Index based on count (Figure 5.3.3.3). Similar results were also achieved using percentage cover-based Barnacle Index, although the declining trend was not as pronounced (Figure 5.3.2.6), this is presumably owing to the large size of surviving adult chthamaloids, i.e. preferential loss of juvenile or small barnacles would impact count-based abundance metrics comparatively more than those based on percentage cover. The overall trend in gradual loss of adults suggests that over much of the study period there was a failure to recruit replacements necessary to compensate against adult mortality (Figure 5.3.3.1). Even in the event of total recruitment failure, the decadal long life cycle of *Chthamalus* spp. should allow protracted adult survivorship (Crisp *et al.*, 1981). The earliest seasons of this study were characterised by extremely low recruitment of *Chthamalus* spp. (Figure 5.3.3.4). In contrast, a dramatic increase was observed in recruitment of *Chthamalus* spp. on intact shores in winter 2015 (Figure 5.3.3.4), as well as using count-based Barnacle Index (Figure 5.3.3.6).

Based on count data, the population of *S. balanoides* was dominated by seasonal recruitment events resulting in large influx of juveniles observed in the summer followed by high seasonal mortality of juveniles before observation occurred in the winter (Figures 5.3.2.2 and 5.3.3.5). Discounting juvenile contribution on intact shores, the adult population of *S. balanoides* was stable with no seasonal trend apparent (Figure 5.3.3.2). There is, however, an increase in observed *S. balanoides* adults in summer 2014, this is consistent with the observation of a 'spike' in juvenile recruitment observed during the previous summer (Figure 5.3.3.5). This very successful period of recruitment appears to have resulted in sufficient numbers of this cohort surviving 12 months later to have boosted the number of adults, although this event is not statistically significant in the adult population (Table 5.3.3.2).

Recruitment failure and rebound in *Chthamalus* spp. and relative stability punctuated by seasons of successful recruitment in *S. balanoides* on WMO may be linked to colder than normal weather experienced on WMO preceded and in the early stages of this study. Specifically, unusually cold AT occurred in consecutive winters in 2009-2010 and 2010-2011, followed by cold summers in 2011 and 2012. Recruitment patterns during this period are consistent with expectations that cold weather will negatively affect chthamaloid populations and that responses to temperature may be most evident following a lag period. This same lagged relationship with temperature might explain the sharp increase in juvenile recruitment of *Chthamalus* spp. following return to warmer conditions.

The lowest 5 percentile of mean daily AT in the winters of 2009-2010 and 2010-2011 (between mid-December and mid-March) were -0.14°C and -0.76°C, respectively, markedly lower than +2.83°C averaged over the following four winters (late 2011-2015). In addition, summer AT in 2011 and 2012 was notably cooler than average in Orkney. The lowest 5 percentile of mean daily AT between mid-June and mid-September in these two summers were +9.66°C and +9.39°C, respectively; the same metric averaged from five summers preceding and following (2009-2010, 2013-2015) was +10.56°C. As mentioned earlier, trends in SST and AT do not always match one another. While lowest 5 percentile of SST was colder than average for winter 2009-2010 and summer 2011, winter 2010-2011 and summer 2012 were marginally warmer than average (over the 6-year period). Although the severity of the cold winters of 2009-2010 and 2010-2011 was nowhere near that experienced in British waters in such past events as the winter of 1962-1963 (Crisp, 1964), rocky shore assemblages may have been affected by these recent extreme cold periods (Figure 5.4.1). Indeed, some analogies were noted between the winters of 1962-1963 and 2009-2010 including that the 10°C contour of monthly average SST between December and March was almost identically positioned in Europe (Wethey *et al*., 2011). Recent evidence from continental Europe includes an expansion of *S. balanoides* range of 75-80 km and a reduction in abundance (but not range) of *Chthamalus* spp. from 2007 to 2010 (Wethey *et al*., 2011). On WMO, after the summer of 2012, winter and summer SST and AT remained consistently warmer than the preceding cooler period.

Figure 5.4.1: ‘Bleaching’ of coralline encrusting red algae peripheral to mid shore rock pool at Billia Croo – 15 January, 2010. Note: submerged section remains pink, suggesting protection from extreme cold atmospheric temperature.

Temperature subhypotheses:

Results described here are consistent with the expectation that colder than average conditions will tend to favour recruitment success in *S. balanoides* over *Chthamalus* spp., and that subsequent warming trends will tend to favour a ‘rebound’ in the chthamaloid population. It was hoped that comparing semi-annual barnacle populations with SST and AT indices might allow specific seasonal effects on recruitment to be identified at the northern distribution limit of *Chthamalus* spp. Previous studies have looked into the relationship between these species and seasonal temperature events, and whether or not recruitment processes follow a lagged response.

Sea surface temperature appears to correlate better than AT with littoral barnacle populations owing to greater sensitivity to short-term temperature changes during larval phases (Barnes, 1956a; Emlet and Sadro, 2006). *Chthamalus* spp. is predicted to increase in abundance and occurrence following warm summer SST and AT (Hiscock *et al*., 2004) through greater adult fecundity (Burrows *et al*., 1992). Research in Ireland, however, identified cold winters as the primary driver of reproductive failures in *Chthamalus* spp. (O'Riordan *et al*., 2012). Previous studies found that the correlation between chthamaloid populations and temperature was most obvious using SST, lagged by either one year (Poloczanska *et al*., 2008) or two years (Southward *et al*., 1995; Wethey *et al*., 2011). In addition to acute local events, Barnacle Index is also strongly linked with long-term climatic trends such as the Atlantic Multidecadal Oscillation (Mieszkowska *et al*., 2014). *S. balanoides* is also strongly correlated with mean SST in June and only marginally less so with mean AT in May and June (Poloczanska *et al*., 2008). In contrast, studies by Jones *et al*. (2012) found that range expansion in *S. balanoides* was chiefly driven by reproductive success following cold winter conditions. With dynamic equilibrium between species influenced by phase-lagged fluctuations in SST and AT, making direct links between recruitment and climatic events can be difficult (Kendall *et al*., 1985). With this in mind, can specific seasonal climatic events be assigned to fluctuations in barnacle recruitment in this study?

In general, when GLMs were modified by substituting lagged temperature indices for year factor, the resulting models did not improve in most scenarios; modified models of

S. balanoides improved less often than those of *Chthamalus* spp. This is not unexpected: failure of *S. balanoides* to correlate with temperature indices might owe to the mid-range of this species' distribution in Orkney waters, i.e. temperature fluctuations witnessed here are well within normal range (Kendall and Bedford, 1987); and the population of *S. balanoides* typically correlates more strongly with season rather than year. Correlation-based conclusions, however, must be met with caution; the possible connection here between cold weather and recruitment failure in *Chthamalus* spp. could be caused by other co-varying factors. Modified GLMs give some support to temperature being a plausible explanation for differences in recruitment during this study but there is not sufficient power to determine when this operates. As such, inferences on which seasonal mechanism might be of greatest importance cannot be made beyond speculation. The study reported here features only 3 years of sampling; longer-term studies are necessary to elucidate any relationship with temperature.

Effects of temperature on processes contributing to barnacle recruitment:

The studies reported here are based only on recruitment data, with consideration of certain assumptions relating to other processes affecting barnacle populations. The processes underpinning temperature-driven changes in littoral barnacle populations are complex and may affect individuals at different life-cycle stages manifest in varying recruitment. As previously stated, fluctuations in recruitment observed 6 or 12 months after settlement could result from changes in adult reproductive output, larval supply to rocky shores, settlement, or post-settlement mortality.

Reproductive output, larval supply and temperature:

In *Chthamalus* spp., increased summer temperatures may lead to greater adult fecundity manifest as prolonged release of larvae and possible additional broods (Burrows *et al*., 1992). Recent range expansion in *S. balanoides* appears to be driven by reproductive success following cold winter conditions (in particular, the severe winter of 2009-2010 (Jones *et al*., 2012)). While Jenkins (2005) concluded that larval settlement of *Chthamalus* spp. in SW England closely matched adult distribution, under certain circumstances, local hydrodynamics can play a leading role in facilitating annual differences in settlement. For example, in embayments, Gaines and Bertness (1992) found no correlation between settlement numbers and adult population but instead variation was chiefly determined by ‘flushing’ of the bay. Fluctuations in barnacle settlement on the Californian coast may be explained by increasingly sophisticated models described by Alexander and Roughgarden (1996) where stronger offshore winds tend to carry larvae away from suitable habitats. Kendall *et al*. (1982) found considerable variation in settlement between study sites owing to differences in topography and prevailing wind directions, with greater uniformity in settlement occurring on relatively linear coasts. On WMO, which features well-mixed waters owing to wave and wind conditions, and general lack of embayments, more homogenous settlement might be expected, given a constant supply of larvae. In future, it would be worth conducting further analysis and research on potential wave and wind effects on barnacle recruitment using meteorological data. Larval supply may also vary as a result of fluctuations in supply of phytoplankton food (Barnes, 1956a; Range and Paula, 2001; Emlet and Sadro, 2006), larval predators and local upwelling (Roughgarden *et al*., 1988).

Settlement and temperature:

After development in the water column and arrival at a suitable habitat, larval settlement is limited by availability of free space (Roughgarden *et al*., 1985). This process may play a major role in barnacle distribution; the competitive interactions between *S. balanoides* and *Chthamalus* spp. may owe to available space left after spring *S. balanoides* recruitment (Poloczanska *et al*., 2008). As such, temperature may indirectly affect recruitment of *Chthamalus* spp. by inhibiting larval settlement months after conditions favourable to successful recruitment of *S. balanoides*. This scenario may have contributed to very low recruitment of *Chthamalus* spp. on intact shores in 2012-2013 on WMO (Figure 5.3.3.4). Settlement behaviours which mediate density also include gregariousness where the presence of conspecific adults will tend to attract larvae (Knight-Jones and Crisp, 1953) (see 5.4.4 Gregariousness).

Post-settlement mortality and temperature:

Causes of post-settlement mortality in littoral barnacles are well established and include temperature-related abiotic factors, such as desiccation (Foster, 1971). In SW Ireland, zonation patterns between *C. stellatus* and *C. montagui* were established by temperature and desiccation driven post-settlement mortality (O'Riordan *et al*., 2010). In SW England, climate was identified as the primary driver of post-settlement mortality in *S. balanoides* (Poloczanska *et al*., 2008). Additional abiotic factors which may contribute to post-settlement mortality and may be affected by climatic conditions include osmotic stress from rainfall (Power *et al.*, 2011), aspect (Wethey, 1984), and sediment impacts (Shanks and Wright, 1986).

Certain biotic causes of post-settlement mortality in littoral barnacles are also influenced by temperature changes including, most obviously, direct interspecies competition for space. *S. balanoides* will outcompete *Chthamalus* spp. by crowding and smothering more slowly growing chthamaloids (Connell, 1961a). The dynamic nature of the equilibrium in the competitive zone between littoral barnacles is primarily-driven by temperature (Southward *et al.*, 1995; Wethey *et al.*, 2011). Additional contributing biotic factors to post-settlement mortality of barnacles, which may be temperature dependant, include predation from *Nucella lapillus* and spat removal by grazing limpets (Connell, 1961b), non-lethal cirral foraging by *Lipophrys pholis* (Harvey *et al.*, 2003), as well as potential cycling in the relationship between fucoids, limpets and barnacles (Hawkins *et al.*, 1992).

5.4.2 Response detection:

Intact shores described in this study are a mosaic of contributing elements including small patches of empty rock surfaces (Figures 5.3.1.1 and 5.3.1.2). In *Chthamalus* spp., low recruitment of juveniles recorded on intact shores during 2012-2014 dramatically changed with observation in winter 2015 (Figures 5.3.2.1 and 5.3.3.4). Recruitment into small patches of free-space on intact rocky shore quadrats increased by greater than an order of magnitude. Similarly, low levels of recruitment were also recorded in 2013 on rocky shores cleared 12 months earlier. However, a substantial increase in recruitment, was first observed on cleared sites in winter 2014 – a year before similar detection on intact sites (Figures 5.3.3.4 and 5.3.4.1). This suggests that experimentally cleared rocky shores, might provide a short-cut to observation of important ecological processes. This early response is also illustrated using Southward's Barnacle Index for intact versus cleared study sites (Figures 5.3.3.6 and 5.3.4.3). Observations of long-term changes driven by recruitment may be expedited by providing greater settlement opportunities. Freeing of available space for settlement provided by clearance methods appears to allow trends in recruitment to be identified earlier than on intact shores. Without clearance experimentation, the presence of long-lived species, like *Chthamalus* spp., might make short-term observations in community structure more difficult.

In *S. balanoides*, the adult population appeared stable over the study years (Figure and Table 5.3.3.2). Although not statistically significant, an increase in adult count was observed in summer 2014. This is consistent with the observation of a 'spike' in *S. balanoides* recruitment observed in summer 2013, particularly apparent on intact shores (Figure 5.3.3.5). This very successful period of recruitment of juveniles appears to have resulted in sufficient survival 12 months later that subsequently matured individuals have boosted the adult population. While this provides a further example where adult population fluctuations may be presaged by observation of juvenile recruitment, there was not a difference in timing of *S. balanoides* recruitment peaks between intact and cleared surfaces. This may be owing to the dominant role of *S. balanoides* on these shores with high density settlement on both cleared surfaces and patches of free space on intact sites. In the current studies, space is not saturated by *S. balanoides* and hummocking, described in early research (Barnes and Powell, 1950), does not occur.

5.4.3 Semi-annual clearance and space resource competition:

Semi-annual clearance methods developed here were followed by observations of barnacle recruitment at 6 months intervals; this may allow some inferences on settlement dynamics. Assuming similar rates of post-settlement mortality, if recruitment onto cleared surfaces is higher (or equal) on quadrats observed 12 months versus 6 months post-settlement, original settlement must have been greater on those quadrats selected for evaluation 12 months later. In contrast, if count is lower in the observations made after 12 months post-settlement, versus 6 months post-settlement, we cannot determine the relative importance of settlement and post-settlement mortality. Larval settlement would be expected to be higher on shores with more unoccupied, ‘free’ space availability (Roughgarden *et al.*, 1985) and reduced on shores pre-occupied by species competing for space resource (Bence and Nisbet, 1989). Free space created by sediment impacts produced during heavy seas in winter months are more likely to occur shortly before settlement of *S. balanoides* (Poloczanska *et al.*, 2008). Competitive interactions between *Chthamalus* spp. and *S. balanoides* appears to be created through resource competition for available space left after spring *S. balanoides* recruitment (Poloczanska *et al.*, 2008) and interference competition by overcrowding of *Chthamalus* spp. by faster growing balanoids (Connell, 1961a).

Looking in greater detail at the *Chthamalus* spp. cohort which settled onto cleared surfaces in approximately August 2013 (represented 6 months later by the population at W14, and 12 months later at S14) (Figure 5.3.4.1), there is a marked difference between the counts; greater count is observed in S14 rather than W14. As described above, this would be expected from either a difference in the original settlement of the same cohort on the same shore, or a difference in post-settlement mortality. Recruitment evidence from the 2013 cohort is directly contradictory to the expectation of lower count observed approximately 12 months post-settlement versus 6 months post-settlement, owing to continuing mortality over time. This suggests that more *Chthamalus* spp. settled on the recently cleared areas (which would be evaluated 12 months later) than on the areas cleared a half year earlier (which would be evaluated 6 months later). This is an expected result owing to competition for free space resource where one species, in this case *S. balanoides*, is provided the first opportunity to settle. Despite the S14 evaluation occurring after a longer post-settlement interval, during which mortality would be expected to continue, the initial settlement of the chthamaloid cohort (in August 2013) evaluated in W14 was sufficiently fewer that higher count was still recorded at S14. This can be explained by greater settlement on to surfaces without prior settlement of *S. balanoides*, whereas the presence of recently settled *S. balanoides* may deter subsequent *Chthamalus* spp. settlement, presumably owing to limitations in free space.

This is further evidenced by the 2012 settlement cohort (represented 6 months later by the population at W13 and 12 months later at S13). While there is not any apparent difference between the cohort counts, post-settlement mortality would be expected to result in lower counts in S13 observations. Equal or higher counts of Chthamalus spp. in 12-month versus 6-month observations on post-cleared surfaced is consistent with increased settlement owing to greater available free space. Alternatively, the pattern observed in the 2012 and 2013 *Chthamalus* spp. cohorts, could occur if post-settlement mortality of juvenile *Chthamalus* spp. was greater on cleared surfaces pre-settled by *S. balanoides* compared with cleared surfaces without *S. balanoides* settlement. It is possible that faster growing *S. balanoides* juveniles could crowd out recently settled chthamaloids in the period between the latter's settlement (in August) and image capture (in the following winter).

What about the reverse scenario? Does high seasonal recruitment of *Chthamalus* spp. affect subsequent *S. balanoides* recruitment by limiting free space? The semi-annual clearance method developed here may allow this to be examined: as explained above, greater count of juveniles observed following 12 months versus 6 months post-clearance might provide evidence of increased settlement on surfaces free from interspecies competition for space resource. This is not apparent in the study presented here (Figure 5.3.4.2), although this process cannot be discounted. Lower counts in the 2013 and 2014 year cohorts, after 12 months compared with 6 months post-settlement, could be the result of either reduced settlement (possibly owing to interspecific space competition) or greater post-settlement mortality, the latter being an expected result.

These data do not provide evidence of reduced *S. balanoides* settlement owing to free space competition with chthamaloid juveniles. Juveniles of *Chthamalus* spp. are much smaller and slower growing than *S. balanoides* and, during most of this study period, recruitment of *Chthamalus* spp. has been very low; unless *S. balanoides* recruitment was markedly reduced by the presence of juvenile chthamaloids, any difference in settlement would be expected to be 'masked' by continuing post-settlement mortality evident at the later observation date. With warmer climatic conditions, greater recruitment of *Chthamalus* spp. might be expected to have a greater impact on subsequent settlement of *S. balanoides*. Towards the end of the study period reported here, *Chthamalus* spp. recruitment dramatically increased (Figure 5.4.3.1). It might be expected that climatic conditions favouring chthamaloid success will result in sufficient recruitment to affect *S.*

balanoides settlement. Svensson *et al*. (2006) simulated this scenario using models informed by recruitment data from *Chthamalus montagui* and *S. balanoides*. Studies by Poloczanska *et al.* (2008), however, did not report changes in *S. balanoides* recruitment based on space pre-emption by *Chthamalus* spp. in SW England. In the current study, additional data from summer 2015 and continuing through 2016, as well as images captured during the reported study series at 6 month post-settlement intervals, may provide evidence to support this. Analysis of these data is beyond the scope of the studentship but is planned for the near future.

5.4.4 Gregariousness:

There is almost total recruitment failure of juvenile *Chthamalus* observed in 2013 on cleared rock surfaces (<10 recruits/10 cm^2) (Figure 5.3.4.1). This is in contrast to observations of juvenile chthamaloids on intact shores where the populations, while still reduced, were not as low (mean 15 recruits/10 cm^2) (Figure 5.3.3.4). This suggests that the reduced number of larvae, following possible reproductive failures of the previous two years, were differentially selected towards settling on intact shores, with only small patches of free space, rather than cleared surfaces, with greater space availability. This would be consistent with what is known of the gregarious nature of barnacle settlement: *S. balanoides* larvae are gregarious and tend to settle in higher densities on surfaces occupied by conspecifics (Knight-Jones and Crisp, 1953); gregariousness of juvenile settlement near remnant adults is also seen in *C. montagui*, although not as strongly (Kent *et al*., 2003). The distance separating balanoid spat will vary with density (Crisp, 1961). As free space begins to fill, distance between settling spat will decrease. Settlement of *S. balanoides* larvae depends on density of intact individuals, where increased density will tend to favour increased settlement (Kent *et al*., 2003). This relationship may provide a marine example of the Allee effect, more commonly seen in ‘closed’ terrestrial populations (Gascoigne and Lipscius, 2004). Hence, during low recruitment periods, settlement of *Chthamalus* spp. may be denser on smaller patches of open rock surface amid remnant adults, and less dense on much larger cleared areas without adult conspecifics. *C. montagui* recruitment correlates with background density, but less so than seen in *S. balanoides* (Kent *et al*., 2003). Gregariousness in *Chthamalus* spp. may help explain observations in SW England where zonation patterns matching adult distribution appear to occur during larval settlement (Jenkins, 2005). Further suggestion of gregarious settlement adjacent to conspecifics can be seen in this study when comparing Barnacle Index from intact and post-clearance juveniles (Figures 5.3.3.6 and 5.3.4.3). Barnacle Index observed in winter was markedly lower on cleared sites, when compared with intact sites containing conspecific chthamaloids, in 2013 and 2015, despite greater available space resource for settlement. No differences in Barnacle Index were seen between intact and cleared sites in winter 2014.

In comparison with *Chthamalus* spp., seasonal recruitment of *S. balanoides* on WMO featured far greater numbers and relatively less annual variation. Evidence of possible gregariousness in *S. balanoides* is found in comparisons of recruitment between intact and cleared shores (Figures 5.3.3.5, 5.3.4.2). Both experimental groups demonstrate clear seasonal patterns with similar maximal counts observed in summer. An important difference may be seen in the contrast between summer and winter counts, there are greater seasonal differences seen on intact sites. Seasonal fluctuations in juvenile count appeared to be ‘blunted’ on post-clearance sites, which also feature lower correlation coefficients in models using season (Table 5.3.4.2). Despite clearance providing almost 100% free space for *S. balanoides* settlement versus intact sites with small patches of available empty spaces, counts recorded in summer 2013 and 2014 were similar. While available space cannot be retrospectively quantified, this suggests greater density of recruitment onto intact shores. Figure 5.4.2 is consistent with findings by Kent *et al.* (2003), where settlement density will decline outwards from areas containing intact adults.

Figure 5.4.2: Evidence of gregariousness in barnacle settlement: the margin between cleared rock surfaces and intact *S. balanoides* features notably higher density of recent conspecific recruits - Northside, Birsay 4 July, 2016.

Gregariousness of settlement in *S. balanoides* to areas with adult conspecifics is the most obvious explanation for apparent different recruitment densities between experimental groups. This might also explain the more dramatic seasonal reductions in juvenile count seen on intact sites; greater settlement density might increase post-settlement mortality as growing conspecifics compete for limited space (Connell, 1985; Roughgarden *et al*., 1985; Jenkins, 2008). In contrast, less dense settlement of *S. balanoides* onto cleared surfaces would be expected to decrease competition for space between growing juveniles and may reduce post-settlement mortality. Alternatively, when comparing intact and cleared sites, other factors contributing to post-settlement mortality might be important, such as preferential targeting by *Nucella lapillus* of intact areas with larger barnacles

(Connell, 1961b). Removal of spat and juveniles by patellid limpets would be expected to affect post-clearance sites more where a film of microscopic algae and larger barnacle-free surfaces would tend to facilitate grazing (Hawkins, 1983; Hawkins *et al*., 1989).

In comparison with intact sites, experimentally-cleared sites may provide earlier detection of responses in barnacle recruitment owing to greater free space availability (Figures 5.3.3.4 and 5.3.4.1). However, differences in settlement density owing to gregariousness may make such interpretation more difficult; greater density of settlement onto less available space (e.g. intact sites) compared with less dense recruitment onto greater available space (e.g. cleared sites) may result in similar counts. On the other hand, interpretations of responses detected on cleared sites might be strengthened if these changes have been observed despite compounding and contrasting consequences of reduced gregariousness.

Results described here of the competitive zone between *Chthamalus* spp. and *S. balanoides* generally support the expected pattern of barnacle zonation with higher Barnacle Index in the upper versus lower zone. However, in these studies, close vertical proximity of upper and lower quadrats and semi-annual observations of recruitment do not allow resolution of whether this pattern was established by non-homogenous settlement (Jenkins, 2005) or through differential post-settlement mortality (Power *et al*., 2006). For example, recruitment of juvenile *Chthamalus* on intact shores is consistently higher in upper shore quadrats (Figures 5.3.3.4 and 5.3.3.6). However, this is not statistically significant, although shore height in Barnacle Index closely approaches significance (Table 5.3.3.6). This might be expected following non-homogenous settlement owing to gregariousness, but equally, post-settlement mortality differences associated with shore height cannot be discounted. Furthermore, juvenile *Chthamalus* spp. on cleared sites also display non-significant preferences in upper quadrat recruitment. Again, the processes of settlement preference and post-settlement mortality cannot be resolved, but clearance of conspecifics might tend to homogenise settlement owing to reduced gregariousness. Inclusion, in future, of 6-month post-clearance data might provide additional support for the role of gregariousness in settlement of *Chthamalus* spp. and *S. balanoides*.

5.4.5 Energy extraction and littoral barnacles:

The experiments described here were designed to provide evidence of long-term change in barnacle zonation and abundance on shores potentially impacted by removal of wave energy. These data are important in providing baseline information before deployment of devices, as well as identifying likely consequences of energy extraction. Wave data during this study could not be applied to recruitment data owing to time constraints but presumably might inform inferences on free space creation during storm events and, with wind data, on conditions during settlement. On sites of greatest wave exposure, barnacle zones are typically broad and extend high up the shore (Lewis, 1964); the *Chthamalu*s zone will tend to be dominated by *C. stellatus*, especially towards the northern range of the genus (Crisp *et al*., 1981). While opportunities to study direct effects of industrial-scale wave energy extraction on *in situ* rocky shores have not yet arisen, the following consequences might be expected in the barnacle zone:

- Narrowing of the zone;
- Lowering of the zone;
- Fewer destructive impacts from large sediment;
- Changes in relative abundance of species.

Expected consequences of extracting wave energy from the sea would include modification of zonation established by exposure levels. Relative to exposed shores, more sheltered conditions are typically associated with narrower zones, found lower on the shore, although vertical distribution is also strongly influenced by tidal range (Lewis, 1964). Energy extraction by WECs should reduce the height difference between the upper and lower zonal boundaries, and shift the zone downslope, relative to mean sea level. Reduction in sediment impacts on rocky shores, an expected consequence of lowering wave exposure, would result in less free space for subsequent barnacle settlement (Roughgarden, *et al.*, 1985). This might shift the relative role in population dynamics from settlement-based towards adult-mortality life-stage processes. How reduction in wave energy might affect overall abundance of barnacles remains unclear. On one hand, on more moderately exposed shores, Hawkins *et al*. (1992) has described cycling of barnacle abundance owing to equilibrium shifts with fucoids and patellid limpets, and variation in barnacle recruitment; over a ten-year study, Jenkins (2005) describes barnacle densities fluctuating by an order of magnitude; and Burrows *et al.* (2010) reported that settlement and population density of *S. balanoides* increased with exposure (as measured via fetch). In contrast, other studies have found that while the composition of the barnacle zone may shift in favour of one species over the other, the overall cover remains similar (Crisp *et al*., 1981; Power *et al*., 2011). A potential effect of reduced wave energy might be a shift in not only the relative distribution of *S. balanoides* and *Chthamalus* spp. but also in the chthamaloid zone, favouring *C. montagui* over *C. stellatus*.

Chthamalus montagui **in Orkney's future?:**

At lower latitudes, *C. montagui* is the dominant chthamaloid at most midshore levels and across the exposure gradient; at higher latitudes, *C. stellatus* is the dominant chthamaloid at higher exposure sites and at lower mid-shore levels (Sousa *et al*., 2000; Range and Paula, 2001). In the Plymouth area, Burrows *et al*. (1992) found that reproductive output differences between *C. stellatus* and *C. montagui* correlated with adult distribution pattern along a gradient of wave exposure. Studies by Power *et al*. (2011) predict that future climatic warming and drying will tend to favour *C. montagui* over *C. stellatus*, owing to greater tolerance to desiccation in the former. Reduction in wave exposure would be expected to increase desiccation stress, particularly on the higher zones. On this basis, large-scale deployment of WECs, as well as continuing increases in SST and AT, might be expected to benefit *C. montagui* over *C. stellatus*, at least in the immediate area 'downstream' of devices. Of course, population changes in chthamaloid congeners can only be addressed if sampling methods include reliable species identification.

Detecting changes in littoral barnacles following wave energy extraction:

How might changes in barnacle populations following industrial-scale extraction of wave energy be manifest using the methods described here? Observations, over many years of fixed height quadrats located in the current upper and lower portion of the transition zone between taxa, would be expected to capture long-term changes. If the barnacle zones were to narrow and lower as expected, the Barnacle Index, as recorded through the fixed height quadrats, will increase. However, even if chthamaloids were identified to species level, this method is unlikely to detect shifts in congeners unless additional shore heights were examined; while localised reduction in exposure might result in an increase in *C. montagui* relative to *C. stellatus*, this would be expected to be manifest mostly on the highest zones, far above the current transition zone.

The role of marine renewable energy devices as additional offshore habitats:

The potential for MREDs to function as ‘stepping-stones’ in facilitating movement of marine organisms has been identified (Shields *et al*., 2011) and is a concern regarding potential transport of non-native species (Nall *et al*., 2015). Furthermore, large-scale deployment of WECs may affect rocky shore ecosystems by providing both novel substrate for larval settlement, and, in turn, additional habitat for larval production by adult organisms (Miller *et al*., 2013; Adams *et al*., 2014). Effects on littoral barnacles would be expected at a highly localised scale; larvae spending longer durations in the water column will be largely unaffected by additional habitats provided by devices (Adams *et al*., 2014). Larger size of *C. stellatus* larvae, compared with *C. montagui*, suggest an adaptation which aids supply on more open shores (Burrows *et al*., 1999), such as those on WMO. MRED sites are selected based on the extreme wave resource created by high onshore winds, blowing across large fetches and driving powerful oceanic swell. While extraction of energy by WECs might affect the shoreline immediately ‘down-stream’ of the devices, as well as potentially create additional substrate for settlement, broad-scale changes in larval supply would not be expected in well-mixed (‘blue’) waters (Burrows *et al*., 1999; Menge, 2000).

5.4.6 Conclusion:

Low recruitment in barnacles could result from reduced fecundity in local adults, decreased larval supply (owing to unfavourable currents, reduced planktonic food, or predation in the water column), changes in behaviour negatively impacting settlement, or increased post-settlement mortality. Climate drives many of these processes making temperature indices suitable proxies for environmental influences on different life stages (Poloczanska *et al*., 2008). The present study shows low recruitment of the 2012 and 2013 cohorts of *Chthamalus* spp. suggesting a much reduced but continuous source of larvae. On WMO, there may have been collapse of reproductive activity of the adult population of *Chthamalus* following two consecutive extreme cold winters (2009-10 and 2010-11) and/or two cold summers (2011-2012). In the event of local collapse in reproduction, the only settlement might be expected from larvae transported by advection and diffusion from viable populations some distance away; sustained upwelling events might carry larvae offshore for sufficiently long enough that settlement does not occur at the adult habitat (Roughgarden *et al.,* 1988). In this case, recruits may have been supplemented from viable populations some distance south (Crisp *et al*., 1981; Gaines *et al.*, 2007). Without examination of reproductive status of this species on WMO and without evidence of larval transport in Orkney waters and, importantly, across the Pentland Firth, origins of settled larvae must remain speculative.

Prevalence of large adult *C. stellatus* individuals has been suggested as a consequence of long life span (10+ years) and irregularity in successful breeding (Crisp *et al*., 1981). As such, decadal-long life spans of *Chthamalus* spp. may allow the population at the extremes of its range to survive through multiple cold seasons (Mieszkowska *et al*., 2014).

When conditions favourably return, resident adults, or larvae from a neighbouring source location, may be able to repopulate losses from normal adult mortality. *Chthamalus* spp. might 'ride-out' several cold seasons with reduced reproductive output but still successfully respond when climatic conditions favourably return. The results on WMO closely match observations made of *Chthamalus* spp. at their northern distribution on continental Europe. Wethey *et al*. (2011) found recruitment failure but sustained adult presence of *C. stellatus* and *C. montagui* over cold periods from 2007-2011. In contrast, *S. balanoides* has a much shorter life span of 2-5 years (Mieszkowska *et al.*, 2014). This would suggest that at the extremes of *S. balanoides* range distribution, several consecutive poor years may have considerable consequences on intact adult populations. Relatively short life-cycle of *S. balanoides* may account for recent large-scale (20-25 km year^{-1}), climate-driven changes in distribution of *S. balanoides* as described by Wethey *et al*. (2011).

There is a clear increase in successful chthamaloid recruitment on intact shores observed in winter 2015 (Figure 5.3.3.4), as well as an upturn in adult *Chthamalus* spp. as suggested by the Barnacle Index (5.3.3.3). This appears to represent a reversal of reproductive success in *Chthamalus,* consistent with a return to warmer winters, two years prior and following release from competition with *S. balanoides* (Poloczanska *et al*., 2008). Overall, modelling outcomes indicate that temperature is more influential on recruitment of *Chthamalus* spp. than *S. balanoides*. These data suggest greater population stability of adult *S. balanoides* and greater differences in recruitment years in *Chthamalus* spp., as expected at its northern-most distribution limit. Climate-driven fluctuations in recruitment might be expected in a species at its latitudinal limit (Hiscock *et al*., 2004; Poloczanska *et al*., 2008; Wethey *et al*., 2011; Mieszkowska *et al*., 2014). In contrast, in

S. balanoides, adults might be expected to remain stable, although seasonal variations in juveniles is demonstrably strong. WMO is at or near the northern distribution limit of the genus *Chthamalus* but very much in the middle of the latitudinal range of *S. balanoides*. These data suggest that recent unusually cold conditions may result in reproductive failure manifest by the shifts in recruitment and adult count described here. Furthermore, temperature-driven successes in *S. balanoides* recruitment limit available space resource for subsequent chthamaloid settlement (Poloczanska *et al.*, 2008). Generalised linear modelling suggested a plausible association between temperature and recruitment but could not determine which specific events were of greatest importance.

Clearance experimentation has been used extensively in previous studies of barnacle settlement and recruitment. Semi-annual clearance methods were developed here as part of wider studies to establish baseline characterisation of important littoral species in an area where industrial-scale extraction of wave energy is planned for the near future. This strategy has allowed recruitment trends to be identified 12 months earlier on cleared versus intact sites. This method was explicitly designed to allow each taxon the opportunity to pre-emptively settle before their competitor, thereby allowing examination of the seasonal relationship with resource competition between *Chthamalus* spp. and *S. balanoides*. However, this method may create differing recruitment densities between intact and post-clearance sites (at least in the first year); inferences must consider the role of gregariousness when comparing experimental groups. Owing to the importance balance between density-mediated repulsion and conspecific-mediated gregariousness in barnacle settlement (Kent *et al.*, 2003), background density and free space may need to be quantified prior to settlement periods to more fully understand these processes

(Minchington and Scheibling, 1993). Burrows *et al*. (2010) has recommended *S. balanoides* as an ideal candidate for studies linking recruitment to adult density.

Recruitment of *Chthamalus* spp. at its northern latitudinal limit is affected by space resource restrictions created by *S. balanoides* settlement earlier in the year. While the reverse scenario does not appear to be important in Orkney, further south, especially towards the southern limit of *S. balanoides* distribution, recruitment of *S. balanoides* might be influenced by competition for space availability following chthamaloid settlement. Perhaps current climatic conditions in Orkney are not compatible with chthamaloid reproduction; Burrows *et al*. (1992) reported that brooding and larval release only occurred in *C. montagui* when SST was >15°C, temperatures almost never seen in these waters. Orkney studies would benefit from seasonal assessment of reproductive status of resident adults.

Long-term changes in exposure through extraction of wave energy did not occur during this pre-deployment experimentation. The methods developed, however, have captured seasonal and annual changes in barnacle recruitment and would be expected to similarly detect responses which might occur following removal of wave energy. Using this model of competitive zonation, reduction in exposure would be expected to lower (vertically) and narrow barnacle zones, and possible result in a population shift in the upper zone from *C. stellatus* to *C. montagui*. Clearance methods used here might be expected to allow responses to wave extraction to be observed earlier than through studying only intact surfaces.

Chthamalus spp. and *S. balanoides* are key components of rocky shore communities in the British Isles and these species are recognised indicators of temperature change. As such, the competitive zone between *Chthamalus* spp. and *S. balanoides* is ideal for long-term studies of energy extraction on WMO, against a background of climatic change. The consequences of reduced exposure by WECs should be limited to local scale processes, ‘downstream’ of deployment; in contrast, anticipated shifts in barnacle populations owing to climatic change, would be expected to occur at a broad scale. BACI-style experimental design should capture data necessary to identify the relative roles of these two long-term forcing agents. Disentangling the effects of energy extraction from WECs and changes due to anticipated temperature increases may be further complicated, however, by increased storminess predicted in some meteorological models (Young *et al*., 2011; Collins *et al*., 2013; Woolf and Wolf, 2013).

Data presented here are limited by the time necessary to analyse images. While the main points have been addressed using this restricted analysis, further information might be gleaned from analysing data gathered at other post-clearance intervals, in particular 6 months and 18-months post-clearance. Once analysed, images from Northside in Birsay will allow spatial comparisons between shores. Furthermore, inclusion of Birsay will provide data from shores of even greater exposure, differently orientated to the prevailing wave direction. Shore height has not been reliably identified as a statistically significant factor; this may owe to the close proximity of upper and lower quadrats in the current transition zone. Future studies would be improved with the inclusion of additional intact and cleared quadrats located above and below current quadrats, although labour may again be a limiting factor.

Consequences of replacement of *S. balanoides* by *Chthamalus* spp. may extend beyond observed changes in the rocky shore barnacle guild. The replacement of a major planktonic food source by another species, i.e. larvae from *Chthamalus* spp. instead of *S. balanoides*, with different reproductive seasons and outputs, may have unpredictable effects on higher trophic levels (Southward, 1991; Hiscock *et al.*, 2004; Hays *et al.*, 2005). In this manner, the use of barnacles as indicators of climatic change may provide ‘early warning’ of ecological changes beyond just the rocky shores.

Chapter 6 - Conclusions and suggestions for further work:

The studies reported in this thesis have examined the relationship between rocky shore assemblages and exposure in an area where industrial-scale extraction of wave energy may be occurring in the near future. During these studies, responses in rocky shore organisms to variations in exposure and other factors that might produce long-term change in the littoral environment were examined. Methods utilised in these studies have included broad-scale assemblage surveys, and monitoring and manipulation of important littoral species found at or near their distribution limits. These studies have been designed to allow a BACI-style characterisation of WMO which may allow comparison with future conditions following energy extraction or climatic change, and to assess select species as potential indicators of changes in the rocky shore community following removal of wave energy, against a background of climatic change.

The western shores of Mainland, Orkney provide an ideal ‘field laboratory’ to develop methodologies for long-term monitoring of rocky shores, specifically in relationship to alterations in wave energy profile. As the major focus of MRED testing and industrial-scale deployment in the foreseeable future, biological studies here are uniquely placed to help assess ecological consequences that may follow these developments. Previous monitoring studies in Orkney, largely associated with the expansion of the oil and gas industries in the 1970s, have examined several habitats around the county, which have been mainly monitored on an annual basis, with some seasonal studies occurring at quarterly intervals (e.g. Baxter *et al.*, 1985). Previous rocky shore studies on Orkney have been conducted at more moderate levels of exposure than the current studies (Baxter, 1982). The location of the Orkney campus of Heriot-Watt University has allowed year-round access possibilities and for study to be conducted by the same observer over several years, mitigating issues of sampling consistency between researchers. The rocky shores of WMO provide a richness of candidate indicator species, inclusive of ‘southern’ and ‘northern’ organisms, living at the edge of their distribution range, and representing important community structuring organisms at different trophic levels. The current studies feature detailed characterisation of many sites not previously described scientifically, and are the first to specifically address the nature of wave energy effects on the rocky shore community in Orkney at the extreme end of the wave energy spectrum. In areas of highest wave resource targeted by the MRE industry, i.e. the northern and western shores of the British Isles, species such as *F. distichus anceps* may be one of only a small number of organisms suitable for use as a long-term monitoring tool. Nevertheless, a suite of indicator species specialised to this extreme environment may be helpful to studies specific to the MRE sector.

6.1 Assessing reduced exposure following wave energy extraction:

Deployment of MREDs is expected to contribute significantly to governmental projections of electricity generation from renewable sources (The Scottish Government, 2013). The ecological consequences of reducing exposure at the large scale associated with this development, however, are not well understood; a potentially important locus for responses to wave energy extraction is the rocky shoreline. While it is reasonable to wish to quantify the degree to which exposure is reduced by the operation of WECs, an ecologically meaningful answer to this question is not yet possible. The design and specifications of WEC devices are often related to particular aspects of the wave climate, such as wave length and frequency, targeted by developers (Twidell and Weir, 2015). Thus, the consequences of extracting wave energy might be expected to differ depending not only upon species-specific exposure adaptations, discussed in this document, but also device-specific energy capture characteristics. Complicating these potential impacts are expected fluctuations in exposure and the biological community owing to seasonal patterns of change, less predictable cyclical community changes, and long-term alterations in climate.

As of early 2017, WEC deployment in Orkney has been limited to testing of individual devices at the EMEC test area off Billia Croo; the consequences of large-scale extraction of wave energy remain to be assessed in practice. One such device tested extensively at EMEC is the Pelamis WEC which generates energy through the flexing of couplings joining several, 3.5 metre-wide, modules floating on the sea surface (Twidell and Weir, 2015). Monthly estimate of power output for a 750 kW Pelamis WEC located off Orkney during the most exposed month (January) is 178.1 kW; an annual power output graph for this device is shown in Figure 6.1 (Neill *et al*., 2014), dependent on the number of modules deployed in a single device. In a hypothetical scenario where 20 of these WECs are deployed along 5 km of Orkney's west coast with an estimated January offshore wave resource of 30.5 kW/m (Neill *et al*., 2014), wave extraction would total 3.56 MW out of an overall resource of 152.5 MW[5]. Whether or not a 2.3% reduction in wave power, as this scenario describes, would result in observable consequences 'down-stream' of the devices remains unknown. Furthermore, the number of devices that may be deployed, and the hydrodynamic implications of different array formations remain theoretical (Stratigaki *et al*., 2015; Forehand *et al*., 2016).

Comparing biological communities between sites of varying topography can provide contrasts in ecological responses to elements of exposure which may augment our ability

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[5] Based on 20 Pelamis devices x 178.1 kW = 3.56 MW; 5,000 m of coast x 30.5 kW/m = 152.5 MW.

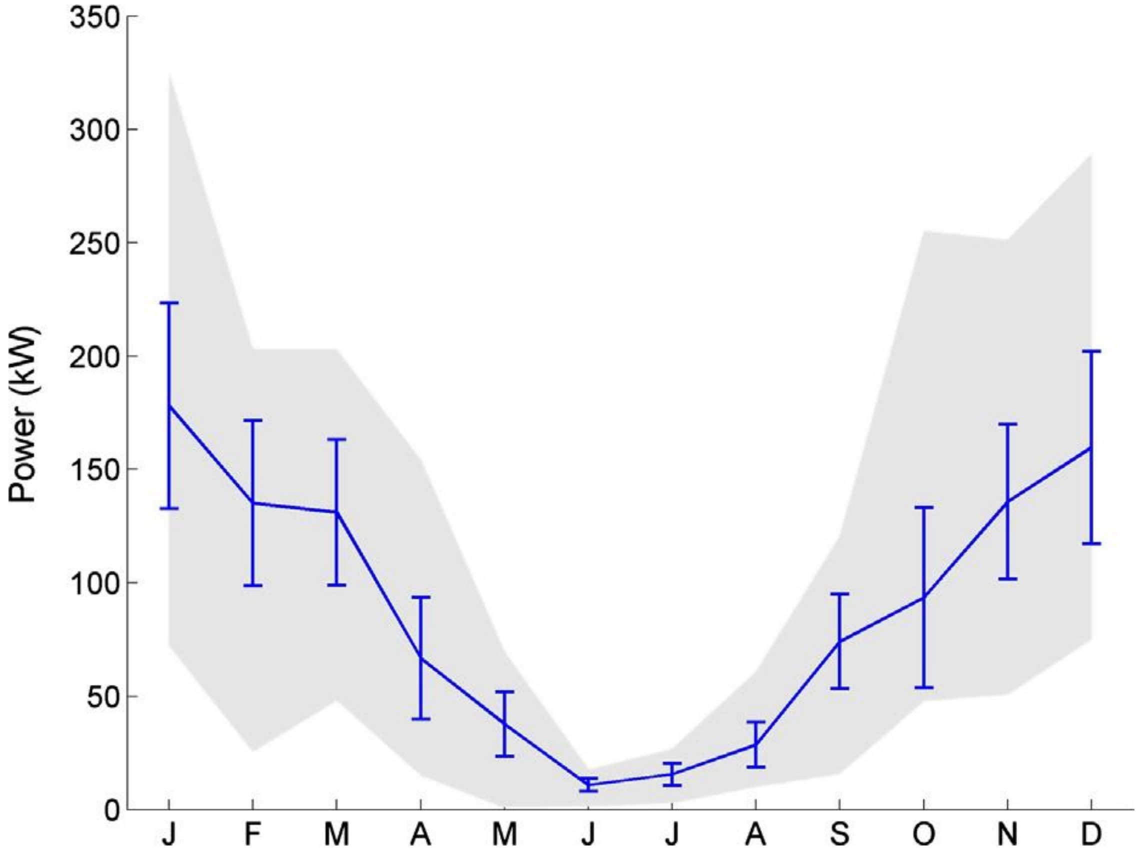

Figure 6.1 Power output for a WEC: Annual cycle of monthly power output for a750 kW Pelamis device located off WMO. Error bars show 90% confidence intervals, and grey shading indicates range. From: Neill *et al*. (2014).

to predict impacts following energy extraction. The littoral community on topographically similar shores in close proximity differing in slope may provide the clearest examples of how organisms respond to varying exposure, recalling that slope affects other ecological processes beyond just those relating to exposure and that the importance of slope may vary with different species (Figure 3.3.1.2). Models of surf-zone interactions between energy and substrate have proved useful (Peregrine, 1983; Smith, 2003), especially when considering biological receptors of exposure (Denny, 1999; Gaylord, 2000; Lindegarth and Gamfeldt, 2005); improvements in quantitative assessments of wave energy in the littoral zone are welcomed. The current studies provide a detailed pre-development assessment of biological conditions to compare with future surveys. Rocky shore assemblages along WMO typically feature organisms adapted to survive extreme wave exposure. This community includes high-energy variant fucoids, a well-defined barnacle zone featuring *C. stellatus*, and mobile molluscs, such as *P. ulyssiponensis* and *N. lapillus*. Following energy extraction, a transition would be expected towards lower energy fucoid species and forms, patchier populations of barnacles featuring a larger proportion of *C. montagui,* and greater diversity of mobile molluscs including *P. vulgata*, and littorinid and trochid snails (see Section 3.3.1).

6.2 Other long-term changes on WMO:

Within the scope of the current studies, energy extraction by WECs did not occur beyond short-term testing of individual devices at the EMEC wave test site at Billia Croo. However, other long-term studies of species distribution suggest that the ranges of certain littoral organisms may be expanding or contracting in and around the Orkney archipelago because of climate change (Mieszkowska *et al*., 2013; Burrows *et al*., 2014; Hawkins *et al*., 2016). Climate change is a multi-factorial alteration in the marine environment, involving changes in sea temperature and increased storminess, amongst other effects, and may shift shoreline communities to those favouring warmer seas and higher-energy, wave exposed conditions. Similar to consequences following energy extraction, exactly how changes in storm events might affect the community is not well understood (Thomas, 1986; Blanchette *et al*., 2008) but will depend upon species' adaptations to exposure: some organisms may be more responsive to changes in average, long-term wave exposure; other organisms may respond more to acute, extreme storm events (Siddon and Witman, 2003; Ruuskanen and Nappu, 2005; Wolcott, 2007). Assessment at fine scale by Helmuth and Denny (2003) demonstrated that on most evaluated sites definable limits to hydrodynamic force were reached as wave height increased, suggesting that increased storm activity may not result in proportional increases in littoral exposure. In addition to sea temperature and storm condition considerations associated with global climatic change, long-term monitoring protocols may need to account for changes in sea level. This may be particularly important in long-term, time-series studies using fixed reference points in the vertical plane such as barnacle clearance studies or intertidal seaweed imaging used in the present work. Recent analysis of the relationship between post-glacial isostatic change of the Scottish landmass and sea level increases due to global temperature increases predict an accelerating rise in relative sea level (RSL), with the Orkney archipelago among the most affected areas with RSL rising by approximately 6 mm/year (Rennie and Hansom, 2011).

Identifying observable long-term changes and distinguishing between the relative roles played by individual forcing agents are the greatest challenges facing this programme. The development of paired-species and multiple indicator monitoring may provide the ability to dissect out the potential effects from energy extraction from those potentially arising from climate change (see Section 2.1: Biological responses to environmental changes). The use of species pairs to provide proportional data offers four main advantages over studying single species responses: (i) it is necessary only to know the relative preferences of the two species to an environmental variable rather than have a detailed knowledge of their response curves – the precise adaptations of rocky shore organisms to energy conditions have not been fully explored; (ii) changes in proportions are easily interpreted in terms of environmental changes, since the response is likely to be highly directional; (iii) measurement of proportions is not dependent on being able to quantify habitat areas on rocky shores; and (iv) proportions may offer higher statistical power to detect changes than single species responses (Want *et al*., 2014). Greater discriminatory power in determining the relative roles of energy extraction and climatic change may be achieved through monitoring a suite of indicator organisms differentially responsive to each environmental variable. Results from the current studies confirm the use of littoral barnacles in time-series data relating to temperature changes, and support the use of *F. distichus anceps* as an indicator of changes in exposure. Additional littoral species, such as *Anemonia viridis*, *G. umbilicalis*, *P. ulyssiponensis*, and *T. testudinalis,* have been identified as suitable subjects for studies of responses to energy extraction or climatic change on WMO, but further data are required to substantiate these potential roles locally.

6.3 Review of cliff survey studies:

Surveys along WMO and Lewis have provided biological and topographic data along extensive areas with limited previous scientific description (see Chapter 3). In summary, these data have provided the following:

- a comprehensive assessment of pre-development biological communities;
- baseline and control data to compare potential future changes following reduced wave exposure or other long-term forcing agents such as climatic change;
- pre-deployment determination of abundance of potential indicator species and identification of suitable locations for further study;
- description of topographic variables which may play important roles in littoral exposure by modifying wave energy dissipation;
- description of biological responses to these modifiers, which may aid prediction of responses to energy extraction;
- development of a novel exposure index based on inclusion of weighted topographic factors (Appendix 6).

Exposure indices:

Despite the clear and long-recognised relationship between wave exposure and the biological community on rocky shores (Ballantine, 1961; Lewis, 1964), quantification of exposure has remained a challenging task (Lindegarth and Gamfeldt, 2005). All too often, marine ecologists accept these difficulties and simply assign broad categorical scales to levels of exposure (Burrows *et al*., 2008). Cartographically-based assessment of exposure can be refined with inclusion of wind and topographic data (Thomas, 1986; Isæus, 2004; Burrows *et al*., 2008; Sundblad *et al*., 2014). In the current studies, an approach has been developed which captures the main facets of variability in wave energy interaction with the shoreline (see Table 3.2.1.2 and Appendix 1). The current studies confirm the importance of modifying fetch-based models with locally derived topographic data. *In situ* recording of topography at individual site-scale provides additional data, not captured through cartographic assessment, which may improve exposure modelling at the scale of metres rather than a broader approach based largely on fetch.

Differences in assemblages between rocky shore sites with similar offshore wave resource are primarily created by topography, in particular structural complexity of the substrate and shore slope (see Section 3.3.5). On the surveyed shores of NW orientated Lewis, high complexity and low slope of rocky shores results in sufficient wave energy reduction prior to reaching the shore that organisms associated with relatively lower exposure can survive. In contrast, on WMO, steeper slopes and uncomplicated platforms tend to be exposed to the relatively unmodified, ‘full force’ of the sea, helping create assemblages featuring extreme wave energy specialists (see Section 3.4: WMO v Lewis). Data from rocky shore surveys on WMO and Lewis have also provided evidence that the role of topographic variables on rocky shore assemblages may be specific to individual community members: the high exposure species *P. ulyssiponensis* and *F. distichus anceps* contrastingly correlate with shore gradients (Section 3.4: *Patella ulyssiponensis* and *Fucus distichus anceps*). In short, exposure may mean different things to different receptor species.

Improvements in current rocky shore survey method:

Several areas for improvement in the current method of rocky shore survey and analysis have been identified. Shore orientation did not perform well in models correlating assemblages with topographic features. This may be owing to current imprecisions in spatially and temporally defining dominant direction of wave energy. In future, wind directional data could be applied to models on a site-specific and temporally-varying scale, and inclusion of local bathymetric data may allow more precise evaluation of energy dissipation through refraction. Future studies could be improved with greater cognisance of testing the correlation of assemblages at different shore heights with exposure. Thomas (1986) found that correlation with exposure was strongest at supralittoral zones when compared with lower zones; quadrat data from the current fucoid studies on WMO support this relationship (Table 4.4.1). Additional collection of data, properly designed to allow comparisons between the biological community, shore heights, and exposure, would complement existing unanalysed barnacle images recorded during the WMO surveys at low, mid, and upper shore heights. This might provide further evidence to support the association between shore heights and exposure.

Technical improvements: quantifying exposure

Development and application of technologies which allow more precise quantification of variables such as wave energy and substrate complexity will improve exposure modelling. The novel ‘Want Index’ incorporates site-specific weighting of wave energy modifying variables to characterise exposure (Appendix 6). Knowledge of local conditions used in this index may allow application to other coastal areas; cognisance of defining scale will be necessary for transferring of exposure indices to novel locations.

Currently, wind speed and directional data are typically used as a proxy for characterising wave resource at a local scale. Broad satellite-based assessment of offshore wave resource at the present, lacks the nearshore resolution necessary for application to biological data at an ecologically meaningful scale (Gulev *et al.*, 2003; Hughes and Heap, 2010; Gallagher *et al*., 2014). The use of wave data collected by buoys to characterise littoral exposure may be limited by restricted deployment of these devices in relatively deep, offshore locations (Folley and Whittaker, 2009). Improvements in characterising nearshore wave resource may remove the need to substitute wind data in estimating exposure.

Quantification of topographic variables, e.g. substrate complexity, will benefit from technical improvements in collection and analysis of data (see Section 3.4: Substrate complexity). Littoral exposure characterisation may be improved through application of emergent technologies currently applied in quantifying sublittoral habitats and the dissipative effects of nearshore features. UAVs and satellites employed in image capture may allow quantification of several topographic variables of importance to exposure modification, e.g. with necessary input data, complexity can be mathematically described as deviations from a planar surface (Pirtle *et al.*, 2015). Remote image sensing technologies may also be applied for rapid, quantifiable assessment of biological communities and topography, and on hard-to-access rocky shores where data collection is impractical or unsafe. Combining broad-based fetch and off-shore bathymetric data with local topographic measurements may allow a more holistic approach to describing exposure. Furthermore, the same principles of nearshore wave dissipative processes affecting littoral habitats could be applied to sublittoral studies related to wave or tidal exposure.

Classification of 'extremely exposed' shores:

Classification systems developed to express community differences over broad geographical regions use energy exposure as one of the main 'top-end' criteria (Connor *et al.*, 2004; EEA, 2008). Rocky shore communities are assigned to biotopes defined partly on a fetch-based evaluation of exposure. Limits in precision of exposure determination used in classification can lead to two shorelines being similarly described ecologically but subject to variable energy regimes (Helmuth and Denny 2003; Ruuskanen and Nappu, 2005); broad categorical descriptors may mask continuous variability in physical mechanisms of exposure (Lindegarth and Gamfeldt, 2005). *In situ* wave quantification on the foreshore of Orkney has shown that rocky shore sites under the same biotope description may contrast with a greater than two-fold difference in average winter wave exposure (Want *et al.*, 2014). It is outside the scope of this thesis to posit a reformed list of biotopes for high wave-energy rocky shores. However, it is relevant to acknowledge that with greater ability to quantify exposure, and to do this at more ecologically meaningful scales, may come a revision of biotope categories. As they stand, existing categories may not always capture all of the parameters necessary to discriminate biological communities as they change in relationship to exposure.

6.4 Review of fucoid studies:

The current fucoid studies have fulfilled the objective of assessing the suitability of *F. distichus anceps* as an indicator species for changes following energy extraction and increased temperature. These studies have successfully utilised several methods to evaluate responses to environmental variables through changes in growth rate and abundance, however, opportunities for improvement have been identified. Image analysis of quadrats (*F. distichus anceps* and *F. vesiculosus* f. *linearis*) and fixed view-point imagery (*F. distichus anceps*) have demonstrated seasonal changes in percentage cover which may be of value in detecting long-term changes, and have captured a zonation shift event in *F. distichus anceps* suggesting recruitment synchrony over a kilometres-scale geographic area. Measurement of individual plant growth through maximum frond length was the most labour-intensive of the methods used in this study. This method also proved problematic in that rate of change in maximum frond length did not correlate as expected with seasonal patterns of growth and regress observed in quadrat percentage cover analysis; maximum frond length may not be a good representative metric of the overall size of the plant (see Section 4.3.5). Perhaps the limit of maximum frond length is set predominantly by hydrodynamic conditions and is less indicative of the growth status of the plant or season of measurement. Additional issues experienced on WMO with measuring individual specimens arose from the loss of *F. distichus anceps* plants on the highest exposure sites and the nebulous concept of ‘individual’, the latter may be especially true in species such as *F. vesiculosus* f. *linearis* where several fronds may grow from a single perennating holdfast. Regarding the issue of high turn-over rate of *F. distichus anceps* individuals however, without these complementary studies at the scale of individual plant, differences between *F. distichus anceps* and *F. vesiculosus* f. *linearis* in the processes underpinning seasonal growth and regress observed in larger scale methods, i.e. quadrat analysis, would have remained unexplained (see Section 4.4: Individual stability of *F. distichus anceps*).

Alternate strategies used by other researchers to determine individual plant size in fucoids have included imaging individuals against a white background and determining planform area through image analysis (Blanchette *et al.*, 2000). While this method is more onerous on data sampling and analysis, it may provide a better assessment of individual size by including additional growth dimensions beyond simply maximum frond length. Other methods of studying fucoid growth worth considering include measuring surface area and fresh weight of apical tips (Schonbeck and Norton, 1980; Twigg, 2011), and measuring other vegetative features known to be responsive to changes in wave exposure, such as number and distance of dichotomies along fronds, and stipe length and width (Schonbeck and Norton, 1981; Rice *et al.,* 1985).

F. distichus anceps presence and abundance demonstrates a strong relationship with exposure manifest in a relatively narrow ‘window’ along the hydrodynamic gradient, and may be of value as an indicator species of changes in wave energy. On WMO, steeply sloped, uncomplicated platforms appear to create the ideal hydrodynamic conditions in the mid shore to allow survival of *F. distichus anceps* (see Section 3.4: *Patella ulyssiponensis* and *Fucus distichus anceps*). Similar topographies with populations of *F. distichus anceps* have been reported in County Clare, Caithness (Powell, 1957a, 1963) and Lewis (Want, pers. obs.). That these populations persist over a decadal-plus scale suggests that local topographic conditions create stable hydrodynamic conditions for survival of this species. On shores with exposure levels below this ‘window’, *F. distichus anceps* is out-competed by other fucoids; with exposure above this ‘window’, the rate of tattering may lead to reproductive failure and whole plant loss may make persistence untenable. On the high exposure shores of WMO, extraction of wave energy might be expected to favour other fucoids, such as *F. vesiculosus* f. *linearis*, at the expense of *F. distichus anceps*.

The role of *F. distichus anceps* as an indicator of climatic change, manifest through increased SST, however, has not been established. Fifty years after Powell described the Orkney population of *F. distichus anceps* (Powell, 1963), its distribution remains stable and limited to the same high energy rocky platforms along West Mainland (see Section 3.4: Population stability of *F. distichus anceps*). Similarly, persistence of highly localised populations on extremely exposed coasts on the west of Ireland, suggest that for a ‘boreal’ species, this organism is surprisingly tolerant of warm seas (Twigg, 2011). Despite its diminutive size, *F. distichus anceps* may play an important role in providing canopy cover and as a food source for grazers; further research would help determine the ecological role of *F. distichus anceps* on high-exposure shores.

Methodological improvements in fucoid studies:

The current studies can be considered an important step in a better understanding of the ecology of fucoids on the extreme wave exposed rocky shores of WMO. It is recommended to continue this long-term monitoring programme, with certain methodological improvements. In addition to utilising alternative individual measurement methods described above, some of the practical issues in the current studies faced on the most exposed shores (e.g. difficulties in accessing quadrats and high loss of individual plants) might be resolved by expanding studies over a careful selected and wider range of exposure sites. In hindsight, quadrat studies would have benefitted from a properly replicated factorial design (Hawkins *et al.*, 1992). Future studies should be designed using multiple sites representative of the full range of energy tolerances and zonal heights for *F. distichus anceps* incorporating within and between shore contrasts within a fully-nested sampling protocol (Wernberg and Thomsen, 2005). This may address unresolved research on individual growth rate in *F. distichus anceps* and response to exposure at different zonal heights, as described above.

Clearance experimentation on fucoids:

In addition to improvements to the current monitoring methods, there is plenty of scope for experimental research of fucoids on WMO, including incorporating patellid limpet studies. Clearance experimentation on macrolagal has a long history (Burrows and Lodge, 1951; Lubchenco, 1980; Schonbeck and Norton, 1980; Hawkins and Harkin, 1985; Hawkins and Hartnoll, 1985) and includes work on *F. distichus* (Edelstein and McLachlan, 1975; Klinger and Fukuyama, 2011). Previous fucoid studies have experimented with removal or exclusion of important grazers including: *P. vulgata* (Jones, 1948; Hawkins, 1981a, b; Jenkins and Hartnoll, 2001; Coleman *et al.*, 2006; Jonsson *et al.*, 2006; Davies *et al.*, 2007; Moore *et al.*, 2007); *P. depressa* (Jenkins *et al.*, 2005; Coleman *et al.*, 2006; Moore *et al.*, 2007); other molluscs (Lubchenco, 1983; Anderson and Underwood, 1994); and echinoids (Lubchenco, 1980). Other researchers have experimented with transplanting fucoids, at times using ingenious experimental designs (Schonbeck and Norton, 1978, 1980; Blanchette *et al.*, 1997; Jonsson *et al.*, 2006).

Clearance experimentation of *F. distichus anceps* has been planned at sites on WMO, including Axna Geo, Northside in Birsay, and Marwick. Axna Geo was selected owing to the presence of an extensive zone of abundant, large *F. distichus anceps* plants providing considerable canopy habitat. Reference markers for dGPS recording of shore height have been secured (Table 4.3.3) and methodological development of individual size determination using planform imagery has been explored. It is hoped that this site will be part of a wider examination of competition between *F. distichus anceps* and other macroalgae, and canopy formation by the latter. Competition from other macroalgae at the upper height limit of *F. distichus anceps* is not expected; zones of *F. spiralis* f. *nanus* (when present) and *Porphyra umbilicalis* are typically located sufficiently far above *F. distichus anceps* for this interaction to be unlikely. Zones below *F. distichus anceps* often feature less densely-populated patches of *Mastocarpus stellatus*; abundant zones of *Himanthalia elongata* are typically found distinctly separate on lower shores. In a similar manner to barnacle clearance experimentation in the present study, observations of recovery following removal of *F. distichus anceps* plants may allow more rapid detection of responses than through monitoring only intact populations.

Grazer studies:

Experimental fucoid studies on WMO may be designed to include research on patellid grazers. Variability in algal recruitment has been shown to temporally affect limpet recruitment success in *P. vulgata* (Baxter, 1982) and the impacts of overall rocky shore grazing (Sousa, 1985), while in turn, grazing by *P. vulgata* mediates percentage cover of fucoids (Hawkins, 1981a, b; Moore *et al*., 2007). On high exposure shores, however, grazing effectiveness may be reduced (Blanchette *et al*., 2000). Studies of *P. vulgata* and

P. depressa show that limpet congeners in similar habitats may display different behavioural response to ecological change (Moore *et al*., 2007); the effects of grazing activity of *P. ulyssiponensis* on the high exposure rocky shores of WMO have not been reported. A relatively simple improvement to the current fucoid study methodology would be to collect data on the abundance, species identification, and congregation patterns of patellid limpets beneath canopies of *F. distichus anceps* and other high-energy variant fucoids. With sufficient resources, manipulative experimentation of *F. distichus anceps* canopy and grazers on high exposure WMO sites (*sensu* Jenkins *et al*., 1999) may provide important new insights into the phenology of *F. distichus anceps* and *P. ulyssiponensis,* and the role of canopy formation and grazing pressure on extreme exposed shores. Such studies should include analysis of substrate owing to the association between *P. ulyssiponensis* and encrusting calcareous red algae (Firth and Crowe, 2010).

Fucoid genomics:

The stability of *F. distichus anceps* populations on geographically-isolated sites, especially at the southern distributional limit, suggests that these populations may be relicts remaining from periods when climatic conditions were more favourable to this species (Powell, 1957b; Coyer *et al*., 2011). Similar conclusions have been reached regarding southern populations of the ‘boreal’ seaweed *Palmaria palmata* (Provan *et al*., 2005). The genetic connectivity of populations of *F. distichus anceps* and other high-energy variant fucoids, e.g. *F. spiralis* f. *nanus*, is unknown (Serrão, pers. comm.). The known strategy of gamete dispersal in *F. distichus* is for external fertilisation and settlement to occur at a scale of metres (Pearson and Brawley, 1996), making the passing of genetic information between more isolated populations of *F. distichus anceps* impossible through this means. Studies of the sea palm, *Postelsia palmaeformis*, by Paine

(1988) suggest that loss of fertile apices with thallus tattering might be an important method for gamete dispersal. Whether or not this reproductive strategy is utilised by *F. distichus anceps* is not known but this may be a means for propagule dispersal between geographically isolated populations (Serrão, pers. comm.). If this is the case, then hydrodynamic connectivity is an important considerations and alterations in water movement may have important consequences to these populations. Phylogenetic studies of *F. distichus* suggest that this organism originated in Pacific waters and migrated across northern Canada into the Atlantic during geologically-recent ice-free periods (Coyer *et al*., 2011). These studies however, do not include samples from Britain or Ireland and do not include published results of *F. distichus anceps*. The phylogenetic relationship between populations of *F. distichus anceps* within British waters and with populations in the wider North Atlantic remain unknown. Genetic characterisation of geographically-isolated populations of this species in British waters might provide important information regarding their long-term history and hydrodynamic connectivity. *F. distichus* is highly prone to self-fertilisation (McLachlan *et al*., 1971); isolated populations may be more genotypically homogenous and therefore increasingly vulnerable to ecological changes.

6.5 Review of barnacle studies:

Barnacle research described here supports the observation that long-term climatic changes and more acute weather events can influence species abundance and distributions (Poloczanska *et al*., 2008; Wethey *et al*., 2011). The current studies include the first experimental research of barnacles in Orkney, located around the northern distribution limit of chthamaloids. The start of these studies coincided with the ending of a series of the coldest winters seen in Europe in almost half a century. This presented both a challenge, to interpret ecological processes occurring during a relatively volatile climatic period, but also an opportunity, to observe responses to more dramatic seasonal temperature events. During the present studies, the juvenile population of *S. balanoides* fluctuated seasonally with large recruitment observed in the summer followed by high mortality before observation in the winter. During the study period, *S. balanoides* recruitment was highest in summer 2013 which may relate to recent prior periods of cold weather (Figure 5.3.3.5). Between 2012 and 2015 adult *Chthamalus* spp. population decreased and recruitment was very low, until a marked increase in juvenile count on intact shores occurred in 2015; on experimentally cleared shores, an increase in juvenile recruitment occurred one year earlier, in 2014 (Figures 5.3.3.4 and 5.3.4.1). Thus, by creating free-space and observing recruitment, this clearance method, helped to detect responses more rapidly than through studying only intact barnacle populations.

In addition to researching acute temperature responses at the northern range limit of *Chthamalus* spp., these studies are believed to be unique in that experimental clearance was conducted semi-annually with the explicit intent of creating free space for recruitment both before and after settlement opportunities provided to each competitive barnacle. These experiments showed that *Chthamalus* recruitment onto recently cleared surfaces pre-settled by *S. balanoides* was reduced owing to free-space competition; the reverse scenario, where pre-settlement by *Chthamalus* may limit *S. balanoides* recruitment by pre-empting free space might occur but could not be determined in this study (see Section 5.4.3). Recruitment of juvenile *Chthamalus* spp. onto cleared surfaces was often reduced compared with recruitment onto small patches found on intact shores, suggesting conspecific gregariousness may promote settlement (see Section 5.4.4).

The clearance methodology, including the use of fixed reference markers to reimage column at the same shore heights at different intervals, was successful. The present studies also explored various methods for analysing barnacle images, as well as describing intact background populations in terms of count, percentage cover and average size of barnacles. Comparisons between image data found that determination of count was as effective as percentage cover in detecting seasonal and annual population changes but far less labour intensive. Direct assessment of response to changing exposure in barnacles was not possible in this study but evidence suggests that barnacle zonation may provide another valuable model for studying the effects of energy extraction (see Section 5.4.5).

Future of time-series barnacle studies at the north range limit of *Chthamalus* spp.:

The most obvious recommendation for future studies is the continuation of the time-series at Marwick and Birsay using the same semi-annual clearance protocol. This has proven an effective means of capturing relevant data and identified responses more rapidly than through observations of intact populations alone. To date, barnacle analysis has been completed on all intact and 12-month post-clearance quadrat images at Marwick. Awaiting analysis are all images from Birsay and additional post-clearance intervals at Marwick. Data from Birsay will allow spatial comparisons between shores, and provide data from populations exposed to greater wave energy and on a differently orientated site. While the main points have been addressed using analysis restricted to intact and 12-month post-clearance data, further information might be gleaned from analysing data gathered at other post-clearance intervals, in particular 6 months and 18-months post-clearance.

While 6-month post-settlement quadrat images only record recruitment of one of the competitive barnacle species, analysis might allow even earlier detection of responses which may otherwise be first apparent after observations made 12 months post-clearance. Observations made 6 months after clearance cannot directly resolve questions regarding settlement processes, but providing data closer to the period of settlement may allow additional inferences about gregariousness and space competition of larvae, as well as offer further insights regarding post-settlement mortality. 18-month post-clearance observations will give the opportunity to assess the role of gregariousness and free-space on cleared patches of rock with and without prior conspecific recruitment one year earlier.

Settlement behaviour of larval barnacle tends to be affected by density-mediated repulsion and conspecific-mediated gregariousness (Kent *et al.*, 2003). To study the relative roles of these processes more fully, quantification of background density and free space availability on intact shores could be included in future study design (Minchington and Scheibling, 1993).

In the current barnacle studies, the percentage cover of *Mytilus edulis* was included in analysis of quadrats (Table 5.3.1.1). Abundance of *Mytilus edulis* was also recorded as SACFOR scores for all survey sites on WMO and Lewis, and included in PCA and RDA. In future, owing to the increased prominence of mussels in higher exposure assemblages (Menge, 1976; Hawkins *et al.*, 1992), more detailed recording and manipulation experiments might be worthwhile considering. Images used in the current studies for barnacle recruitment studies can be used to compare intact and post-clearance abundance of mussels over the same seasonal intervals.

Additional future barnacle studies on WMO:

There are a wide range of options to further explore the responses of littoral barnacles in Orkney. The inclusion of studying reproductive processes in indicator species is of particular importance as early life-cycle periods may be the most sensitive to environmental stressors and observable changes may occur over a shorter period of time (Hiscock *et al.*, 2001). Fluctuations observed in recruitment of *Chthamalus* spp. on Orkney might be better explained with the help of seasonal assessment of reproductive status in resident adults. When compared with *C. montagui*, the larvae of *C. stellatus* are larger and develop in the water column over a longer period of time which may account for higher recruitment of the latter on exposed shores (Burrows *et al*., 1999). Modelling of local currents, especially across the tides of the Pentland Firth, coupled with reproductive status data, may help determine the likely source of chthamaloid recruits on WMO. Wind data have been used recently to model larval transport and predict potential dispersal distances on the west of Scotland (Adams *et al*., 2014). These models should be cognisant of the potential role that MREDs may play as ‘stepping-stones’ for range-expanding organisms (Shields *et al*., 2011; Nall *et al*., 2015). In future, inclusion of local wind data may support findings on barnacle recruitment dynamics. In particular, seasonal wind direction and speed might be expected to inform assumptions on larval settlement on WMO, e.g. March-April for *S. balanoides*; and July-August for *Chthamalus* spp.

Between chthamaloid species, reduction in exposure following energy extraction might preferentially favour *C. montagui* over *C. stellatus*. Changes which may occur between chthamaloid congeners can only be addressed if species identification is included during sampling or analysis; in future studies on WMO, the benefits of identifying chthamaloid species may need to be compared against the costs in time necessary for analysis, especially when studying hard-to-distinguish juveniles. While the current studies confirm the dominance of *S. balanoides* on lower barnacle zones, shore height has not been reliably identified as a statistically significant factor in recruitment analysis. This may simply owe to the close proximity of upper and lower quadrats in the studied transition zone. Future studies would be improved with the inclusion of additional intact and cleared quadrats located above and below current quadrats, although time resource may again be a limiting factor. As mentioned above, long-term studies using fixed height quadrats need to account for expected changes in RSL (Hansom and Rennie, 2011). Study of size and growth of individual barnacles could also be considered and is possible using photograph-based biometrics. In past studies, individual size has been determined by measuring the rostro-carinal axis (Barnes, 1956b) but owing to age-independent variation created by crowding, the length of the operculum may be a preferred metric (Burrows, *et al*., 2010).

Automated image analysis of barnacle populations:

In certain conditions of light intensity and 'wetness', the optical qualities displayed by *S. balanoides* and *Chthamalus* spp. are distinctive enough to allow quantification using supervised classification software (Want *et al*., 2014). However in most cases, quantification of percentage cover must be performed manually which, as described in Chapter 5 (Section 5.2.3: Image analysis), is extremely labour-intensive. Image analysis software is currently being developed specifically for this research study in collaboration with the School of Mathematics and Computer Sciences at Heriot Watt University to investigate the feasibility of using species-specific differences in shell shape to inform image recognition software. Similar to 'face-recognition' software, this analysis compares several anatomical features, in particular, the shape of the operculum and the intersection of the tergal and scutal plates along the longitudinal axis of the operculum (see Figure 5.1.1). These structures are more conserved than wall plates, i.e. these features are less affected by the individual's age or density of settlement, and may prove to be reliable markers for the software to differentiate and allow for accurate analysis delivered in a fraction of the time. This work has produced some encouraging results (data not presented here) – the application of rotation invariant software assists in identification regardless of barnacle orientation. It is hoped that this research will be further developed in the future.

6.6 Conclusion:

The current studies have included an extensive survey of rocky shore sites on WMO available as background data by which potential future environments impacts can be compared. Separation of the relative roles of different forcing agents, such as energy extraction and climatic change, will be challenging but will benefit from the study of suitable indicator species. Important study organisms, differentially responsive to changes in exposure and temperature have been identified: presence of *F. distichus anceps* appears to strongly correlate with wave exposure but is not particularly responsive to temperature; *Chthamalus* spp. is acutely responsive to changes in temperature, while sensitivity to exposure changes has not been sufficiently tested. This monitoring programme would be enhanced through the development of a broader suite of indicator species. As previously discussed, data from *P. ulyssiponensis* and *G. umbilicalis* have been recorded on WMO and Lewis but properly designed hierarchical studies featuring treatments and controls at sites within shores and between shores, would be welcomed. *Anemonia viridis* and *T. testudinalis* may be considered for climatic change studies but their absence from the open rock surfaces on WMO limits their applicability for exposure-related work. The kelp *Alaria esculenta* has been suggested as a potential candidate for climatic change research (Mieszkowska *et al*., 2006), and its association with high exposure shores might make it valuable for inclusion in future WMO rocky shore and sublittoral studies. Fucoids are conspicuous, important community structuring organisms and have already shown to respond to climatic change (Ladah *et al*., 2003; Nicastro *et al*., 2013). Owing to its association with high exposed shores, species such as *F. spiralis* f. *nanus* might be considered for more detailed study.

In producing a comprehensive survey along an extensive coast, important background data for both control and impact study sites have been obtained. Continued studies of selected sites along this shore will allow monitoring of areas expected to be developed for commercial scale removal of wave energy, as well as similar areas at a considerable distance from these developments. Inter-annual variation appears to be less than the variation between sites, suggesting that detection of variation at a scale that exists between sites should be possible using this beyond BACI-style study. Development of more sophisticated exposure indices, incorporating topographic modifiers in a quantitative framework and higher resolution wave energy input data, may be applied to characterise littoral exposure more accurately. The use of exposure indices may be transferable to other locations using weighting factors for topographic variables based on local conditions (see Appendix 6).

Many of these procedures should be looked upon as establishing a baseline for long-term monitoring while at the same time addressing common issues which may allow these methods to be transferred to different shores with potentially different species. While long-term monitoring may be necessary in identifying community population dynamics, governmental and business decision-making typically requires data delivery in a shorter time frame – methodologies such as barnacle clearances may short-circuit normal community responses, potentially providing a more rapid observable change.

The comprehensive rocky shore survey and research described here comes at a critical time as the MRE industry prepares to launch industrial-scale deployments of devices in local waters (Meygen, 2016) and marine ecosystems are coming under increasing threat from climatic changes and other anthropogenic developments (Frost *et al*., 2016). With increasing pressure from multiple users of the marine resource and global changes in climate affecting marine communities, the effects of changes in exposure on species distribution will become increasingly important (Blanchette *et al*., 2008).

Appendices:

Appendix 1: Main research sites on WMO (see Figure 2.4.2).

Billia Croo (OSGB: 101040 N; 322273 E):

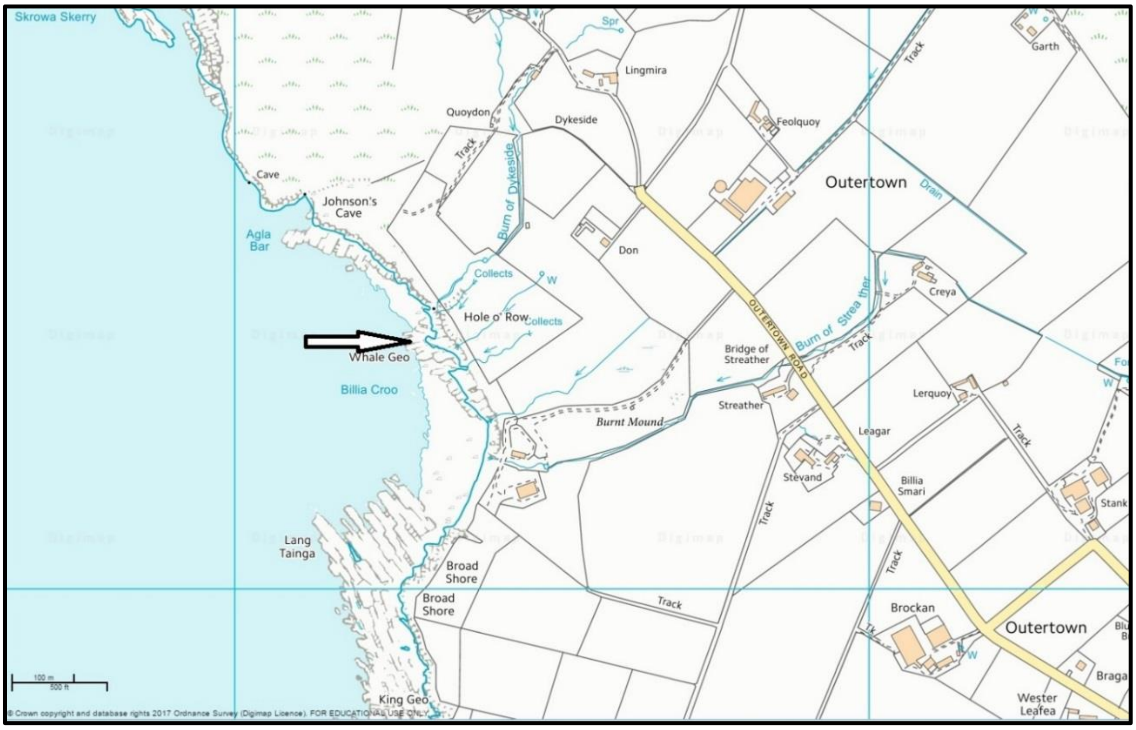

Figure A1.1: Billia Croo. Arrow indicates Billia Croo research site. © Crown Copyright and Database Right [2017]; Ordnance Survey (Digimap Licence).

Billia Croo is the location of the EMEC wave test site where wave energy extraction is presently limited to individual devices during sea trials. Billia Croo forms a slight embayment bordered by rocky promontories (open to 118° of fetch) with a boulder field occupying the southern half of the embayment. The Billia Croo research site is characterised by stepped platforms dipping seaward at approximately 14° with numerous rock pools. Fetch from south and south-westerly directions is reduced by the high hills of the neighbouring island of Hoy (Figure A1.2).

Figure A1.2: Billia Croo, looking south to Hoy.

Based on quantitative measurement of littoral exposure using the Terobuoy device compared with other sites on WMO (Want *et al*., 2014) and the presence of wave-modifying features (see 3.2.1: Littoral site survey), the Billia Croo research site was assigned a Want Exposure Index value of 2 and a complexity score of 5. Subsequent biological characterisation determined that: fucoid cover is predominantly *F. vesiculosus* f. *linearis* with rare *F. distichus anceps* and *F. spiralis* f. *nanus* common in a few discrete locations; limpets are frequent on open shores and in rock pools, and are represented almost exclusively by *P. vulgata*; barnacles are frequent but do not form well-defined extensive zones.

Marwick (OSGB: 102448 N; 322510 E):

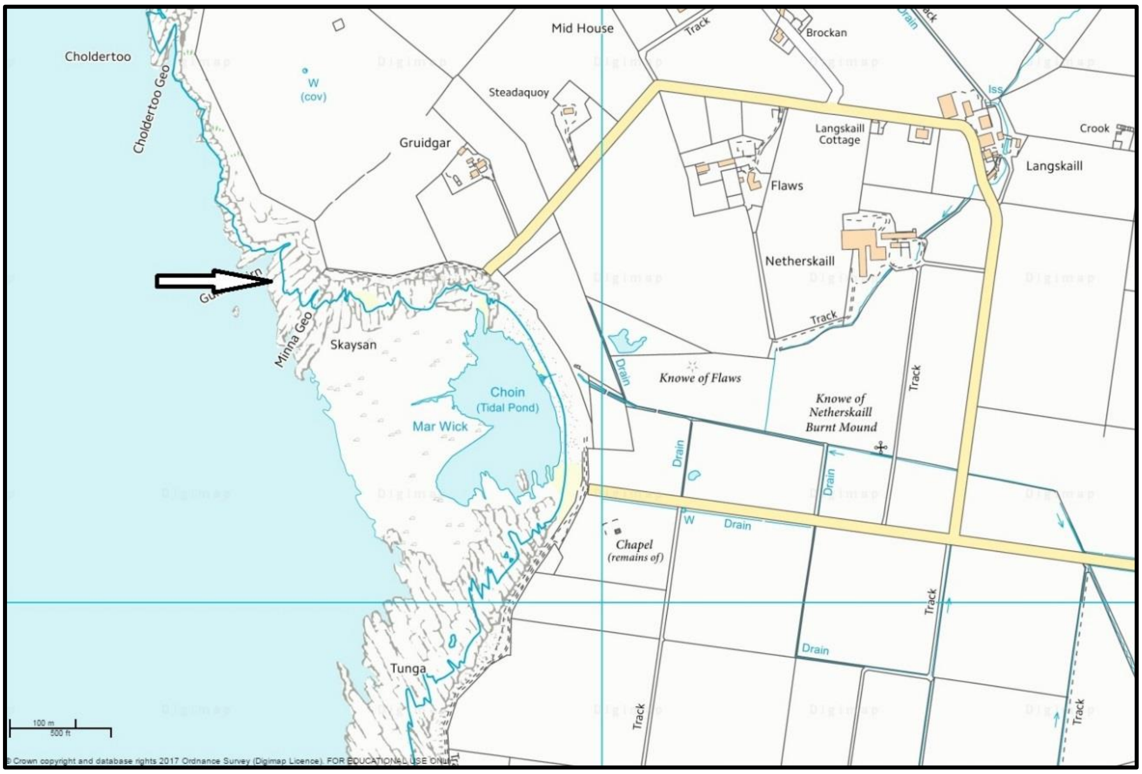

Figure A1.3: Marwick. Arrow indicates Marwick research site. © Crown Copyright and Database Right [2017]; Ordnance Survey (Digimap Licence).

Marwick is onshore from the proposed site of the largest WEC array to date, where industrial scale extraction is proposed (TCE, 2015). The research site is located approximately 200m north of the edge of Marwick Bay – one of the largest embayments on WMO, featuring an extensive boulder field. The site is characterised by stepped planar rock formations, dipping seaward at approximately 12° with a few rock pools (Figure A1.4). Offshore, two prominent reefs complicate the formation of breaking waves through shoaling and refraction (Figure A1.5). This site is open to oceanic swell over 147° with no obstructing landmasses closer than the Scottish Mainland, a minimum of 55 km away to the south-west.

Figure A1.4: looking east at Marwick from offshore. Note: a distinct zone of barnacles is visible as a light brown band above a darker zone of macroalgae.

Based on comparisons between sites using Terobuoy data (Want *et al*., 2014) and the presence of wave-modifying features (see 3.2.1: Littoral site survey), the Marwick research site was assigned a Want Exposure Index value of 3 and a complexity score of 6. Subsequent biological characterisation determined that: fucoid cover is mixed between abundance of common *F. distichus anceps* and frequent clumps of *F. vesiculosus* f. *linearis*, with *F. serratus* frequently found in lower shore rock pools; limpets are common and represented by an even proportion of *P. ulyssiponensis* and *P. vulgata*; an extensive band of superabundant barnacles is present (Figure A1.4) featuring a well-defined lower zone of *S. balanoides* and upper zone of *Chthamalus* spp.

Figure A1.5: looking west off Marwick.

Northside in Birsay (OSGB: 102885 N; 325418 E):

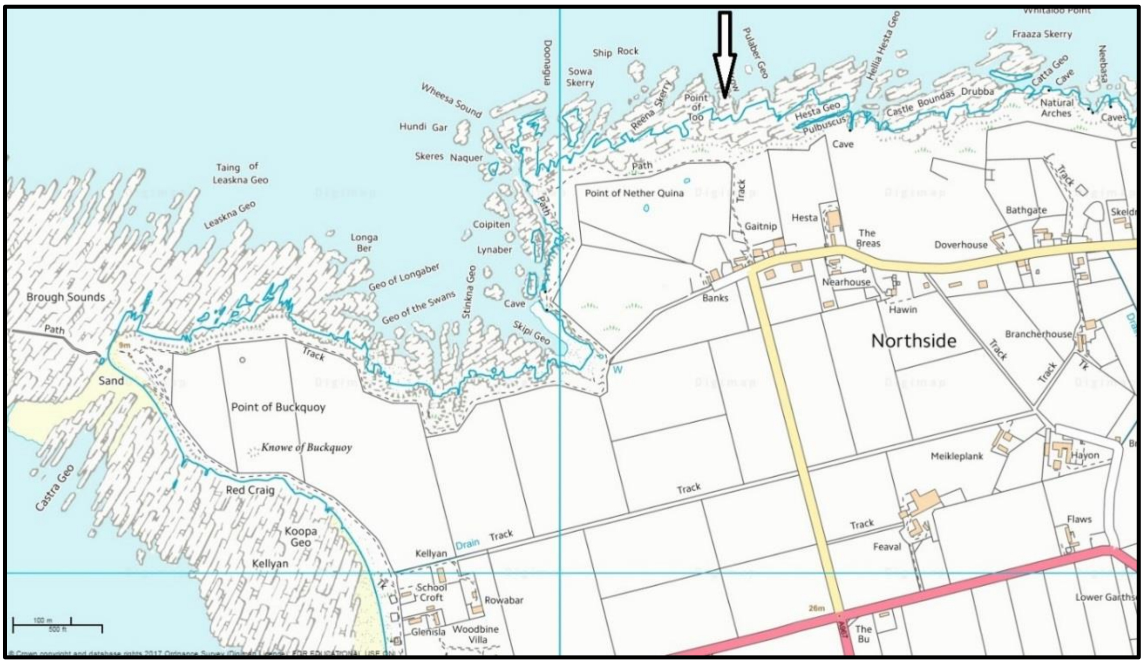

Figure A1.6: Northside in Birsay. Arrow indicates Northside in Birsay research site. © Crown Copyright and Database Right [2017]; Ordnance Survey (Digimap Licence).

The NW orientated coast of Birsay is located approximately 8 km distant from Marwick, where the first phase of WEC deployment is planned. Owing to distance and differences in orientation from Marwick, the impacts of wave energy extraction are not expected at Birsay which may thus serve as a control site. The Northside research site in Birsay is located on rock shores (open to 136° of fetch) featuring substantial platforms of rock separated into discrete units by fracturing features including numerous rocky inlets or geos. Beside Hesta Geo, the research site is located on large platforms dipping seaward at approximately 11° (Figure A1.7). Small offshore reefs and the edge of a neighbouring rocky promontory may modestly reduce wave exposure on the main platform (Figure A1.8).

Figure A1.7: looking east across Northside.

Based on comparisons between sites using Terobuoy data (Beharie, unpublished data) and the presence of wave-modifying features (see 3.2.1: Littoral site survey), the Northside research site was assigned a Want Exposure Index value of 4 and a complexity score of 5. Subsequent biological characterisation determined that: fucoid cover is provided by a superabundant zone of *F. distichus anceps* and occasional *F. spiralis* f. *nanus*; limpets are common and represented by an approximate 2:1 ratio of *P. vulgata* and *P. ulyssiponensis;* a band of abundant barnacles is present featuring a lower zone of *S. balanoides* and a more extensive upper zone of *Chthamalus* spp.

Figure A1.8: looking NW off from Northside.

Appendix 2a: survey site locations and survey dates on West Mainland, Orkney (Ordnance Survey Gird Reference [OSGB36]).

Survey Site	**OS East**	**OS North**	**Survey Date**
Billia Croo	322273	1010387	25/04/2013
Borwick	322379	1016898	26/04/2013
Cauldrus - North	322160	1016800	26/04/2013
Marwick	322513	1024466	08/05/2013
Tunga	322680	1023808	08/05/2013
Saed Geo	322691	1023237	08/05/2013
Skrowa Skerry	321810	1010901	09/05/2013
Eastalet	321746	1012432	09/05/2013
Neban Point	321584	1013249	09/05/2013
Lyre Geo	321761	1013897	09/05/2013
Bo Skerry	321890	1015843	09/05/2013
Hesta Geo	325289	1028759	06/06/2013
Outshore Point	322443	1022680	07/06/2013
Inga Ness	321631	1014949	10/06/2013
Point of Qui Ayre	321755	1015411	10/06/2013
Howana Geo	322706	1020237	11/07/2013
Nebo Geo	322695	1020744	11/07/2013
Hole o' Row	322594	1019009	22/07/2013
Axna Geo	322820	1021134	22/07/2013
Alga Bar	322093	1010547	23/07/2013
Cut Taing	321995	1016323	25/07/2013
Cauldrus - South	322012	1016695	25/07/2013
North of Ness of Ramna Geo	322620	1017587	25/07/2013
Latha Skerry	323127	1026077	27/07/2013
Between Latha and Choldertoo	322746	1025680	27/07/2013
Choldertoo	322329	1024841	27/07/2013
North of Marwick Research Site	322458	1024532	27/07/2013
Yettna Skerry	322322	1018533	27/07/2013
Costa Head	331351	1030258	13/06/2014
Loop of Crooie - East	327350	1029277	13/06/2014
Loop of Crooie - West	326541	1028869	13/06/2014
Ramley Geo	327741	1029454	13/06/2014
West of Imyala Helliar	329397	1030184	13/06/2014
Brough of Birsay	323359	1028521	13/07/2014
Garson - Birsay Bay	323890	1026463	28/07/2014
Breckness	322012	1009434	18/05/2015
Pulse Skerry	323436	1008406	18/05/2015
Sole Geo	331991	1029689	02/06/2015
Clay Geo	334254	1028256	02/06/2015
Oyce	328502	1029690	18/06/2015
East of Little Ramley Geo	328148	1029575	18/06/2015

Appendix 2b: survey site locations and dates on Lewis (Ordnance Survey Gird Reference [OSGB36]).

Survey Site	**OS East**	**OS North**	**Survey Dates**	
Roinn a'Bhuic	40706	57545	25/06/2013	27/05/2014
Rubha Blanisgaidh	37851	55216	25/06/2013	27/05/2014
Tada Ghabhsainn	43321	59431	25/06/2013	27/05/2014
Bad an Fhithich	48155	62618	26/06/2013	28/05/2014
Sgeir Coidlt	50723	64163	26/06/2013	28/05/2014
Stathanais	52536	66182	26/06/2013	28/05/2014
Upper Barvas	34597	51950	27/06/2013	29/05/2014
West of Siadar	36986	54394	27/06/2013	29/05/2014

Appendix 3: abundance scales used for intertidal organisms, after Crisp and Southward (1958) modified by Hiscock (1981). S: super abundant; A: abundant; C: common; F: frequent; O: occasional; R: rare. Organisms not seen during a 45 minute site visit despite searching were recorded as N: absent.

Barnacles
S: 300–499 per 0.01 m2, 3–4 cm–2
A: 100–299 per 0.01 m2, 1–2 cm–2
C: 10–99 0.01 m–2
F: 1–9 per 0.01 m2
O: 1–99 m–2
R: <1 m–2

Patella spp. ≥10 mm,
Littorina littorea (juveniles & adults),
L. mariae/obtusata (adults)
S: 10–19 per 0.1 m2
A: 5–9 per 0.1 m2
C: 1–4 per 0.1 m2
F: 5–9 m–2
O: 1–4 m–2
R: <1 m–2

Littorina 'saxatilis ',
Patella <10 mm, L.mariae/obtusata juv.
S: 20–49 per 0.1 m2
A: 10–19 per 0.1 m2
C: 5–9 per 0.1 m2
F: 1–4 per 0.1 m2
O: 1–9 m–2
R: <1 m–2

Nucella lapillus (>3 mm), Gibbula spp.
S: 5–9 0.1 m–2
A: 1–4 0.1 m–2
C: 5–9 m–2, sometimes more
F: 1–4 m–2, locally sometimes more
O: <1 m–2, locally sometimes more
R: Always <1 m–2

Mytilus edulis
S: 50–79% cover
A: 20–49% cover
C: 5–19% cover
F: Small patches, 5%; ≥10 small ind. per 0.1 m2; ≥1 large ind. per 0.1 m2
O: 1–9 small ind. per 0.1 m2: 1–9 large ind. m–2; no patches except small ind. in crevices
R: <1 m–2

Pomatoceros sp.
A: ≥50 tubes per 0.01 m2
C: 1–49 tubes per 0.01 m2
F: 1–9 tubes per 0.1 m2
O: 1–9 tubes m2
R: <1 tube m–2

Spirorbinidae
A: ≥5 cm–2 on appropriate substrata; >100 per 0.01 m2 generally
C: Patches of ≥5 cm–2; 1–100 per 0.1 m2 generally
F: Widely scattered small groups; 1–9 per 0.1 m2 generally
O: Widely scattered small groups; <1 per 0.1 m2 generally
R: <1 m–1

Sponges, hydroids, bryozoa
A: Present on ≥20% of suitable surfaces
C: Present on 5–19% of suitable surfaces
F: Scattered patches; <5% cover
O: Small patch or single sprig in 0.1 m2
R: <1 patch over strip; 1 small patch or sprig per 0.1 m2

Lichens, lithothamnia
S: 50–79% cover
A: 20–49% cover
C: 1–19% cover
F: Large scattered patches
O: Widely scattered patches all small
R: Only 1 or 2 patches

Algae
S: 60–89% cover
A: 30–59% cover
C: 5–29% cover
F: <5% cover, zone still apparent
O: Scattered plants, zone indistinct
R: Only 1 or 2 plants

Appendix 4: species list used for abundance recording in this study.

Crustacea
Chthamalus montagui
Chthamalus stellatus
Semibalanus balanoides

Mollusca
Calliostoma zizyphinum
Gibbula cineraria
Gibbula umbilicalis
Littorinidae
Mytilus edulis
Nucella lapillus
Patella ulyssiponensis
Patella vulgata
Tectura testudinalis

Cnidaria
Actinia equina
Urticina felina

Porifera
Halichondria panicea

Chlorophyta
Cladophora sp.
Ulva intestinalis
Ulva lactuca

Rhodophyta
Callithamnion sp.
Ceramium sp.
Chondrus crispus
Corallina officinalis
Dumontia cortorta
Lomentaria articulata
Mastocarpus stellatus
Osmundea hybrida
Osmundea pinnatifida
Palmaria palmata
Polysiphonia sp.
Porphyra umbilicalis

Phaeophyceae
Alaria esculenta
Ascophyllum nodosum
Fucus distichus anceps
Fucus serratus
Fucus spiralis
Fucus spiralis f. *nanus*
Fucus vesiculosus
Fucus vesiculosus f. *linearis*
Halidrys siliquosa
Himanthalia elongata
Laminaria digitata
Laminaria hyperborea
Leathesia difformis
Pelvetia canaliculata
Scytosiphon lomentaria

Appendix 5: exposure values for survey site locations on West Mainland, Orkney described by the following exposure indices: Ballantine (Ballan.); Thomas (Tho.): Thomas modified with littoral slope (Tho.-M); Burrows (Burr.); Burrows modified with foreshore extent (Burr.-M); and Want semi-quantitative description (WantSQ).

Survey Site	**Ballan.**	**Tho.**	**Tho.-M**	**Burr.**	**Burr.-M**	**WantSQ**
Billia Croo	2	8.99	2.29	154.2	3.28	2
Borwick	2	10.79	2.06	189.8	4.41	3
Cauldrus - North	1	18.50	3.60	188.4	5.38	4
Marwick	2	15.13	3.22	138.5	2.04	3
Tunga	3	14.99	2.16	288.9	1.19	3
Saed Geo	2	14.81	1.40	260.0	2.08	3
Skrowa Skerry	1	18.67	6.32	318.7	13.28	5
Eastalet	1	17.21	2.33	303.2	6.19	5
Neban Point	1	9.46	2.27	352.0	16.00	4
Lyre Geo	1	15.92	1.53	285.7	6.80	4
Bo Skerry	1	10.48	2.96	300.7	11.57	5
Hesta Geo	1	10.03	1.99	306.5	3.23	4
Outshore Point	3	7.93	0.58	288.4	1.41	4
Inga Ness	2	17.46	2.48	351.0	6.75	4
Point of Qui Ayre	1	18.32	4.16	366.7	9.40	4
Howana Geo	2	6.98	0.98	307.3	2.13	4
Nebo Geo	2	14.43	2.91	309.2	2.64	4
Hole o' Row	1	15.46	1.98	117.6	2.31	4
Axna Geo	1	14.76	2.79	321.8	5.65	5
Alga Bar	1	17.72	2.46	187.1	6.68	3
Cut Taing	1	16.19	2.91	305.9	7.11	4
Cauldrus - South	1	17.48	2.58	241.1	4.38	5
North of Ness of Ramna Geo	1	7.64	0.88	206.6	3.18	3
Latha Skerry	1	14.41	2.80	243.6	4.06	4
Between Latha and Choldertoo	1	16.57	2.36	267.4	7.04	4
Choldertoo	1	17.52	5.12	370.0	9.49	5
North of MRS	1	9.96	2.03	241.8	7.11	4
Yettna Skerry	1	7.74	0.92	366.7	8.33	4
Costa Head	1	9.99	1.46	352.4	6.18	3
Loop of Crooie - East	1	7.33	0.28	301.8	3.87	4
Loop of Crooie - West	1	7.40	0.43	268.5	2.56	4
Ramley Geo	2	7.54	0.82	285.1	10.56	3
West of Imyala Helliar	1	8.41	0.37	219.8	2.29	3
Brough of Birsay	1	7.01	1.67	270.4	3.30	5
Garson - Birsay Bay	1	8.13	2.80	155.7	5.19	3
Breckness	4	19.47	3.78	328.1	2.29	1
Pulse Skerry	4	12.17	1.69	255.6	0.88	1
Sole Geo	2	2.96	0.13	233.3	1.90	2
Clay Geo	2	1.87	0.11	152.8	1.74	1
Oyce	1	6.78	0.37	250.7	2.04	5
East of Little Ramley Geo	1	7.44	0.39	285.1	7.13	5

Appendix 6: ‘Want Index’ of Exposure:

Development of a novel exposure index began with a simple overview of shoreline exposure:

$$E_X = E_W \text{ x } T$$

Where: E_X is a measure of wave energy reaching the littoral zone, i.e. exposure; E_W is a measure of offshore wave energy approaching the shore prior to modification from topographic variables in question; and T is a modifying factor owing to topographically-derived dissipation of wave energy. This basic relationship can be populated with quantifiable input data gathered during shore surveys and from meteorological studies, as shown in the following example formula:

$$E_x = E_W \text{ x } \left(I_S \text{ x } I_{Op} \text{ x } I_B \text{ x } I_A \text{ x } I_C\right)$$

Where the following indices refer to topographic variables examined in the present study which may modify the dissipation of energy as waves approach and break in the littoral zone, namely: I_S, index of slope; I_{Op}, index of openness; I_B, index of bearing; I_A, index of aspect; and, I_C, index of complexity – the latter being semi-quantitatively determined in the present study.

Offshore wave energy (E_W) can be substituted by a suitable proxy such as significant wave height or by other wave, wind, or fetch-based metrics. Each topographic index is based on a 0-1 point scale where: 0.0 refers to maximal dissipation of wave energy by the variable; and 1.0 refers to no dissipation of wave energy by the variable. In reality, it is unlikely that any topographic variable described here could result in total removal of wave energy; indices can be rescaled using a weighting factor (λ):

$$I_i' = (1 - \lambda_i) + \lambda_i I_i$$

Where I_i, I_i', and λ_i are the unweighted, weighted, and weighting factor for, topographic variable i, respectively. Weighting factors were not empirically quantified in the current study, but help to illustrate the potential of developing more sophisticated models using hydrodynamic and other quantifiable data. A graphic example of the relationship between a topographic variable (in this case, substrate complexity) and wave energy dissipation using a weighting factor is provided in Figure A6.1. In this example, a perfect planar surface will have a complexity of 1 and produce no modification of wave energy owing to substrate heterogeneity. Based on a working assertion that maximal observed complexity has the capacity to reduce wave energy by 60%, the weighting factor for complexity (λ_C) is defined as 0.6. Whether the relationship between each variable and energy dissipation is linear or non-linear remains to be determined. Non-linear relationships can be encompassed using exponent values for the indices. Exponent >1 give convex curves; those <1 give concave curves (Figure A6.1).

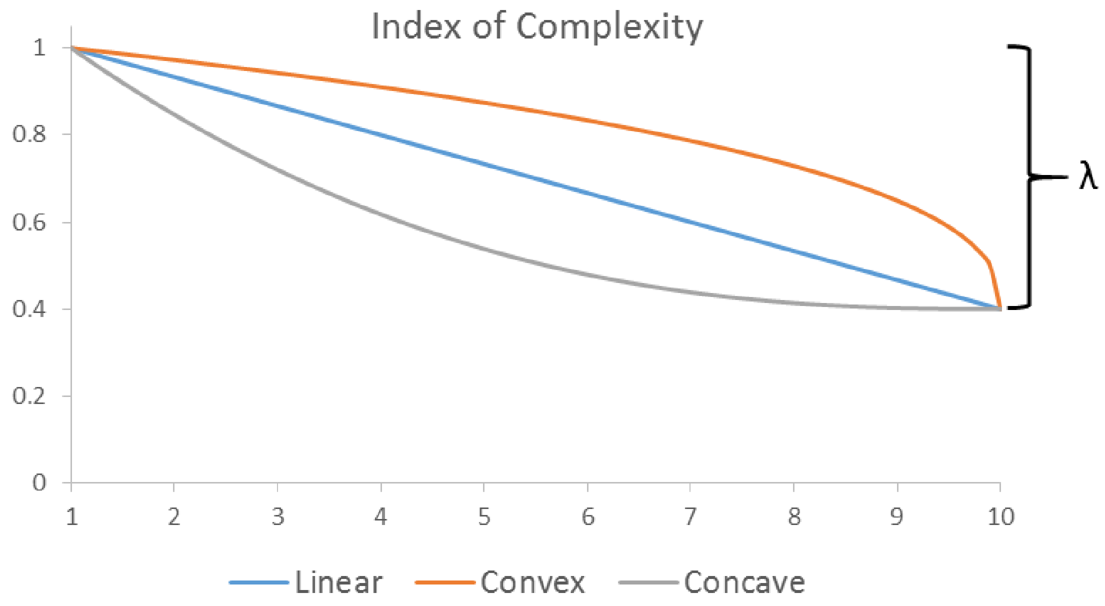

Figure A6.1: Dissipation of wave energy as a function of substrate complexity, using linear and non-linear examples. Weighting factor for complexity (λ_C) = 0.6.

The topographic indices considered in the current study are defined as follows:

-I_S is the index of slope; a 90° slope will score 1.0, i.e. no wave energy is removed owing to the slope of the substrate; a 0° gradient will score 0.0, i.e. all wave energy is removed; and λ_S is a weighting factor for slope.

-I_{Op} is the index of openness; 360° will score 1.0; a hypothetical beach at the end of a narrow rocky inlet open to 1° will produce a score approaching 0.0; and λ_{Op} is a weighting factor for openness.

-I_B is the index of bearing, defined as the deviation of mean direction of openness from direction of maximum wave energy approaching the shore; 0° indicates that the mean bearing is parallel to incoming waves and will score 1.0, i.e. the shore in maximally orientated to wave direction such that no dissipation occurs as a result of this factor; shores orientated perpendicular (90°) to wave direction will score 0.0; and λ_B is a weighting factor for bearing.

-I_A is the index of aspect; defined as the deviation of direction of substrate aspect from direction of maximum wave energy approaching the shore; 0° indicates that the aspect is parallel to incoming waves and will score 1.0; aspect perpendicular (90°) to wave direction will score 0.0; and λ_A is a weighting factor for aspect.

-I_C is the index of complexity; substrate complexity score of 1.0 is assigned to a perfect planar surface which produces no modification of wave energy; shores of maximum complexity score 0.0; and λ_C is a weighting factor for complexity.

Note: in the absence of directional wave data, when calculating I_B and I_A, wind or fetch-based data may be substituted to determine angles of deviation. Direction of maximum wave energy will temporally and spatially vary. Statistical methods may be used to tailor weighting factors when applying the index to particular situations.

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