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Stability and variability of the ecosystem engineer Sabellaria alveolata on differing temporal and spatial scales

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Stability and variability of the ecosystem engineer *Sabellaria alveolata* on differing temporal and spatial scales.

A thesis presented by

Laura Elizabeth Bush B.Sc. M.Sc.

to the School of Ocean Sciences, Bangor University

in partial fulfilment of the requirements for the award of Doctor of Philosophy

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Being a typical PhD student I didn’t just utilise all available pots of money, I also dipped all available wells of knowledge, and mined both friends and acquaintances for their expertise at every turn: Dr Andrew Davies and Professor Steve Hawkins, I couldn’t have done it without you; Dr Gay Mitchelson-Jacob, many thanks for being my supervisor; Stephen Balestrini, Elisha Slater, Farng Kringpaka, and Abby Gilson, your enthusiasm got me through some dark and muddy times; Dr Louise Firth, I will forever associate ‘broad-scale, long-term’ with you; and my family and friends, those who are still with me and those who aren’t, to all of you, there may have been points when I took you thoughtlessly for granted but believe me when I say your endless patience has been appreciated every long step of the way.

III. Abstract

Climate change is directly and indirectly impacting biota, A common prediction is that biogeographic ranges will extend poleward, with increases in abundance near the leading edge. Understanding how marine species will respond is hindered by a scarcity of long-term datasets. However, within the British Isles there is a long history of well-documented intertidal research. Historical data are stored in a variety of forms from grey-literature and national databases to published journals. *Sabellaria alveolata* is a conservationally important biogenic reef-forming species that reaches its northern range limit within the British Isles. The aim of this thesis was to establish if *S. alveolata* has responded predictably to climate change, and to investigate abiotic and biotic drivers of observed change. Through comparisons with historical and contemporary collated and collected data on different spatial scales, it was clear that *S. alveolata* has exhibited persistence in distribution, and stability in abundance and morphology on a long term, broad spatial scale with no significant difference in distribution, abundance or reef-forming morphology exhibited from the 1980s to the 2010s (>50 % stability in all paired data; Bush et al., Chapter 2). Within this, *S. alveolata* populations have demonstrated change on reduced spatial scales, increasing in response to increased temperature near the northern range edge, with some decreases in response to increased wave exposure well within the range (explaining ~ 50 % of the variance in both instances; Bush et al., Chapter 3). Through long-term monitoring studies, this study demonstrated high within-site variability. Additionally evidence was provided that, within Britain, the intertidal ecosystem engineers *S. alveolata* and *Mytilus edulis* are alternative stable state communities on pebble shores, with complete change of state from *S. alveolata* dominated to *M. edulis* dominated reef in 1 year (Bush & Davies, Chapter 4). State is partially maintained by settlement success in both instances ($R^2 \geq 0.55$). Finally, through a combination of traditional monitoring and laboratory techniques with state of the art modelling approaches, this study provided insights into reproductive strategy, larval dispersal and population connectivity patterns of *S. alveolata* and provided evidence of subpopulations of reef-forming species on British coastlines (e.g. Scotland to North Wales, Mid Wales, and South Wales to Southwest England; Bush et al., Chapter 5).

Index

1. Introduction

The intertidal region is essentially a boundary between the terrestrial and marine environment that is exposed to the natural stressors of both (Thompson et al., 2002; Helmuth et al., 2006), in addition to the anthropogenic stressors of an expanding and developing human population (Hawkins et al., 2009; Firth et al., 2013). Coastal biological communities are determined by numerous abiotic processes (e.g. temperature, wave exposure), in addition to biotic processes (e.g. competition, reproduction). In temperate intertidal zones, the magnitude and extent of both abiotic and biotic stress varies daily (e.g. with the ebb and flow of the tide; Denny & Paine, 1998; Thompson et al., 2002), seasonally (e.g. summer to winter; Helmuth, 1999), and annually (e.g. global atmospheric oscillations, extreme weather events; Cardoso et al., 2008; Firth et al., 2011; Wethey et al., 2011), in addition to longer term (e.g. climate change; Thompson et al., 2002; Hawkins et al., 2008; 2009).

Understanding governing mechanisms behind species distribution patterns, particularly of ecosystem engineers, is fundamental to coastal ecology, and is often confused by the interaction of many variables on multiple spatial and temporal scales (Crain et al., 2004; Saldaña et al., 2007). The overall aim of this thesis was to investigate the stability and variability of a conservationally important coastal marine habitat (intertidal *Sabellaria alveolata* reef) in relation to changes in the physical environment (i.e. climate change and extreme weather events), in addition to biological interactions (i.e. competition, reproductive ability and larval dispersal), on long-term broad-spatial scales.

1.1. Importance of long-term datasets

Sustained biological observations across broad spatial scales are essential to separate climate driven changes from natural variations, with time-series data an invaluable resource (Mieszkowska et al., 2014; Firth et al., 2015). Whilst long-term broad-spatial scale observations are generally rare, a rich history of sustained biological observations is available from the coastlines of the British Isles, dating back to the 1950s (e.g. Southward & Crisp, 1954; Crisp & Southward, 1958; reviewed in Mieszkowska et al., 2014). Several broad-scale and/or long-term datasets have been collected by numerous scientific observers (e.g. individually or as part of the Marine Nature Conservation Review, under the MarClim Project, or during environmental monitoring by national environment agencies, or government funded organisations). However, data are dispersed in a wide variety of resources (e.g. grey literature, national or organisational databases, published papers) and until recently have rarely been collated (e.g. Mieszkowska et al., 2006; 2007; 2014; Firth et al., 2015; Yesson et al., 2015).

In the past decade, through collation of historical data and resurveys of historical sites, observers have demonstrated some rapid range shifts in intertidal species in response to climate change. For example, poleward range extensions of the southern species of macroalgae *Bifurcaria bifurcata,* limpet *Patella depressa*, barnacle *Perforatus perforatus,* and gastropods *Phorcus lineatus*, and *Gibbula umbilicalis*; and equatorial range retractions of the northern species of macroalgae *Alaria esculenta* and barnacle *Semibalanus balanoides* have been demonstrated from MarClim data (Mieszkowska et al., 2006; 2007; 2014). Whilst the impact of extreme weather events has been historically reported (e.g. Crisp, 1964), the investigation of the long-term impacts and subsequent recovery from such events is minimal and again requires sustained biological observations (e.g. Firth et al., 2015).

1.2. Stability and variability of coastal marine habitats

Intertidal species are predominantly of marine origin, and adapted to tolerate some degree of aerial exposure (Southward et al., 1995; Raffaelli & Hawkins, 1996; Helmuth et al., 2006; Seabra et al., 2011). The morphological and physiological adaptations required for life in an environment of constant change allow intertidal organisms to buffer a certain degree of environmental stress (Thompson et al., 2002), but inherent vulnerability to aerial stress makes such species naturally susceptible to additional environmental change (Fields et al., 1993; Helmuth et al., 2006; Firth et al., 2011). Consequently, it has been predicted that intertidal species may be amongst the first to respond to present and future climate change (Helmuth et al., 2006; Power et al., 2011).

Many species reach their distribution limits on the coastlines of the British Isles. Several Lusitanian species reach their northern limits, whilst some boreal species reach their southern equivalent (Figure 1.1). For many, biogeographical boundaries occur between St Davids Head, South Wales and Anglesey, North Wales, and between Plymouth and the Isle of Wight, South England (Hawkins et al., 2009; Figure 1.1). Major biological changes have occurred across these boundaries, in response to both climate change and extreme weather events (Helmuth et al., 2006; Hawkins et al., 2009). For example, poleward range shifts (northward range extensions by southern species, and range retractions by northern species) with associated increases in the abundance of southern species near their leading edge and reductions in northern species near their trailing edges have been frequently reported in association with climate warming (reviewed in Southward et al., 2005; Mieszkowska et al., 2006; Hawkins et al., 2009). In temperate regions, a temperature increase of ~1 °C is the equivalent of a poleward shift of climate zones of 100s of kilometres (Figure 1.1; Mieszkowska et al., 2006; Hawkins et al., 2008; Beukema et al., 2009). A ~50 km per decade poleward movement of intertidal biota is predicted in temperate regions from long-term monitoring (Helmuth et al., 2006). More species are currently advancing than retreating poleward (Parmesan, 1996; Parmesan and Yohe, 2003; Mieszkowska et al., 2005; Helmuth et al., 2006). Within the UK, where northern and southern species co-occur within the same niche, the abundance ratios generally alter in favour of the southern species (Helmuth et al., 2006). Decreases in abundance have also been reported in association with extreme weather events, particularly cold winters (e.g. Crisp, 1964) and increased storminess (e.g. Smale & Vance, 2015). Marine biodiversity and ecosystems are responding to global climate change.

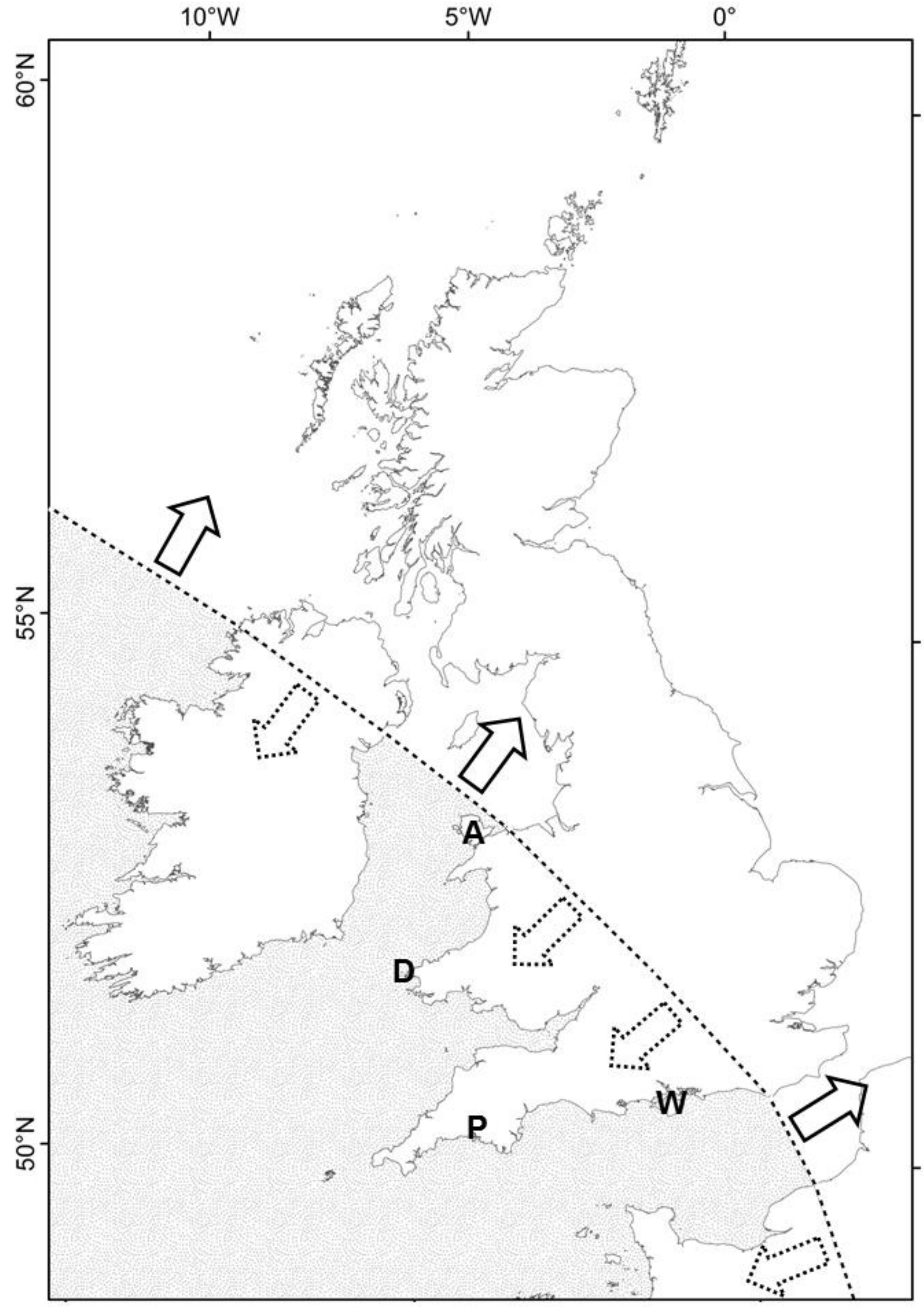


Figure 1.1: Approximate position of the general boundary between Lusitanian waters (grey) and boreal waters (white) in the British Isles (coastline in grey), adapted from Forbes (1858) and Hiscock et al. (2004). Many species currently reach their biogeographic range limit between Saint Davids Head (D) and Anglesey (A), and between Plymouth (P) and the Isle of Wight (W). Under a warming climate, biogeographic range extensions of southern species are predicted, although extreme weather events may counteract this (black arrows represent range extension of ~100 km, whilst dashed arrows represent an equivalent range contraction).

1.3. Ecosystem Engineers

An ecosystem engineer can be defined as an organism that directly or indirectly controls resource availability to other organisms by altering the environmental state through changes in biotic or abiotic components, physically modifying, maintaining or creating habitats (Jones et al., 1994; 1997; Hastings et al., 2007). Ecosystem engineers physically alter their environment in one of two ways. Autogenic engineers directly transform the ecosystem by modifying themselves, with the engineer remaining a component of the ecosystem (e.g. kelp), whilst allogenic engineers physically alter their environment by transforming (a)biotic material from one state to another and do not necessarily remain a component of the ecosystem (e.g. bioturbating worms; Jones et al., 1997; Eklof et al., 2015).

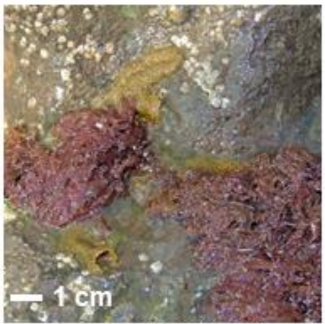
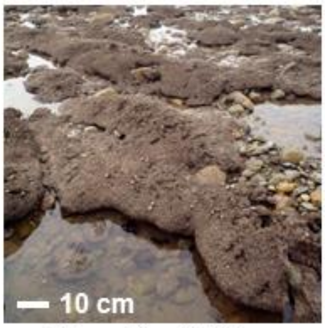
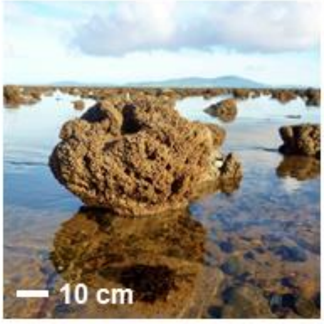
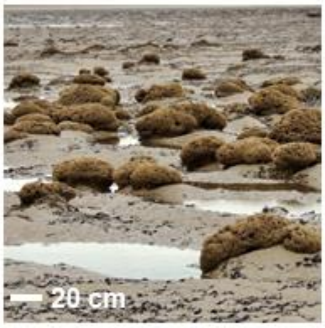
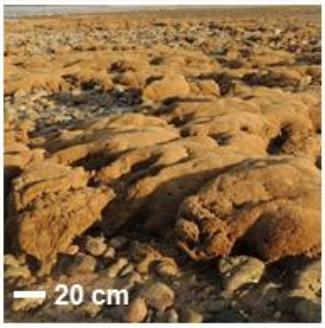
By creating habitat, ecosystem engineers may have small or large impacts on biodiversity, and that impact is not necessarily positive on a local scale. However, through the provision of an alternative habitat, on a global scale, ecosystem engineers may have a net positive benefit (Jones et al., 1997). The overall impact of ecosystem engineers stems from several factors, highlighted in Jones et al. (1994). These include the individual lifetime of the engineering organisms, and the engineered ecosystem in the absence of its founders, the population density, the spatial extent of the engineered ecosystem, the persistence of the population, the type and rate of engineering, and the resources utilised (Jones et al., 1994; 1997). Thus, engineers with large per capita effects, high population densities, large spatial area, and high persistence will have a greater impact (Jones et al., 1994).

1.4. *Sabellaria alveolata*

1.4.1. Importance of habitat

Sabellaria alveolata is an allogenic ecosystem engineer, creating biogenic reef structures from suspended sand and shell fragments affixed to hard substrata. These biogenic structures take many forms; from the tube of an individual, through aggregated low lying encrusting sheets, to raised hummocks and platforms (Table 1.1; Gruet, 1982; 1986; Naylor & Viles, 2000; Dubois et al., 2002). Encrusting

Table 1.1: Visual examples of *Sabellaria alveolata* morphology (Images copyright Laura Bush).

Morphology	**Examples**
Individual Tubes, Small Patches	 Tarn Bank, 2012  Paviland Cliff, 2013
Sheet, Veneer	 Moss Bay, 2012  Llanwit Manor, 2013
Hummock, Mushroom, Ball	 Ellison Scar, 2012  Foot Scar, 2013
Platform, Reef	 Duckpool, 2013  Llanddulas, 2013

structures may be no more than 1 cm to over 10 cm in height, and from tens of cm^2 (small patches) to tens of m^2 in area (extensive veneers). Such structures are prevalent in populations on homogeneous exposed shores (e.g. affixed to bedrock or binding pebble scars; Table 1.1; Cunningham et al., 1984; Bush, per. obs.). Hummocks are isolated three-dimensional raised structures, typically mushroom shaped, and more than 30 cm in diameter (Table 1.1; Cunningham et al., 1984; Gruet, 1986). These generally occur on heterogeneous shores where suitable substrate is a minority (e.g. affixed to boulders on predominantly sandy beaches; Cunningham et al., 1984), or during population initiation (e.g. after primary settlement; Gruet, 1986; Bush, pers. obs.). Platforms are larger raised structures, more than 65 cm in height, and for the purpose of this study, more than 1 m in diameter (Table 1.1; Cunningham et al., 1984; Gruet, 1986).

The known spatial extent of *S. alveolata* habitat covers less than 0.5% of the British coastline making it by definition a “nationally rare” habitat (Sanderson, 1996; Naylor & Viles, 2000). The reef structures created by *S. alveolata* are protected under Annex 1 of the EU Habitats Directive (Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora), directly as “biogenic reefs” and in some instances additionally, as part of broader features, such as “intertidal mudflat and sandflats”. *Sabellaria alveolata* reef habitats were subsequently listed as a Priority Habitat under the UK Biodiversity Action Plan (1994), and designated as a unique biotope in the Marine Nature Conservation Review (Connor et al., 2004). Reef-forming *S. alveolata* are considered a “Habitat of Principal Importance” under the UK Natural Environment and Rural Communities Act (2006). Within British waters, they are present in many Special Areas of Conservations (SACs), including the Solway Firth, Cardigan Bay, Pen Llŷn a’r Sarnau, and Morecambe Bay. However, despite the high conservation status of the resultant habitat, *S. alveolata* have been the subject of minimal research throughout their biogeographic range.

Adult *S. alveolata* populations are typically found within the low to mid-shore, although it can survive at higher shore levels (Bush., pers. obs.), and has also been found in subtidal areas such as within the Severn Estuary (Mettam et al., 1994; De

Grave & Whitaker, 1997; Holt et al., 1998). It encrusts a variety of hard substrata, living epifaunally on bedrock, boulders or pebbles, in addition to anthropogenically created hard structures, predominantly building on or near established tube structures or degraded reef scars (Firth et al., 2015). It has also been known to settle on sedimentary substrata that has been stabilised sufficiently (e.g. by *Lanice conchilega*; Larsonneur, 1994) in addition to mobile dead shell (e.g. oyster shells in Morecambe Bay; Bush, pers. obs.).

As an ecosystem engineer, *S. alveolata* generates small-scale topographic environmental complexity creating numerous spatial and trophic niches for colonisation by other species (Dubois et al., 2006b). They provide shelter from physical and chemical stresses; protection from predators and competitors; and alter resource availability (Porras et al., 1996). Consequently, these reefs host highly diverse and unique species assemblages, composed of species originating from hard substrata, muddy and sandy sedimentary habitats, in addition to both subtidal and intertidal habitats (Dubois et al., 2002; 2006b), and are broadly considered as local hotspots of biodiversity (Ayata et al., 2009). Whilst the resultant dense and solid structures do not produce carbonate in the same manner as bivalve or coral reefs, they are known to trap carbonate-rich sediments (reefs have been reported to be 60-80% calcium carbonate; Caline et al., 1992; Gruet & Bodeur, 1994), and to actively control the composition of the surrounding sediments through preferential selection of sand grains (Gruet & Bodeur, 1994; Naylor & Viles, 2000; Noernberg et al., 2010; Le Cam et al., 2011).

A cycle of *S. alveolata* reef development from reef initiation, as a result of successful primary settlement, to potential reef destruction, with age and in the absence of successful secondary settlement, was suggested by Gruet (1986). Following initial settlement, a rapid reef growth phase occurs, followed by a decrease in expansion as individuals age, become lethargic and the reef enters a stagnation phase. Reef recovery is predicted with successful secondary settlement, but in the absence of this, destruction begins (Wilson, 1976; Gruet, 1986) The elevation of biodiversity, and the balance of these assemblages, is related to the developmental phase of the reef, with healthy rapidly growing reefs dominated by *S. alveolata*, physically limiting the space for microhabitat formation and larval settlement of other organisms (Gruet. 1986; La Porta & Nicoletti, 2009). In addition, actively feeding *S. alveolata* may directly consume the larvae of other invertebrates through indiscriminate filter feeding activity thus reducing competition (Porta & Nicoletti, 2009). Conversely, degrading reefs tend to feature a lower abundance of *S. alveolata*, habitat fragmentation and, consequently, an increase in microhabitats, such as crevices, sedimentation, and pools (La Porta & Nicoletti, 2009). Whilst individual *S. alveolata* live for an average of 3-5 years (Gruet, 1986), the resultant reef structures can persist over long temporal scales (e.g. decades to centuries) in varying degrees of health partially dependent on environmental conditions (Naylor & Viles, 2000), and consequently, they play a large role in ecosystem and community structure (Porras et al., 1996). When conditions become unsuitable, the direct effects of the biogenic reef generated by *S. alveolata* can outlive the polychaetes themselves, although species diversity tends to decline as the reef degrades (Hastings et al., 2007).

1.4.2. Biology

Sabellaria alveolata is a sedentary, tube-dwelling intertidal polychaete. In response to physical disturbance (e.g. trampling, predation), or emersion (e.g. low tide; Figure 1.2 a), *S. alveolata* retract completely into their protective tubes (Bush, pers. obs.). When submerged, although the majority of the body remains within the protective tube, the anterior region of active worms is emergent from the tube aperture (Figure 1.2 b, c; Bush, pers. obs.). Whilst inhabiting such a tube offers protection, adaptations are required for feeding, excretion and respiration (Giangrande, 1991). *S. alveolata* are segmented worms, with a distinct anterior, thoracic and abdominal region (Figure 1.2 c, d). The most posterior abdominal section, the caudal appendage, lies folded forward within the tube, with the anus facing anteriorly, potentially aiding waste removal through tube aperture (Bush, pers. obs.). Sabellids can actively irrigate their tubes through waves of muscular contraction flushing waste from the tube and creating an influx of clean water for respiration (Giangrande, 1991). In *S. alveolata*, the dorsal cirri of parapodium, from the second segment onwards, are partially modified into lamella to function as gills,

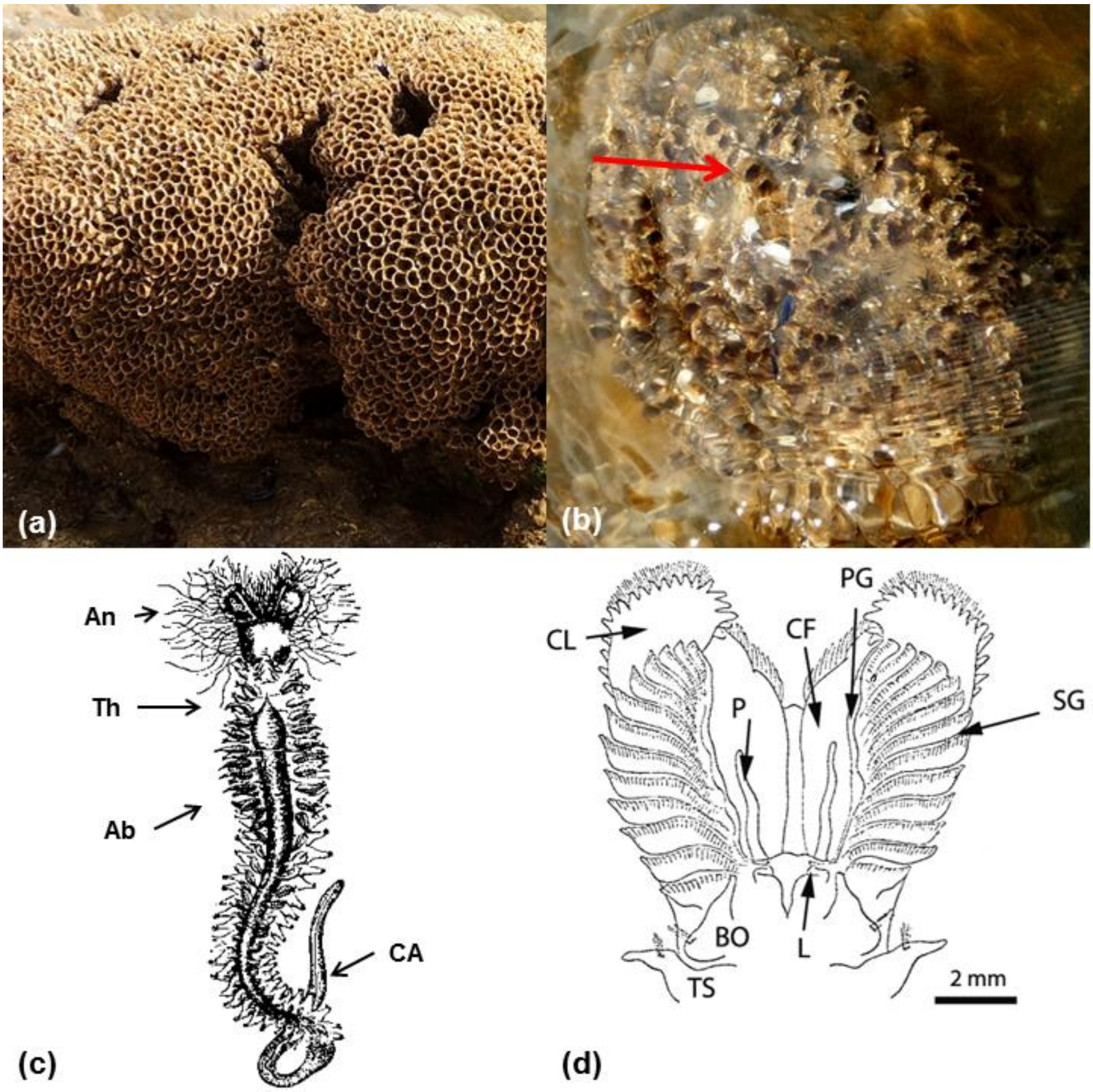


Figure 1.2: *Sabellaria alveolata* reef and individual morphology. (a)Emersed reef (Image copyright Laura Bush), (b) Submerged reef with emergent actively filtering individuals (↑; Image copyright Laura Bush), (c) Illustration of adult with anterior region (An), thoracic region (Th), abdominal region (Ab) and caudal appendage (CA) which terminates in an anus (image adapted from http://www.zoofirma.ru, accessed 14 Mar 2016), (d) Anterior region with tentacles excluded. Two cephalic ventral lobes (CL) equate to the feeding organ. Each lobe is composed of a primary groove (PG) that collects small particulates for transportation to the mouth. These are divided into secondary grooves (SG). Two palps are positioned behind the upper lips (L, internal and external lips; CF, cephalic floor;BO, building organ; TS, first thoracic segment; image from Dubois et al., 2005).

increasing the surface area available for respiration (Figure 1.2 c; Bilej et al., 1993). Additionally, the prostomium is reduced and fused with the peristomium forming a crown of ~250 flexible ciliated tentacles (Dubois et al., 2003; 2005), with potential respiration, feeding and tube construction functions (Giangrande, 1991; Kicklighter & Hay, 2007).

Although little research has occurred on the role of tentacles in respiration, their role in feeding and tube construction has been well documented. When submerged, *S. alveolata* actively filter particulates from the water column with great efficiency (Dubois et al., 2003; 2005). Once collected from the water column, particles are stuck to tentacles with highly viscous mucus preventing resuspension until they are transported to the mouth, to the building organs or rejected (Dubois et al., 2005). Prior to tentacle formation, tactile palps are utilised by juveniles as feeding appendages. Palps of both adult and juvenile *S. alveolata* actively select sand-sized particles from available suspended sediment for tube construction (sand and shell fragments of 0.5 – 5 mm in diameter; Wilson, 1971; Naylor & Viles, 2000; Dubois et al., 2006a), with suitable sized particles transported directly to the building organs. Palps are also used to clean the tentacle area and cephalic floor (Dubois et al., 2005; 2006b), with clearing rate reduced in conditions of increased suspended particulate matter (Dubois et al., 2009).

Like many coastal benthic invertebrates, *S. alveolata* feature a complex life cycle, with several planktonic larval stages, in addition to a sessile bottom dwelling juvenile and subsequent adult stage (Figure 1.3; Wilson, 1929; Cazaux, 1964; Bush et al., 2015) (Figure 1.3). *Sabellaria alveolata* is a gonochoric broadcast spawning species, becoming reproductively active within its first year (Ayata et al., 2009). Gruet (1982) suggested that individuals reproduce only once in approximately 3 years and consequently that the average individual would only reproduce twice in its lifetime. *Sabellaria alveolata* populations may display semi-continuous spawning throughout the year (Dubois et al., 2007). Fertilisation is external, with fertilised eggs hatching and developing into free swimming trochophore larvae rapidly. Within the laboratory Pawlik (1988) found larvae developed to young trochophore stage within 12-18 hours at 20 °C, or 18-24 hours at 15 °C, whilst Wilson (1929) found larvae developed to an equivalent stage in 2 days at room temperature (around 17 °C). The trochophore larvae develop into obligate metatrochophore larvae, and then facultative erpochete larvae that are ready to settle and metamorphose into benthic juveniles (Figure 1.3; Dubois et al., 2007, Elkin & Marshall, 2007; Bush et al., 2015). Eye spots develop with progression to metatrochophore stage (Bush et al., 2015). Settlement stage larvae are attracted to

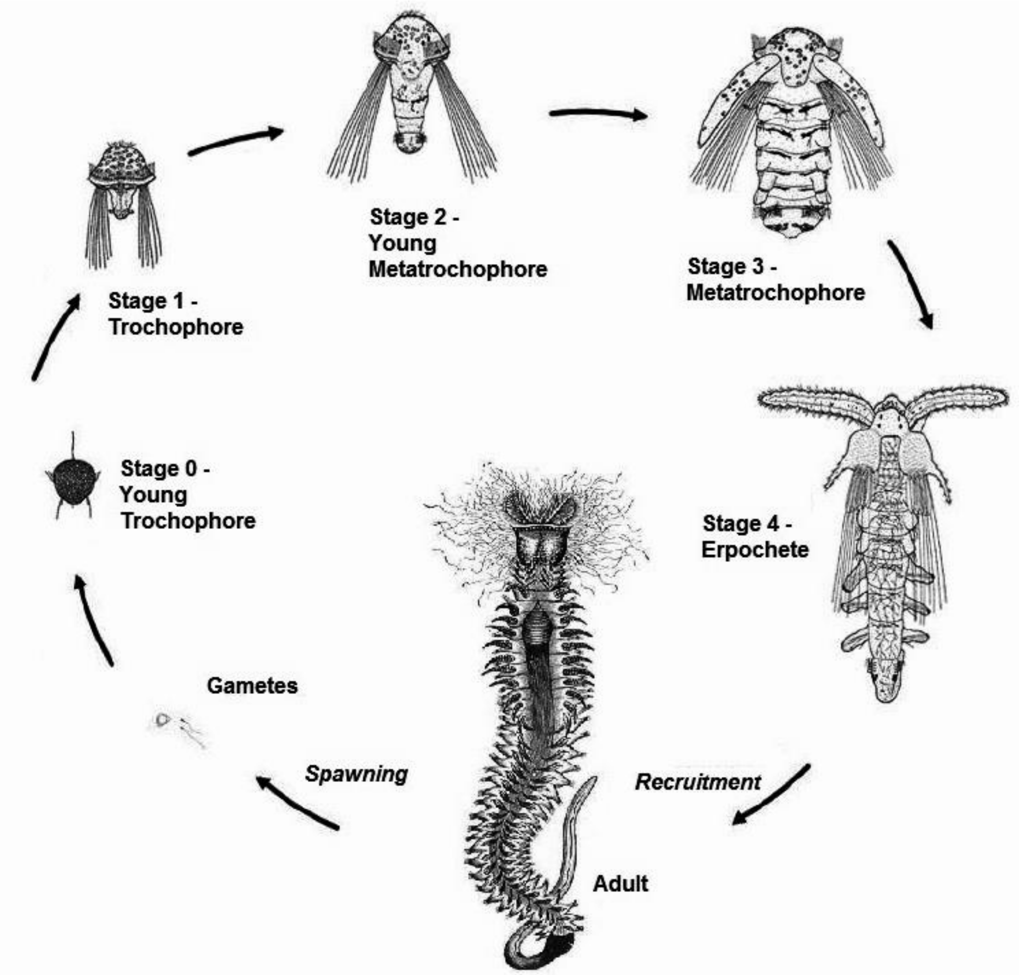


Figure 1.3: Life cycle of *Sabellaria alveolata* (Stages not drawn to scale). Adult males and females (image adapted from http://www.zoofirma.ru, accessed 14 Mar 2016) spawn gametes directly into the water column. External fertilization occurs and eggs hatch into a free swimming early trochophore larvae (Stage 0) within 2 days. These develop into trochophore larvae (Stage 1), reaching ~120 µm in length. The larvae continue to develop into the early metatrochophore (Stage 2) reaching 350 µm in length. The metatrochophore larvae (Stage 3) continues to develop with the initiating of tentacular palp formation, reaching ~500 µm before transforming into the erpochete larvae (Stage 4). The erpochete is the settlement stage larvae, which seek out a suitable settlement site to recruit to and begin tube construction (Wilson, 1929; Dubois et al., 2007; Slater, 2013; Bush et al., 2015).

conspecific reef structures, both alive and dead (Wilson, 1968), and have been observed to actively seek such habitat within the laboratory (Wilson, 1968; Pawlik, 1988; Bush et al., 2015), potentially delaying settlement (Wilson, 1986 a, b). Consequently, settlement is generally gregarious (Wilson, 1968a, b; 1970; 1976; Pawlik, 1988).

Ultimately, the distribution of any species is determined by dispersal ability and tolerance to the numerous gradients of stress (Thompson et al., 2002). Contradictory information is available regarding larval dispersal strategy, with spawning reported from just one summer month (e.g. Wilson, 1971) or extended throughout several summer months (e.g. Culloty et al., 2010; Bush et al., 2015), potentially with bimodal peaks in summer and autumn (e.g. Gruet & Lassus, 1983; Dubois et al., 2007), to semi-continuously (Gruet & Lassus 1983; Dubois et al., 2003; 2007; Culloty et al., 2010; Bush et al., 2015), and planktonic larval durations have been reported of between one month (e.g. Dubois et al., 2007; Bush et al., 2015) and 8.5 months (e.g. Wilson, 1968a; b). Larval settlement has been reported within the UK in spring to summer (Bush et al., 2015), and in autumn to winter (Wilson, 1976).

1.4.3. Potential for changes to biogeography

Sabellaria alveolata is a widely distributed Lusitanian species, extending from Scotland in the north, to Morocco in the south (Firth et al., 2015), and reaching its biogeographic range within the British Isles where it is confined to southwestern coasts and shallow waters (from the Isle of Wight in the southeast to the Mull of Galloway in the northwest; Gubbay, 1988; Bamber & Irvine, 1997). *Sabellaria alveolata* is a southern species that is known to be sensitive to extreme cold (Gruet, 1982; Bamber & Irvine, 1997). Under a warming scenario, a poleward range extension and an increase in abundance near the leading edge would be expected (Hawkins et al., 2009). Regional increases in distribution and abundance have been reported from northwest England since the 1980s, during a period of warming (Allen et al., 2002; Frost et al., 2004; Firth et al., 2015). Additionally, it has been suggested that historical absences and extirpations of *S. alveolata* in the north of its range, specifically along the Welsh, Wirral and Lancashire coastlines were likely to be in response to extremely cold air and sea water temperatures (Crisp, 1964; Gubbay, 1988; Frost et al., 2004; Mieszkowska et al., 2006; Firth et al., 2015). However, *S. alveolata* reefs are subjected to numerous other stresses. For example, *S. alveolata* are known to require a certain degree of wave action in order to suspend particulates into the water column for food and tube construction (Cunningham et al., 1984). By contrast, high wave exposure has been reported to damage intertidal species (Denny, 1995), including *S. alveolata* (Wilson, 1971). The impact of a changed wind regime, as is often reported under climate change scenarios is largely unknown (e.g. Giorgi et al., 2004; Beniston et al., 2007).

Climate change investigations required substantial time-series data (Mieszkowska et al., 2014). Within the British Isles, an extensive review of *S. alveolata* presence and abundance was completed by Cunningham et al. (1984), from available grey literature, reports by other researchers and collected data. This review documented records of *S. alveolata* over a period of approximately 70 years from 1919 to 1984. Consequently, it is widely regarded as providing a baseline dataset of *S. alveolata* distribution and abundance within Britain (Frost et al., 2004; Firth et al., 2015). Regional studies have built on this valuable baseline dataset with a focus in northwest England where several distinct reports have documented *S. alveolata* abundances from a range of sites (e.g. Allen et al., 2002; Frost et al., 2004; Firth et al., 2015). In addition, many scientific observers have reported presence and/or abundance records for this enigmatic species (e.g. during the Marine Nature Conservation Review, MarClim, environment agencies etc.). Despite being a conservationally important and enigmatic species, the overall impact of environmental change on the distribution and abundance *S. alveolata* in the north of its range is largely unknown. However, there is an abundance of time-series data available to be collated, that would facilitate long-term broad-spatial scale comparisons.

1.5. The *Sabellaria alveolata* community as an alternative stable state

The alternative stable state model attempts to explain why two different natural assemblages of species can co-occur in the same space through time (Petraitis & Dudgeon, 1999; 2004; 2005). It is theorised that these states exist in equilibrium, whereby the existent state suppresses the alternative state through feed-back mechanisms (Petraitis & Latham, 1999), thus communities tend to display resilience to state shifts (Holling, 1973). It is theorised that an assemblage can move from one stable state to another in one of two ways. Firstly, the change in state is the result of a sufficiently large perturbation applied directly to the assemblage (e.g. a physical disturbance that alters population densities), and secondly, the change in state is the result of a change in the parameters that determine the assemblage behaviour and thus interactions with the alternative state (e.g. altered birth or death rates, predation; Beisner et al., 2003). Either way, a change in state is often the result of a combination of biological processes and external perturbations (Scheffer et al., 2001), the process of which is often rapid (Petraitis et al., 2009).

Sabellaria alveolata is known to co-occur with *Mytilus edulis* on the coastlines of NW Europe (Cunningham et al., 1984; Allen et al., 1999; 2002; Dubois et al., 2006b; Desroy et al., 2011) Cunningham et al. (1984) reported the presence of large numbers of *M. edulis* on older, degrading populations of *S. alveolata* in several localities throughout the range, and suggested a "*Sabellaria*/*Mytilus*" succession may occur, particularly in such populations. Chapman (2008) noted competition for space with *M. edulis* was a potential threat to *S. alveolata* populations, particularly on boulder scars, where heavy settlement of the former has been suspected to destabilise the latter. This relationship has been studied in four successive years (2011 to 2014) within Morecambe Bay. In this embayment, both Egerton (2014) and Foster (2015) reported a negative correlation between *M. edulis* and *S. alveolata* through time, with sites at which *S. alveolata* thrived featuring a low density of *M. edulis* (Figure 1.4).

The habitats produced by *S. alveolata* and *M. edulis* biogenic reefs are both protected under Annex 1 of the EU Habitats Directive (Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora), but they provide subtly different ecosystem services. Both species are invertebrate suspension feeders (Dubois et al., 2003; 2005; Folmer et al., 2014). Developed *S. alveolata* reefs are physically raised solid structures containing numerous surface microhabitats (e.g. pools, crevices, overhangs, sedimentary pockets, and solid substrata; La Porta & Nicoletti, 2009). Developed *M. edulis* reefs also add structural heterogeneity (Folmer et al., 2014), but in comparison with *S. alveolata* populations, *M. edulis* beds are relatively homogeneous in surface view (Bush, pers. obs.), and dominated by fine sediments, partially due to pseudofaeces (Dubois et al., 2009; Folmer et al., 2014), with the exception of the *M. edulis* shells. Little is known with regards secondary production and predators of *S. alveolata* reefs (Taylor et al., 1962; Wilson, 1971; Bamber & Irving, 1997), however *M. edulis* are an important food resource for numerous wild fowl, crustaceans and other invertebrates (Egerton, 2014; Folmer et al., 2014).

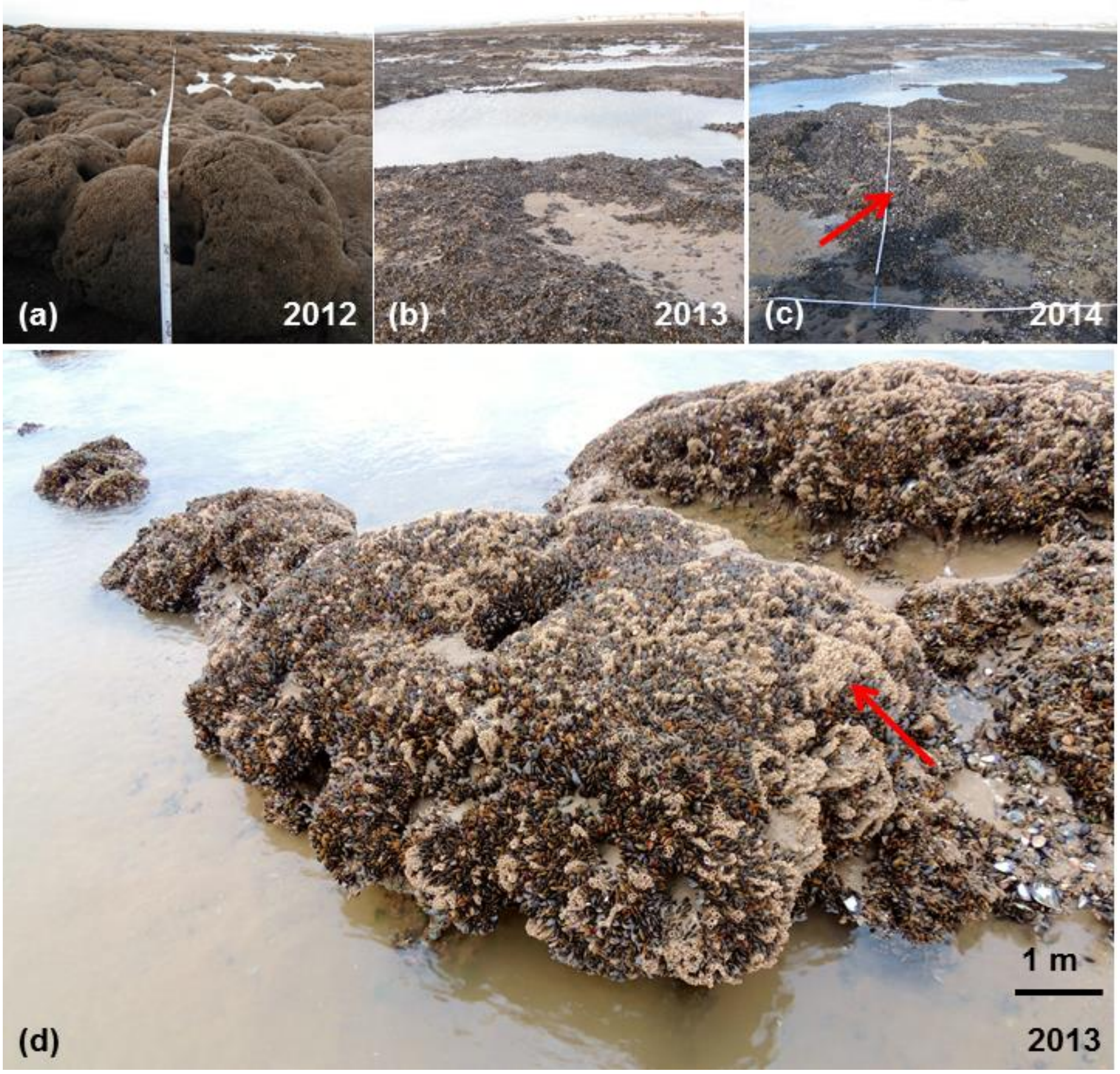


Figure 1.4: *Sabellaria alveolata*/*Mytilus edulis* assemblages. (a-c) Time series of a transect within Morecambe Bay. (a) dominated by *S. alveolata* in 2012. (b) dominated by *M. edulis* in 2013. (c) dominated by *M. edulis* in 2014 but with small patches of *S. alveolata* (↑). (d) detail of a *S. alveolata* reef (↑) in Morecambe Bay, in 2013, featuring dense *M. edulis* recruitment. Images copyright Laura Bush

The alternative stable state model suggests that disruption to negative feedback processes of the original stable state (e.g. *S. alveolata*), combined with significant recruitment of the alternative stable state (e.g. *M. edulis*), may result in a change of state, and vice versa (Petraitis & Dudgeon, 1999). On rocky shores of the Gulf of Maine, *M. edulis* has been reported to form an alternative stable state to *Ascophyllum nodosum* canopy (Pertraitis & Latham, 1999; Bertness et al., 2002), with ice scour combined with heavy *M. edulis* settlement driving the transition from an algal dominated to an invertebrate dominated community. It is theorised that the alternative *M. edulis* stable state is maintained as a result of *M. edulis* biology as larvae settle gregariously, and can move laterally to rapidly fill vacant space. However, an exceptional algal recruitment, or a reduction in grazing may result in a switch back to an algal dominated state (Bertness et al., 2002).

If *S. alveolata* and *M. edulis* exist as alternative stable states on British coastlines, the feedback mechanisms controlling state change are largely not understood. On pebble shores, *S. alveolata* actively stabilises the substrata providing a solid substrate upon which secondary settlement of both *S. alveolata* and *M. edulis* can occur*,* in addition to other species. Recently settled *S. alveolata* populations exhibit rapid growth for a period of up to 3 years (Wilson, 1976; Gruet, 1986). During growth phase, *S. alveolata* have been observed to out-compete all associated biota for space (Wilson, 1976). Petraitis and Latham (1999) suggested that a switch between stable states would be scale dependent, initiated by a large spatial or long temporal removal of the original assemblage, sufficient to allow the settlement and establishment of the alternative state. In the absence of reoccurring secondary settlement, active *S. alveolata* reef growth is reduced after 1.5-3 years (Wilson, 1976; Gruet, 1986). *Sabellaria alveolata* settlement is known to be highly spatially and temporally variable (Wilson, 1971, 1974). Failed recruitment to large areas of an established *S. alveolata* population and/or failed recruitment over successive years may facilitate a change of state as older individuals will die, and uninhabited biogenic structures will begin to degrade. Additionally *S. alveolata* has suffered local extirpation historically as a result of extreme cold (Crisp, 1964). The solid reef scar will persist beyond the life-time of the individual and remains suitable for colonisation by epilithic/episammic organisms such as *M. edulis* (Cunningham et al., 1984). Decreases in the distribution of *M. edulis* have been reported from northern Atlantic coasts in recent decades (Jones et al., 2009; 2010). Additionally, within Morecambe Bay, the return to a *S. alveolata* dominated state may be favoured by the annual removal of the majority of the *M. edulis* population, either through commercially harvesting or winter storms (Egerton, 2014).

1.6. Outline of thesis

Climate change is impacting species both directly and indirectly, through long-term warming, and an increased magnitude and duration of extreme weather events. Intertidal organisms are predicted to be particularly sensitive to this change, and the overall impact on the intertidal ecosystem will be largely dependent on the species, habitats and communities affected. Through a combination of long-term broad-scale monitoring approaches, on temporal scales of months to decades, and spatial scales of metres to hundreds of kilometres, this thesis attempts to untangle physical and biological drivers of change in the distribution and abundance of a Lusitanian ecosystem engineer at its northern range edge.

The first question explored in this thesis was “Has the Lusitanian ecosystem engineer, *S. alveolata*, increased within the British Isles since the 1980s?” (Bush et al., Chapter 2). As *S. alveolata* is a southern species, it was hypothesised that an expansion in distribution and abundance would have occurred throughout the British Isles since the 1980s in response to warming temperatures. Through collation of all available time-series data within the British Isles, and collection of contemporary present day data from 327 sites, comparisons of both distribution and abundance were possible through time. The concept of morphology was also considered as this species is only protected in reef-form. For all investigations, data were pooled into decades, and compared pairwise through time. For distribution, abundance and morphology, data were considered in three distinct ways: (1) comparisons between all available data, (2) comparisons between specific 1 km^2 areas, (3) comparisons between the baseline dataset and contemporary dataset (Bush et al., Chapter 2)

National analysis indicated regional patterns of change had occurred through time. Additionally, increases in both distribution and abundance had been previously reported from the northwest of England, close to the range edge (e.g. Frost et al., 2004; Firth et al., 2015). Consequently, the second question explored in this thesis was “Have populations of *S. alveolata* at the range edge responded differently to climate change to those within the range, and if so why?” (Bush et al., Chapter 3). It was hypothesised that at the range edge, populations will have increased in response to warming, whilst within the range, no change will have occurred. Utilising regional components of the previously collated dataset (e.g. in Bush et al., Chapter 2), comparisons of decadal distribution, abundance and morphology were made between populations near the range edge (i.e. north Wales to southwest Scotland) and within the range (i.e. south Wales to southwest Scotland). Changes were related to site-specific changes in both wave exposure (i.e. due to average wind speed, and the frequency of wind events) and regional changes in temperature (i.e. average temperature, minimum temperature, and the frequency of negative temperature events; Bush et al., Chapter 3).

National analysis also indicated that highly variable changes in abundance and distribution occurred at some sites on short-term small-spatial scales, with some reef-forming populations effectively transient (e.g. reported as present in one year but absent the next). Additionally, Gruet (1986) reported a natural cycle of reef development from reef initiation to reef degradation over a period of 10 years. Settlement success is reportedly variable (Wilson, 1971; 1974), thus reef initiation (primary settlement) and reef replenishment (secondary settlement) can be assumed to be variable. Additionally, a natural succession from *S. alveolata* reef to *Mytilus edulis* dominated reef has been suggested (Cunningham et al., 1984). Consequently, the third question investigated in this thesis was “Are *S. alveolata* reefs morphologically stable on seasonal to annual time scales, and if not what are the drivers of this change? Do intertidal biogenic reefs within the British Isles exist as alternative stable states?” (Bush & Davies, Chapter 4). It was hypothesised that *S. alveolata* and *M. edulis* function as alternative stable states, both varying in abundance on small-spatial scales through time in association with settlement success. Abundance (percentage cover) and community structure (settlement success) of *S. alveolata* and *M. edulis*, in addition to reef height were observed at four reefs near the range edge over a period of three years. Comparisons were made between *S. alveolata* and *M. edulis* dominance, in addition to dominance of each ecosystem engineer in relation to settlement success (Bush & Davies, Chapter 4).

The importance of settlement success in establishment and persistence of a *S. alveolata* dominated states was highlighted in Bush & Davies (Chapter 4). Due to contradictory information being available regarding adult fecundity, spawning season, and larval dispersal (e.g. Wilson, 1968a; b; 1970; 1971; Cazaux, 1970; Gruet & Lassus, 1983; Dubois et al., 2007; Culloty et al., 2010), the final questions investigated in this thesis were "What is adult fecundity and larval spawning season of *S. alveolata* within the British Isles? Do larvae exhibit vertical migration?" and "Is successful settlement predominantly the result of self-recruitment or population connectivity?" (Bush et al., Chapter 5). It was hypothesised that semi-continuous spawning with a peak in summer months would be observed, and that larvae would be rapidly dispersed from their source sites with substantial connectivity between neighbouring populations. Adult fecundity and larval abundance were monitored monthly at three sites within Wales. Larvae were raised in the laboratory and their response to light investigated throughout development. And finally both passive and active particle dispersal was simulated from known abundant sites within the Irish Sea (Bush et al., Chapter 5).

Finally, the results were discussed in a broader context, and the known factors determining stability and variability of *S. alveolata* reef-forming populations at the north of their range are depicted in a conceptual model, linking the effects of competition, settlement success, and climate change in intertidal biogenic reef-forming populations (Bush, Chapter 6).

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2. Persistence and stability of the biogenic reef-forming polychaete, *Sabellaria alveolata* (L.) in the British Isles

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Declaration

I declare that this manuscript is entirely my own work. L.B.F assisted with fieldwork from North Wales to South Scotland. S.J.H. and A.J.D. provided supervision.

It is intended that this manuscript will be submitted to the Journal of the Marine Biological Association of the United Kingdom

2.1. Abstract

Climate change is predicted to directly and indirectly impact biota, including species of conservational importance (e.g. reef-forming species). Biogeographic ranges are predicted to extend poleward, with increases in abundance near the leading edge. Understanding how marine species will respond is difficult as long-term datasets are scarce, but there is a long history of well-documented intertidal research within the British Isles, stored in a variety of forms from grey-literature and national databases to published journals. *Sabellaria alveolata* is a biogenic reef-forming species that reaches its northern range limit within the British Isles. Through comparisons with historical and contemporary collated and collected data, this study documented long-term patterns in both the distribution and abundance of *S. alveolata* within the British Isles. No significant difference in distribution occurred nationally in all available or paired data, from the 1980s to the 2010s with > 60 % of paired data in all comparisons exhibiting persistence. Despite this, a decrease in distribution occurred in all available data from the 2000s to 2010s. Similarly no significant differences in abundance or reef-forming morphology occurred in paired area or site-specific data from the 1980s to the 2010s with > 60 % of paired data in all comparisons exhibiting stability. Despite this, from the 1980s to the 1990s a decrease in both were observed, whilst opposing increases were observed from the 1990s to both the 2000s and 2010s. In contrast to predictions, *S. alveolata* has exhibited persistence in distribution, and stability in abundance and morphology (e.g. little change from crust to reef form), on a long term (e.g. from the 1980s to the 2010s), broad spatial (e.g. national) scale within the British Isles.

2.2. Introduction

Climate change is one of the greatest challenges of our time, with a wealth of literature reporting on the redistribution of species in response to warming temperatures and extreme weather events (e.g. Southward et al. 1995; Hawkins et al., 2003; 2009). There has been an increase in global average surface temperatures in recent years, in the northeast Atlantic, surpassing previous warming periods (e.g. from the 1930s to the 1950s). The 5-year running mean temperature of the northeast Atlantic has increased since the 1980s (Pörtner et al., 2014), as has sea surface temperature around the British Isles (Hawkins et al., 2009; Philippart et al., 2011). Reid et al. (2016) reported a major regime shift in the Earths biophysical processes, particularly a sudden increase in temperature occurred around in the 1980s (1985-1988). As the climate continues to warm, biogeographic ranges are predicted to extend poleward, with an associated retraction at the trailing range edge, and increases in abundance are expected near the leading edge. For example, the northern range limit of many southern (i.e. Lusitanian) species has been observed to extend northward, whilst the southern range limit of many northern (i.e. Boreal) species has been observed to retract (Mieszkowska et al. 2005, 2006; Kordas et al., 2011; Pörtner et al., 2014).

Range changes are predicted to accelerate. However, extreme weather events can also provoke biological responses. Whilst average temperatures drive physiology, understanding long term responses to climate change can be confounded by extreme weather events. The previous cold-spell (1960s – 1980s) was heralded by the 200 year extreme cold winter of 1962-1963 (Wethey et al., 2011). The next three decades were punctuated by cold winters (e.g. 1978-9, 1985-6, and 1987-8). Even the recent spell of rapid warming has included cold winters (1995-6, 2009-10, 2010-11, the latter being the coldest winter since 1978-9; Wethey et al., 2011). Extreme low air temperatures cause stress and mortality for a variety of intertidal organisms. For southern species, the reproductive output is less and recruitment is less successful during cold periods and more successful when warmer (Crisp, 1964). During the cold spell of the 1960s-1980s several warm water Lusitanian species decreased in abundance (Southward, 1967; 1991; Southward et al., 1995; Kendall et al., 1987; 2004; Hawkins et al., 2009).

Investigations of the impacts of climate change are difficult as they inherently require the collation of long-term biological and physical datasets. Such biological datasets are scarce, but there is a long history of well-documented intertidal research within the British Isles, where presence and abundance data have been reported for many species, from numerous sources, over several decades (e.g. Marine Nature Conservation Review, MarClim, scientific research; sources reviewed in Southward et al., 1995; 2005; Helmuth et al., 2006; Hawkins et al. 2009). The UK straddles the biogeographic boundary zone, where many northern and southern (Boreal and Lusitanian) species reach their northern and southern limits respectively (Figure 2.1 a; Forbes, 1858; Hiscock et al., 2004). For example, *Sabellaria alveolata* is a Lusitanian species that reaches its northern biogeographic range within the British Isles, extending from Morocco in the south, to Scotland in the north (Gruet, 1982; Cunningham et al., 1984; Dubois et al., 2007). This biogenic reef-forming species constructs robust tubes from sand and shell fragments on solid substrata, predominantly in the intertidal zone. Due to gregarious settlement, *S. alveolata* can create highly morphologically variable three-dimensional structures ranging from the tube of an individual through to aggregated low-lying encrusting constructions commonly known as sheets or veneers, to raised platforms or reefs (Gruet, 1982; 1986; Naylor & Viles, 2000; Dubois et al., 2002). *S. alveolata* can stabilise sand and pebble habitats, providing hard substrata for inhabitation by both infaunal and episammic biota. Increased species richness has been reported within the resultant habitat (Dubois et al., 2002), and consequently, the resultant habitat is protected internationally (e.g. OSPAR as a threatened or declining habitat type). Although *Sabellaria alveolata* is the most common Sabellariid species on European shores (Pawlik, 1988), within the British Isles, the known area occupied by this ecosystem engineer is less than 0.5% of the overall coastline making it by definition a “nationally rare” habitat (Sanderson, 1996; Naylor & Viles, 2000).

Despite the conservational importance of this species, and it’s nationally rare status, no long-term broad-scale analysis of changes in either distribution or abundance has been carried out within the British Isles. Cunningham et al. (1984) documented the distribution and abundance of *S. alveolata* within the British Isles from the 1900s to the early 1980s. Since the 1980s, a series of short-term, small-scale, predominantly unpublished studies have built upon this baseline (e.g. Hammond, 2000; Allen et al., 2002; Frost et al., 2004; Boyes et al., 2008; Moore, 2010; Allen et al., 2014; Firth et al., 2015a). Consequently, a unique long-term broad-scale dataset of abundance and distribution of a Lusitanian ecosystem engineer at the north of its range is available. Small-scale comparisons of *S. alveolata* on eastern Irish Sea coasts have reported increases in distribution and abundance at selected sites since the 1980s, indicative that this species is responding in a predictable manner to climate change (Allen et al., 2002; Frost et al., 2004; Firth et al., 2015a).

Historical ‘extirpations’ (e.g. local, potentially temporary absences at previously inhabited sites) and prolonged absence of *S. alveolata* along some coastlines were likely to be in response to extremely cold air and reduced seawater temperatures (Crisp, 1964; Gubbay, 1988; Frost et al., 2004; Mieszkowska et al., 2006; Firth et al., 2015a). Healthy populations were reliably reported within these areas prior to 1962 (Cunningham et al., 1984; Crisp & Southward, unpublished; Firth et al., 2015a) but mass mortality of several populations was reported following the extremely cold winter of 1962-1963 (Crisp, 1964). This winter heralded a prolonged cooler period dominated by North Atlantic Oscillation repetitive winters with strong continental influence. Subsequent to this period, recolonisations of locations near the northern range edge have been reported for many intertidal species (Southward, 1991; Herbert et al., 2003; Kendall et al., 2004; Frost et al., 2004; Mieszkowska et al., 2006; Lima et al., 2007). Cunningham et al. (1984) completed an extensive review of *S. alveolata* presence and abundance within the United Kingdom. Whilst they concluded that the extreme winter of 1962-1963 had had little long-term broad-scale adverse effects with full recovery of populations at the majority of sites, recolonisation had not occurred at some sites (e.g. in North Wales).

This study expanded on previous work by Firth et al. (2015a) who investigated change in northwest England, and collated available historical data of *S. alveolata* within Britain, allowing for a national spatio-temporal comparison, over a period of approximately thirty years of both distribution and abundance. Reef morphology was also considered. More than 300 locations with historical data were revisited in this study, and sampled using the same procedure as the baseline survey of Cunningham et al. (1984). The goal of this long-term broad-scale study was to document changes in the distribution and abundance of *S. alveolata* on the west coast of the British Isles, from the southwest of England to the northwest of its range in southwest Scotland (Figure 2.1). It was hypothesised that at the north of its range, on British coastlines, *S. alveolata* will have populated additional suitable sites and will have increased in abundance from the 1980s, although a retraction in distribution and a decrease in abundance may have occurred in recent years.

2.3. Methodology

2.3.1. Historical *Sabellaria alveolata* data

Historical distribution and abundance data for *S. alveolata* within Britain, were collated from a variety of sources, including nationwide, regional and site specific surveys, published and grey literature, and national and regional records databases (e.g. National Biodiversity Network Gateway website, http://www.nbn.org.uk; hereafter NBN). The authors note that under-reporting of presence is possible if an untrained observer was aware of only the reef-forming morphology of *S. alveolata.* Additionally, when collating data from numerous data sources, there is inherent observer bias and incorrect abundance may be assigned. To minimise this, data were quality controlled through selection from scientific observers only, generally collected as a targeted survey, or part of larger biodiversity studies. Data sources are listed in Appendix 2.1 and a full listing of all data points is archived in Appendix 2.2.

Collated abundance data were predominantly reported on the semi-quantitative SACFOR scale, from ‘Rare’ to ‘Superabundant’ (Table 2.1; originally described in Crisp & Southward, 1958). This scale is commonly utilised, as it is a rapid and relatively reliable method of assigning quantitative abundance with limited observer bias (Southward & Crisp, 1954; 1956; Crisp & Southward, 1958; Simkanin et al., 2005). Cunningham et al., (1984) subsequently clearly described the six categories of the SACFOR scale for application to *S. alveolata*, modifying the original scale and defining wide clear categories. A 30-minute search is required, and the witnessed zone of maximum abundance reported, consistent with previous methodology thus minimising observer error, whilst providing a level of quantification (Simkanin et al., 2005).

Some abundance records were reported on an alternative ‘type’ scale, applied by UK statutory bodies to assess both *S. alveolata* abundance and health post 2000 (e.g. Allen et al., 2002; Boyes et al., 2008). Both ‘type’ and SACFOR describe reef size, shape and percentage cover, allowing direct conversion to SACFOR (‘Type’, Table 2.1). Additionally, some abundance records were reported as descriptive comments.

Table 2.1: Comparison and standardisation of several categorical scales for measuring the abundance of *Sabellaria alveolata* and biogenic reefs. Column 'SACFOR': The use of a modified SACFOR semi-quantitative abundance scale was described by Cunningham et al. (1984), adapted from Crisp & Southward (1958). Column 'Type': An alternative Type scale was used by English Nature and Natural Resources Wales (previously Countryside Council of Wales) and was defined by Allen et al. (2002). Morphological descriptors for type can be related to SACFOR abundance by size and coverage. Column 'Reef': The UK Marine SACs Project provided a definition of reef (Holt et al., 1998) which is assumed to correspond to Common to Superabundant categories. Column 'PA': Alternatively just presence absence (PA) data may be reported where mention of *S. alveolata* is made at any level.

SACFOR		Type		Reef		PA
Superabundant (7)	Massive reefs 2-3 ft thick. >50% cover at maximum abundance.	Type 1	Individual reefs <10 m^2, generally >30 cm height (always >10 cm). >90% coverage.	Reef-forming (2)	Solid, massive structures. Clearly forming a substantial, discrete community or habitat.	Present (1)
		Type 2	Individual reefs >10 m^2, and >30 cm height. >90% coverage.			
Abundant (6)	Hummocks >1 ft. across. >20% cover at maximum abundance.	Type 3	>10 m^2 patchy area. Reef[s] >10 cm diameter/height >50% coverage.			
		Type 4	>10 m^2 very patchy area. Reef[s] >10 cm diameter/height 20-50% coverage			
Common (5)	Large sheets or patches. No large hummocks.	Type 5	>10 m^2 extremely patchy area. Recognisable area of proper reef. Reef[s] >10 cm diameter/height <20% coverage			
		Type 6	Low lying patches/areas			
Freq-uent (4)	Many individuals. Small patches.	Type 7	Low lying, heavily silted and predominantly dead areas	Non-reef-forming (Encrusting) (1)	Not as above (i.e. sparse cover, isolated small patches or individuals)	
Occas-ional (3)	Scattered individuals. No patches					
Ra-re (2)	<10 found in search					
Remains (1)	No living individuals found. Tube remains present	-	-	Assumed Absent (0)	-	Assumed Absent (0)
Not Seen (0)	None found.					

Where these comments described morphology as depicted by the SACFOR scale ('SACFOR', Table 2.1), records were allocated a SACFOR abundance category.

However, where a category was not clear (e.g. size of patch or percentage cover was not explicitly reported), no abundance was allocated and records were considered as presence only data ('PA', Table 2.1). 'Remains' were occasionally reported if the reef structure remained but was degraded with no sign of any living individual. These records were considered as an additional category of the SACFOR scale for the purposes of abundance analyses in all available data, but were treated as absence records for the purpose of presence absence analyses as although indicative of presence in the recent past, the longevity of the remains is unknown. Records at which the species were reported as Not Seen were assumed to be absence records.

All data were quality controlled to only include records with a coordinate precision of less than or equal to 1 km^2. Spatial data were standardised to the British National Grid, to correspond with the majority of historical data. Due to the multiple sources of data, duplicate historical records existed. True duplicates were removed, but in some instances, surveyors reported multiple abundances at the same 'site' on the same date (i.e. if a 'site' was surveyed on a smaller spatial scale than 1 km^2, for example, along an intertidal transect; Appendix 2.2). These spatially duplicated records were combined, and maximum (rather than median) abundance retained, as the SACFOR scale requires an assessment of the zone of maximal abundance (e.g. where one section of a reef was reported as 'Common' but another section as 'Abundant', only the 'Abundant' record was retained).

Despite vigorous data quality control, eight locations in areas that were clearly spatially distinct from the majority of *S. alveolata* were detected (Figure 2.1 a). These were clear geographical outliers and, for the purposes of this manuscript, it was assumed that these records were as misidentifications or data entry errors, likely confusion with the sister species *S. spinulosa* known to occur intertidally in some areas (Cunningham et al., 1984) and were excluded from further analysis. Although

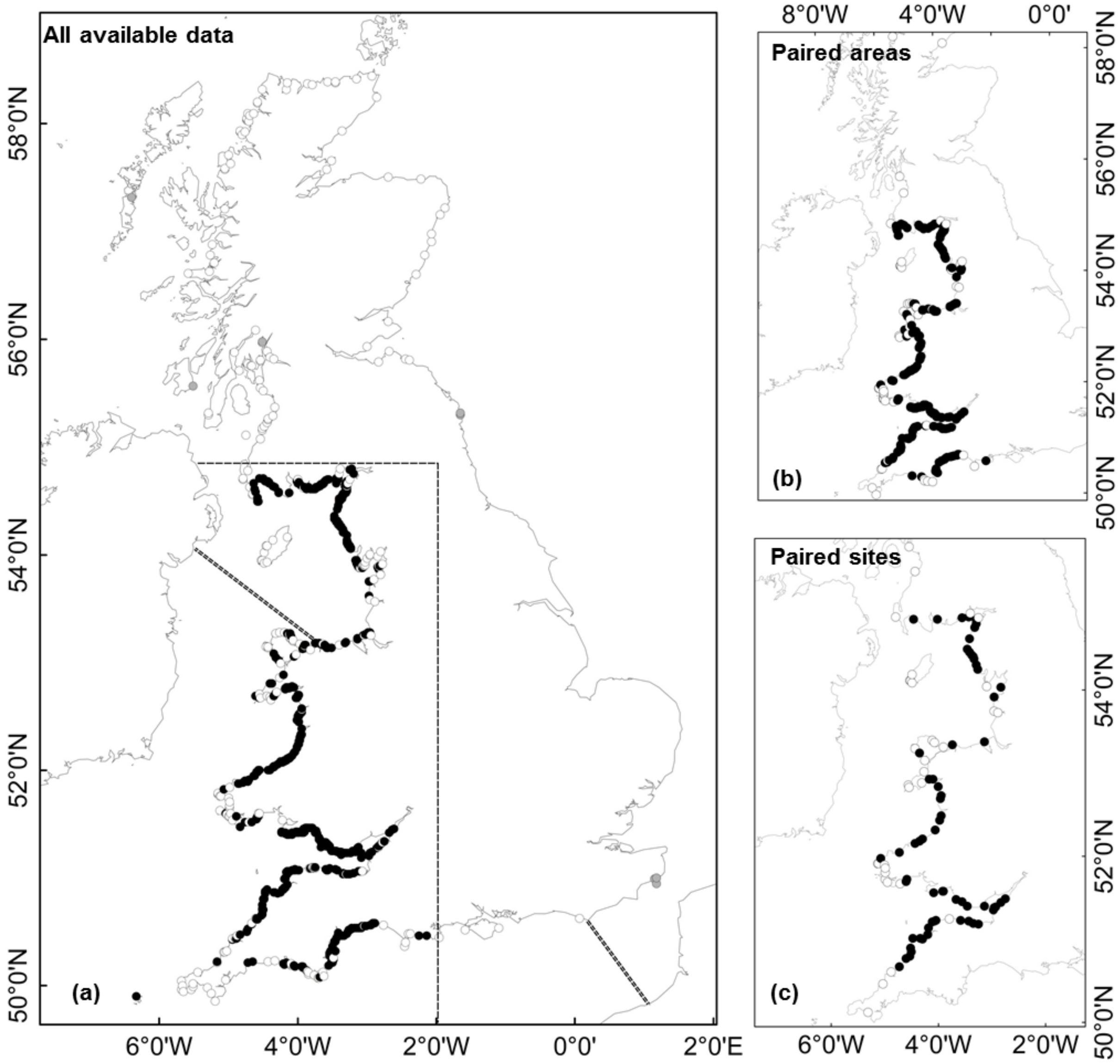


Figure 2.1: Reported locations of *Sabellaria alveolata* presence (black circles) and absence (white circles) within Britain (probable misidentifications depicted as grey circles). The recognised general limit of many southern and northern species (line adapted from Forbes, 1858; Hiscock et al., 2004) is approximated by a double dashed line, with the predicted range edge of *S. alveolata* approximated by a dashed box: (a) All locations from which *S. alveolata* presence or absence has been reported from the 1900s to the 2010s, (b) Locations from which *S. alveolata* presence or absence has been reported in more than 1 decade from the 1970s to the 2010s. (c) Locations from which *S. alveolata* presence or absence has been reported in both the baseline survey of Cunningham et al., (1984) and a contemporary survey completed this study.

present in Appendix 2.2, sites at which *S. alveolata* has never been reported as present (e.g. only Not Seen records collated), were excluded from further analysis as they were assumed to be sites of ‘unsuitable’ (e.g. soft, exposed) or ‘unconnected’ (e.g. not reached by settlement stage larvae) habitat.

2.3.2. *Sabellaria alveolata* data collection

Distribution and abundance data were collected from 327 sites on the west coast of the UK, from Machrihanish in western Scotland (north of the known range edge of *S. alveolata*) to Porthleven in southwest England, in the summer of 2012 to summer 2014. Sites were predominantly selected based on those surveyed historically. The geographic coordinates of historical data were often reported at resolutions greater than 1 km^2. *Sabellaria alveolata* are known to require a sufficient supply of suspended sediment for tube construction and maintenance, and a hard, stable substratum for physical attachment (Gruet, 1971, 1972, 1986; Porras et al., 1996; Holt et al., 1998). Consequently, where coordinate resolution was low, potentially 'suitable' sites (e.g. areas of hard substratum adjacent to, or intermixed with, sedimentary substratum) were identified by local knowledge, Google Earth searches and Ordnance Survey maps, within 1 km^2 of the named historical location prior to survey.

Collection of contemporary data utilised the methodology devised by one of the authors (SJH) of Cunningham et al. (1984). At each site a 30 minute search was completed within 2 hours of low water (surveys were all carried out within 3 days of the fortnightly peak spring tide). The zone of maximum *S. alveolata* abundance was categorised at each site using the modified SACFOR abundance scale (Table 2.1). If no *S. alveolata* was found within the allocated search time, it was recorded as 'Not Seen' and assumed to be absent. If dead reef was present that contained no living individuals, the species was recorded as 'Remains'. This survey technique enabled the assessment of *S. alveolata* abundance on a large spatial scale over a relatively short time-period, whilst allowing a direct temporal comparison between historical and contemporary surveys.

2.3.3. Defining "reefs" within qualitative observations

There is a naturally continuous morphological gradient between "non-reef" and "reef" communities, with mosaics often occurring over a small spatial scale (Bush, pers. obs.). Whilst changes in *S. alveolata* distribution and abundance are of ecological importance, changes in morphology between reef and non-reef state are also of conservation importance. The UK Marine SACs Project defined ‘biogenic reef’ as “*solid, massive structures which are created by accumulations of organisms*” and “*clearly forming a substantial, discrete community or habitat which is very different from the surrounding seabed*” (Holt et al., 1998). Within the British Isles, historical abundance of *S. alveolata* has predominantly been assessed on the semi-quantitative SACFOR categorical scale (Table 2.1, Appendix 2.1) dependent on the maximum morphology of the population. To be classified as ‘Common’ abundance requires “*large sheets or patches*” (e.g. veneers, hummocks or reefs in Table 1.1; Cunningham et al., 1984). Consequently, any population categorised with ‘Common’ or greater abundance on the SACFOR scale was assumed equivalent to the “reef” defined by the UK Marine SACs Project. Conversely to be classified as ‘Frequent’ requires “*small patches*” and so any population categorised as ‘Frequent’ or less is assumed to be ‘non-reef’ forming, and in the case of *S. alveolata*, ‘encrusting’ (Table 2.1).

2.3.4. Assessing change in distribution and abundance

Collated data were compared by decade through time (e.g. data were grouped into discrete decade classes and pair-wise comparisons performed). Data were considered as presence absence data allowing assessment of changes in distribution, and as both SACFOR and morphological data allowing assessment of changes in abundance. Data were considered in three distinct ways: (a) decadal comparisons of all available data; (b) area-specific decadal comparisons; and (c) site-specific comparisons between the baseline dataset of Cunningham et al., (1984) and the contemporary dataset collected in this study.

Decadal comparisons of all available data:

To evaluate long-term temporal variability in *S. alveolata* populations, decadal subsets of data (1980s, 1990s, 2000s, 2010s) from known suitable sites (i.e. sites from which presence was reported at least once) were compared. Records from known suitable sites are subsequently referred to as ‘all available data’ (Figure 2.1 a, listed in Appendix 2.3). The 1990s was excluded from distribution analysis as it was assumed to be ‘presence biased’ (biased by reporting of presence records only). No species targeted survey was carried out in this decade and the assumption is justified as absences were infrequently reported. For abundance and morphological analysis (e.g. “reef” and “non-reef”) more than 50% of presence data in all decades were reported with associated abundance. However, in all decades some presence records were reported without associated abundance. Due to the reporting of the majority of SACFOR categories, including low abundance categories, in all decades, it was assumed that available abundance data was representative of existing abundance in all decades, including the 1990s. Cumulative percentages of presence to absence, SACFOR, and morphological abundance data were compared between decades as stacked column bar charts. The Wilcoxon rank-sum test with continuity correction (WRS) was carried out to assess if changes in the proportions of presence, abundance or morphology categories varied between decades. Data for the WRS required assignment of categorical numbers to distribution, abundance and morphology data following the methodology of Simkanin et al. (2005) and Yesson et al. (2015) (Table 2.1).

Area-specific decadal comparisons:

To facilitate area-specific comparisons through time, records within the same 1 km^2 British National Grid square were grouped spatially (i.e. into 1 km^2 ‘areas’). Maximum presence and abundance classes were retained. Limited data were lost by this approach (Less than 25% of collated records were not directly retained by this approach, of which only ~40% contained data less than that retained). The resultant dataset of spatially and temporally paired suitable areas are subsequently referred to as ‘paired area data’ (Figure 2.1 b, listed in Appendix 2.4). Decadal changes in distribution, abundance, and morphology in paired areas from the 1980s, 2000s, and 2010s were plotted geographically. In consideration of the semi-quantitative nature of the SACFOR scale, a change in abundance was only assigned if the area exhibited a change in abundance of more than one category (e.g. Common to Occasional or Superabundant, not Common to Frequent). Additionally, reported changes in abundance between Rare and Not Seen were not considered a change due to the difficulties in observing and accurately identifying individual specimens. One-tailed sign tests (OTS) were used to compare the number of locations demonstrating a change in distribution (colonisation or extirpation), change in abundance (increase or decrease of greater than one category of the SACFOR scale; as in Firth et al., 2015a) or change in morphology (increase or decrease from encrusting to reef) between decades within regions.

Site-specific comparisons from baseline to the contemporary data:

The national baseline data of Cunningham et al (1984) were compared with contemporary data from the same sites collected using directly comparable methodology (Fieldworkers were trained in the use of the modified SACFOR scale by SJH, one of the original surveyors). The aim of both surveys was to assess the abundance of *S. alveolata* at potentially suitable locations. Consequently, assessment of abundance was consistent between these datasets with minimal observer bias. Site-specific data collected by Cunningham et al. (1984), from 1980 to 1984, were compared with paired site-specific data collected by the authors, from 2012 to 2014 (Figure 2.1 c, listed in Appendix 2.5). Cumulative percentages of presence to absence, SACFOR, and morphological data were compared as stacked column bar charts. Changes in distribution and abundance at paired sites were plotted geographically. As with area-specific comparisons, pair-wise comparisons were carried out with OTS to assess if distribution, SACFOR abundance or morphology varied significantly between datasets.

2.4. Results

2.4.1. Change in distribution

Decadal temporal change in distribution in all available data:

In all comparable decades (1980s, 2000s and 2010s; 1990s not considered for distribution comparisons as assumed to be biased by presence only reporting), presence sightings dominated records from known suitable sites (Figure 2.2 a). No significant difference in the proportion of presence to absence records was demonstrated from the 1980s to either the 2000s or 2010s, but a significant difference occurred from the 2000s to the 2010s due to an increased number of absence reports in the 2010s (WRS, Table 2.2; Figure 2.2 a). The distribution of absence data was relatively consistent between comparable decades, with the exception of (re)colonisations in North Wales from the 1980s to the 2000s (Figure 2.3 a, b). A temporally stable northern range edge occurred in southwest Scotland, with no confirmed presence records reported north of 55 ˚N (Figure 2.3 a – c).

Decadal temporal change in distribution at paired areas:

Sabellaria alveolata was persistent at the majority of suitable areas through time. Changes in state (between populated and unpopulated) were in the minority (>75% of all suitable areas in decadal comparisons between the 1980s, 2000s, and 2010s demonstrated no change in state; Figure 2.3 d). There was no significant difference in the proportion of presence to absence records from paired areas between any decade from the 1980s to the 2010s (OTS, Table 2.2). More colonisations than extirpations occurred from the 1980s to 2000s. Conversely, more extirpations occurred than colonisations from the 1980s to 2010s. At paired areas, equivalent numbers of colonisations and extirpations occurred from the 2000s to the 2010s (Figure 2.3 d). Colonisations dominated change in the north, but extirpations in the centre and south of the British range, from the 1980s to both the 2000s (Figure 2.3 e) and 2010s (Figure 2.3 f). No clear spatial pattern was visible from the 2000s to the 2010s with extirpations and colonisation occurring in roughly equivalent numbers and geographically dispersed (Figure 2.3 d, g).

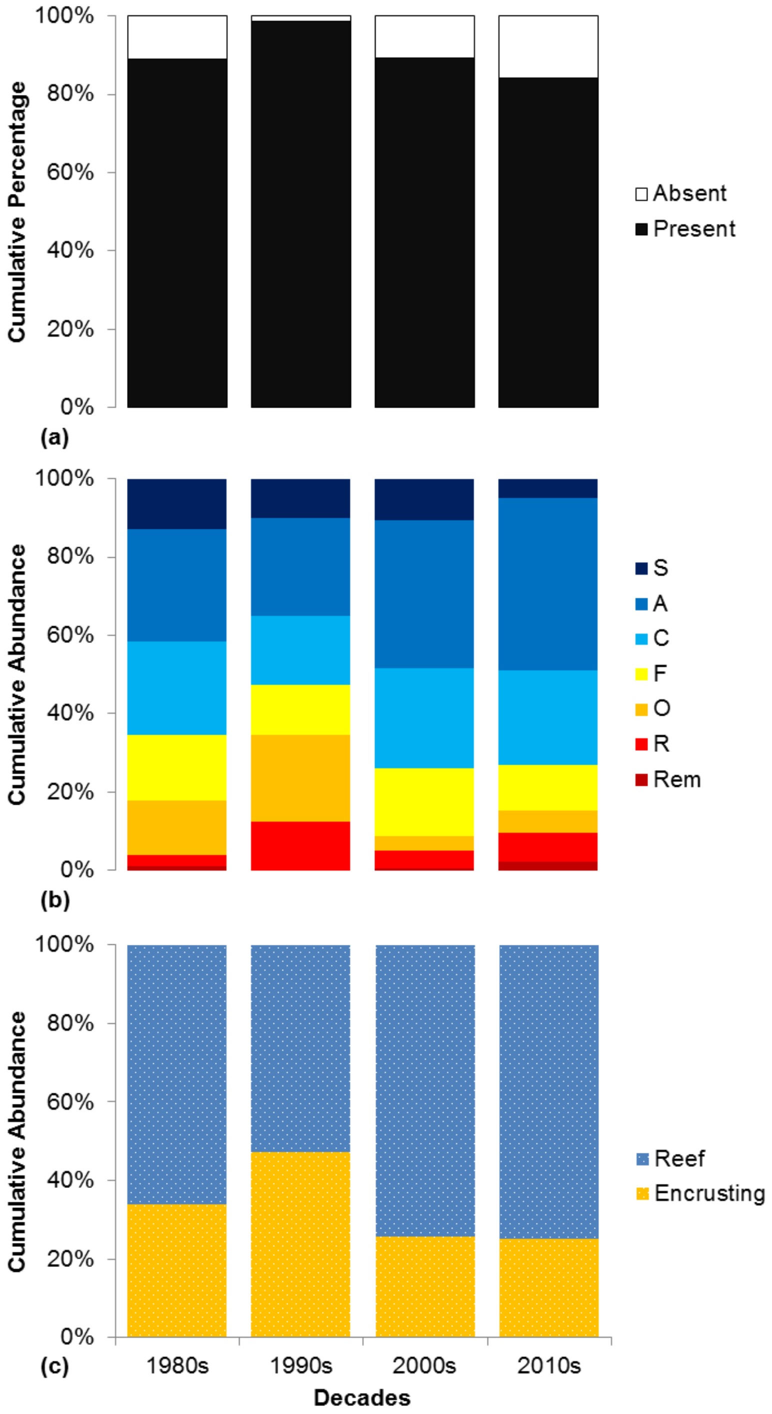
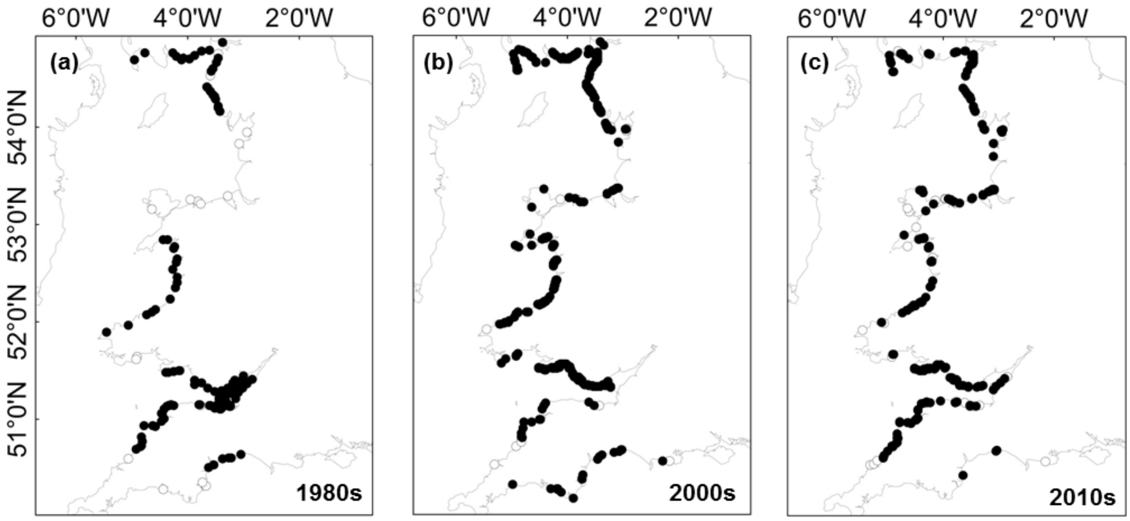


Figure 2.2: National decadal proportions of *Sabellaria alveolata* presence and abundance through time. (a) Percentage of suitable sites where *S. alveolata* was reported as present or absent (n_{1980s} = 174, n_{1990s} = 224, n_{2000s} = 487, and n_{2010s} = 314); (b) Percentage of SACFOR abundance reported from occupied sites (n_{1980s} = 102, n_{1990s} = 177, n_{2000s} = 255, and n_{2010s} = 222); (c) Percentage of reef-forming and encrusting (non-reef-forming) populations reported at occupied sites(n as b).

Decadal distribution data



Change in distribution

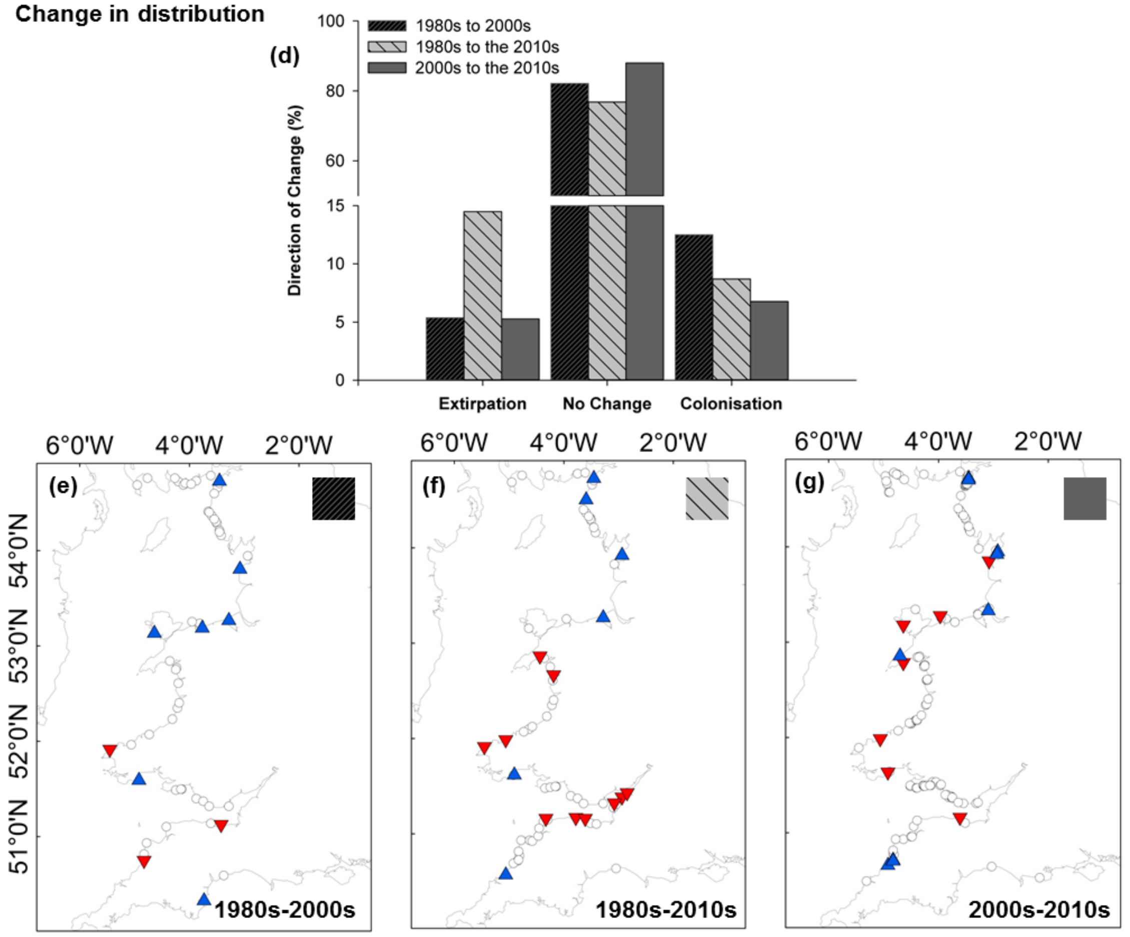


Figure 2.3: *Sabellaria alveolata* distribution, within the British Isles, from the 1980s to the 2010s. (a - c) Reports of *S. alveolata* presence (black) and absence (white) from known suitable sites in the: (a) 1980s; (b) 2000s; and (c) 2010s. (d) Reported changes in the presence to absence ratio at paired 1 km^2 areas from the 1980s to the 2010s ($n_{1980s\text{-}2000s}$ = 56, $n_{1980s\text{-}2010s}$ = 69, and $n_{2000s\text{-}2010s}$ = 133). (e - g) Spatial distribution of reported changes (circle = no change; up = colonisation; down = extirpation) from: (d) 1980s to 2000s; (e) 1980s to 2010s; and (f) 2000s to 2010s.

Table 2.2: National changes in distribution, abundance and morphology of *Sabellaria alveolata* in the British Isles, in comparisons from the 1980s to the 2010s. Changes were considered in all available data on decadal timescales, decadal site-specific data and from the baseline to the contemporary (Contemp.). The 1990s were assumed biased by presence only reporting, and changes in distribution to this decade are not considered further (grey). However, the 1990s were included for abundance and morphology comparisons as the majority of records were reported with associated abundance. Significance in all available data were assessed with a Wilcoxon rank sum test with continuity correction, whilst significance of paired data (areas and sites) were assessed using a one-tailed sign test, with the null hypothesis that no change had occurred (df = 1). Significant increases (↑) are highlighted in blue, decreases (↓) in red (p-value < 0.05), and no significant differences (↔) in white.

Analysis	Dataset	1980s – 1990s	1980s – 2000s	1980s – 2010s	1990s – 2000s	1990s – 2010s	2000s – 2010s	Baseline – Contemp.
Distribution	All	*↑(W = 17466, P <0.001)*	↔ (W = 42421.5, P = 0.917)	↔ (W = 28685, P = 0.129)	*↓(W = 59318, P <0.001)*	*↓ (W = 39933, P <0.001)*	↓ (W = 80834, P = 0.028)	↔ (W = 18568, P = 0.135)
	Pair	↔ (P = 0.168)	↔ (P = 0.104)	↔ (P = 0.086)	↔ (P = 0.087)	↔ (P = 0.105)	↔ (P = 0.070)	↔ (P = 0.088)
Abundance	All	↓ (W = 10392, P = 0.022)	↔ (W = 11798, P = 0.183)	↔ (W = 10814, P = 0.596)	↑ (W = 17251, P <0.001)	↑ (W = 16146, P = 0.002)	↔ (W = 29703, P = 0.371)	↔ (W = 18238, P = 0.173)
	Pair	↔ (P = 0.07)	↔ (P = 0.1)	↔ (P = 0.096)	↔ (P = 0.105)	↔ (P = 0.106)	↔ (P = 0.068)	↔ (P = 0.099)
Morphology	All	↓(W = 10083, P = 0.038)	↔ (W = 11832, P = 0.11)	↔ (W = 10356, P = 0.164)	↑ (W = 17833, P < 0.001)	↑ (W = 15633, P < 0.001)	↔ (W = 12458, P = 0.951)	↔ (W = 10928, P = 0.072)
	Pair	↔ (P = 0.120)	↔ (P = 0.111)	↔ (P = 0.093)	↔ (P = 0.122)	↔ (P = 0.106)	↔ (P = 0.086)	↔ (P = 0.082)

Temporal change in distribution from the baseline to the contemporary data:

Sabellaria alveolata populations demonstrated long-term broad-scale persistence from the baseline data of Cunningham et al. (1984) to the contemporary. No significant difference was demonstrated in the proportion of presence to absence data (OTS, Table 2.2). No change of state was reported from the majority of paired sites, and more extirpations occurred than colonisations (Figure 2.4 a). Although fewer sites demonstrated no change, geographic patterns of change in distribution from the baseline to the contemporary (Figure 2.4 c) mirrored change from the 1980s to 2010s in all paired site data (i.e. colonisations dominated in the north, and extirpations dominated in the centre of the British range; Figure 2.3 f).

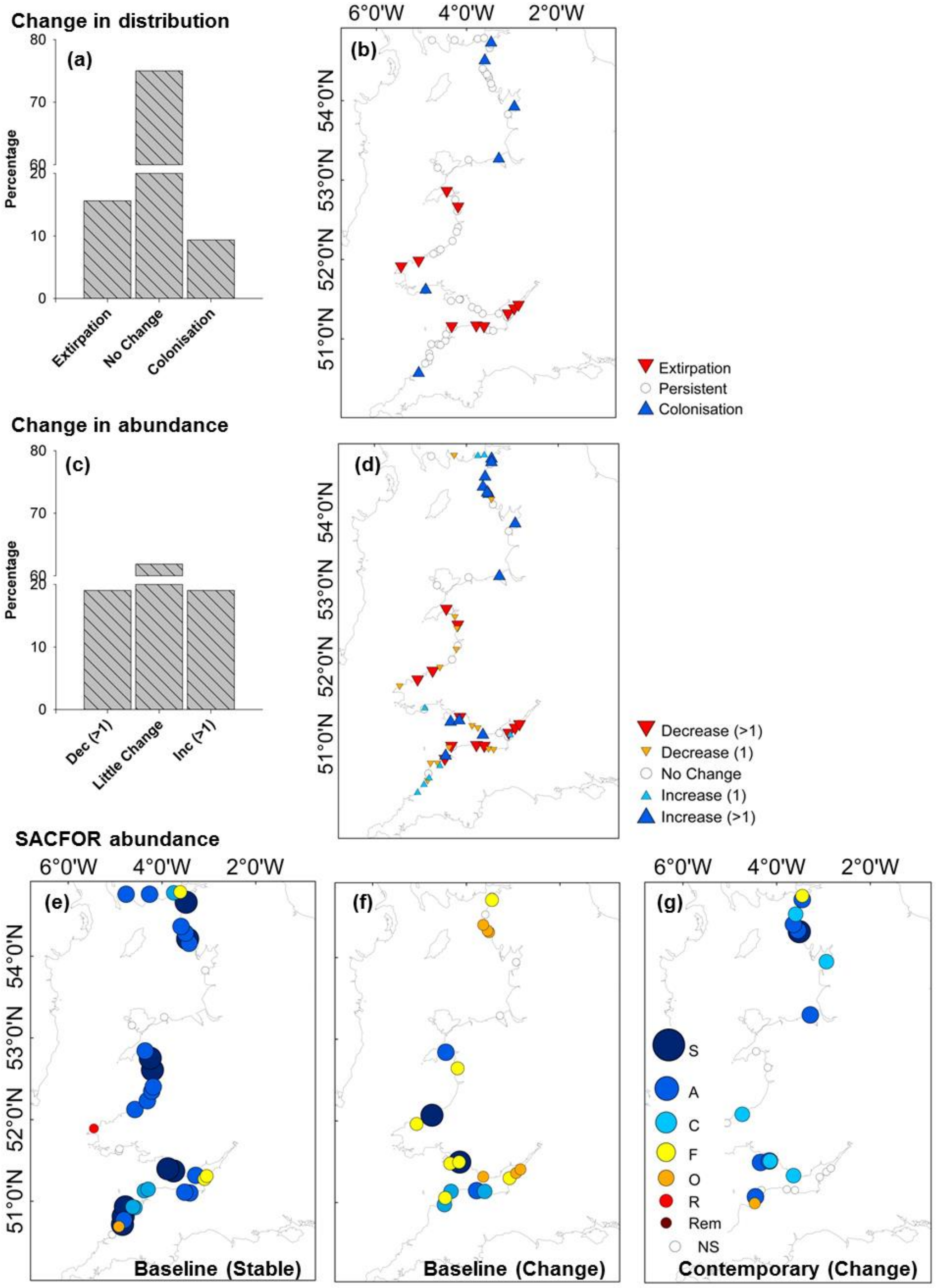


Figure 2.4: *Sabellaria alveolata* distribution and abundance from baseline to contemporary data at paired sites. (a) Reported changes in distribution (n = 64). (b) Reported changes in abundance (n = 63). (c) Spatial patterns of changes in distribution (○ = no change; △ = colonisation; ▽ = extirpation). (d) Spatial patterns of changes in abundance (○ = no change; △/▽= little change of 1 SACFOR category (not considered further); △/▽= increase/decrease of ≥ 2 SACFOR category). (e) SACFOR abundance at sites that demonstrated no or little change (baseline). (f - g) SACFOR abundance at sites where change in abundance occurred. (f) baseline dataset. (g) contemporary dataset.

2.4.2. Change in SACFOR abundance and morphology

Decadal temporal change in abundance and morphology in all available data:

In all decades, the majority of *S. alveolata* populations were of ‘Common’ abundance (or higher) and thus assumed reef-forming morphology. ‘Abundant’ abundance was the most commonly reported category, whilst median abundance was consistently ‘Common’ (Figure 2.2 b). Despite no significant differences in the proportions of SACFOR abundance or morphology categories from the 1980s to either the 2000s or 2010s, significant differences were demonstrated from the 1990s to all other decades (WRS; Table 2.2; Figure 2.2 b). The greatest proportions of ‘Rare’ and ‘Occasional’ abundance occurred in the 1990s when almost half of reported populations were of encrusting morphology (Figure 2.2 b, c). The 1990s also featured the lowest proportion of ‘Common’ and ‘Abundant’ abundance and thus reef-forming populations (Figure 2.2 b, c). Conversely the 2000s and 2010s featured the highest proportion of reef-forming records (the highest percentage of ‘Common’ in the 2000s, and of ‘Abundant’ in the 2010s (Figure 2.2 b, c). Strongholds of high abundance reef-forming *S. alveolata* populations have persisted within southwest and northwest England and mid Wales through time, for example Duckpool, Criccieth and Allonby Bay respectively. Additional, often transient, reef-forming and low abundance encrusting populations have occurred in intervening regions through time (Appendix 2.6).

Decadal temporal change in abundance and morphology at paired areas:

Sabellaria alveolata abundance was stable at the majority of suitable areas through time (Figure 2.5), with no significant difference demonstrated between any decades (OST, Table 2.2). Changes were in the minority in all comparisons (>60% of sites demonstrated little or no change in abundance; Figure 2.5 a - c). More decreases occurred than increases from the 1980s to the 1990s (Figure 2.5 a), and more increases than decreases from the 1990s to both the 2000s and 2010s (Figure 2.5 a, b), again suggesting that a decrease in abundance occurred nationally from the 1980s to the 1990s with recovery to the 2000s and 2010s. As with changes in

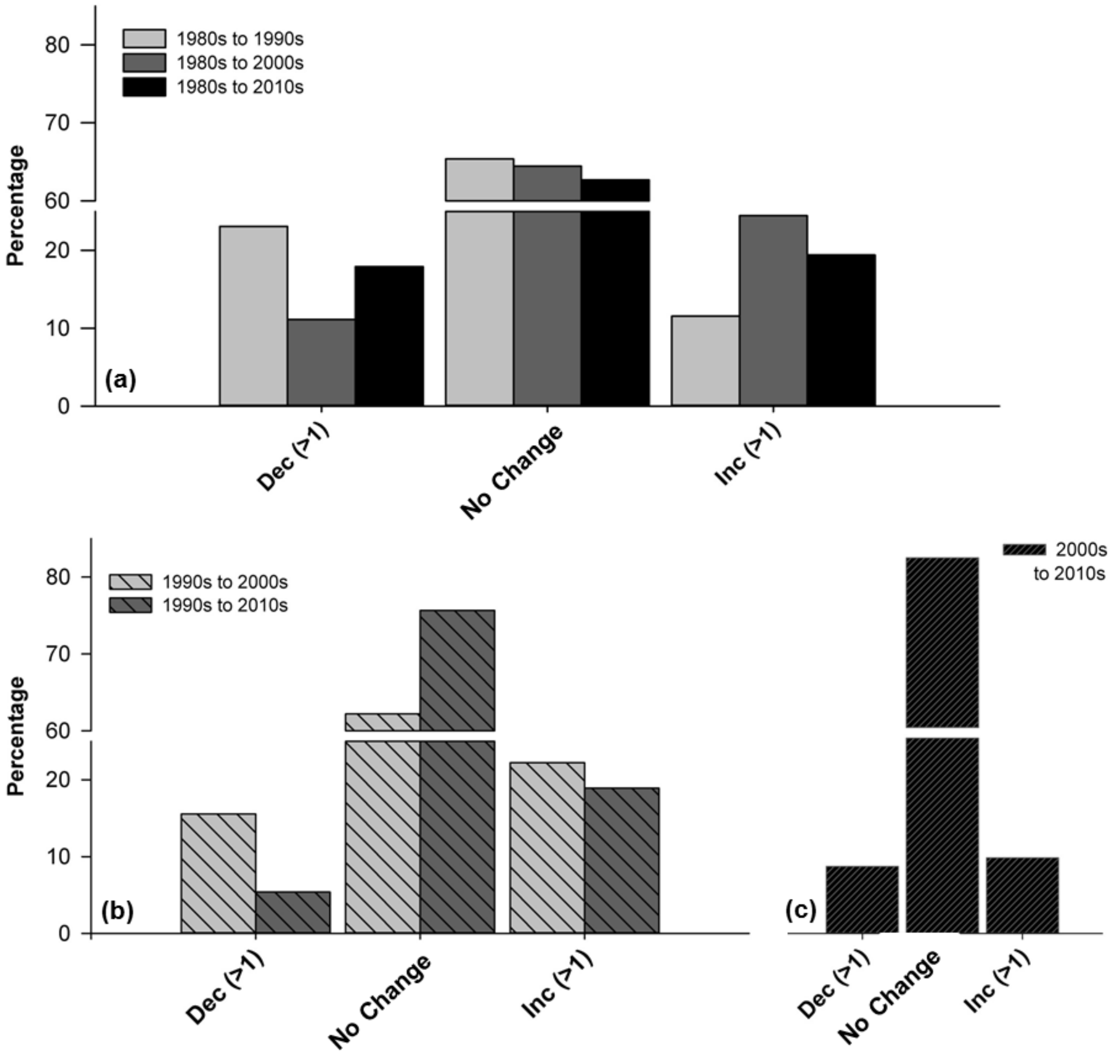


Figure 2.5: Changes in *Sabellaria alveolata* SACFOR abundance within the British Isles, at paired 1 km^2 areas from the 1980s to the 2010s. (a) 1980s to subsequent decades ($n_{1980s\text{-}1990s} = 26$, $n_{1980s\text{-}2000s} = 45$, and $n_{1980s\text{-}2010s} = 67$); (b) 1990s to subsequent decades ($n_{1990s\text{-}2000s} = 45$, and $n_{1990s\text{-}2010s} = 37$); (c) 2000s to 2010s ($n_{2000s\text{-}2010s} = 93$).

distribution, changes in abundance demonstrated regional patterns. From the 1980s to the 1990s decreases occurred throughout Britain, with increases confined to the south coast (Figure 2.6 a). From the 1980s to the 2000s and 2010s decreases in abundance dominated change in southern populations, but increases dominated change in the north (Figure 2.6 b, c). From the 1990s, changes in abundance were geographically dispersed throughout the range (Figure 2.6 d - f); but in contrast to changes from the 1980s, increases dominated change in mid Wales (Figure 2.6 d - e).

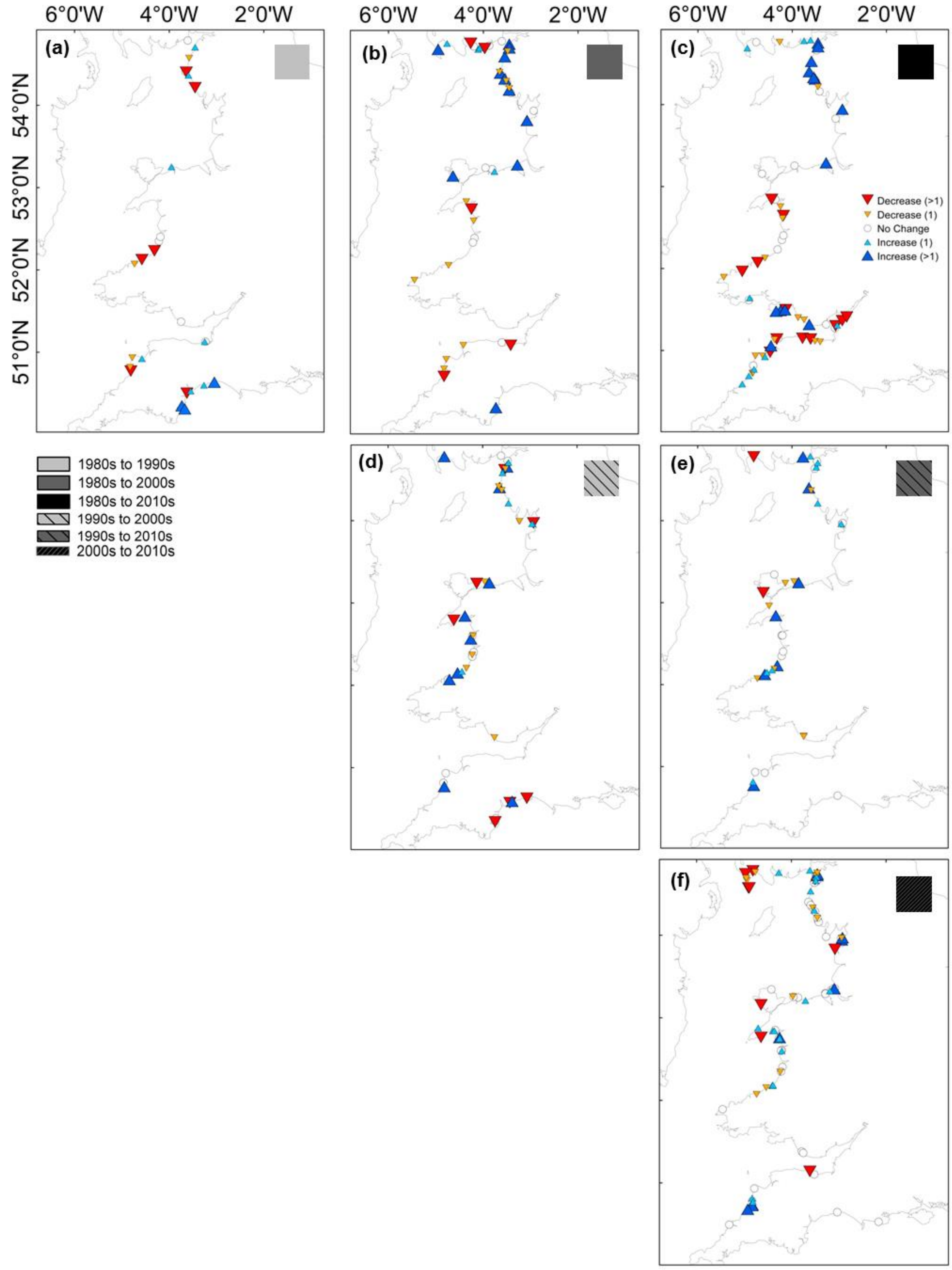


Figure 2.6: Distribution of changes in *Sabellaria alveolata* SACFOR abundance in Britain, at paired 1 km^2 areas, from the 1980s to the 2010s (○ = no change; △/▽= little change of 1 SACFOR category (not considered further); △/▽= increase/decrease of ≥ 2 SACFOR category). (a-c) 1980s to subsequent decades; (d-e) 1990s to subsequent decades; and (f) 2000s to subsequent decades.

Temporal change in abundance from the baseline to the contemporary data:

No significant difference was demonstrated in the relative proportion of raw SACFOR abundance or morphology (OTS, Table 2.2) from the baseline to the contemporary survey. The majority of *S. alveolata* populations demonstrated stability in SACFOR abundance and thus morphology between the baseline data and the contemporary (Figure 2.4 b); particularly at reef-forming populations clustered in mid Wales, southwest England, and from northwest England into Scotland (Figure 2.4 e). The majority of decreases in abundance were extirpations (Figure 2.4 c, d). Sites where a change in morphology occurred were predominantly reported as encrusting populations in the baseline data (Figure 2.4 f) and had subsequently either died out or thrived and been reported as reef-forming populations in the contemporary (Figure 2.4 g).

2.5. Discussion

Through comparisons of best available historical data and contemporary data, this study provided an account of long-term (three decades) and broad-scale (from 50 to 55 °N) changes in the distribution and abundance of a Lusitanian ecosystem engineer within the British Isles where it reaches its northern range edge. Whilst it is impossible to state definitive causes of any change without experimental manipulation, findings are discussed in relation to observed changes in temperature (cold winters and recent warming), and wind-driven wave exposure.

2.5.1. Persistence and stability

Sabellaria alveolata was highly persistent at suitable sites near its range edge (i.e. at sites where *S. alveolata* was reported once, it was consistently reported through time). Although there are concerns regarding both human impacts (Dubois et al., 2002; 2006; Desroy et al., 2011; Strachan, 2013) and the effects of extreme weather events (Crisp, 1964; Cunningham et al., 1984; Frost et al., 2004; Firth et al, 2015), *S. alveolata* might be expected to prosper in a warming world. The 1980s baseline reflected its range and occurrence at the end of a prolonged cold spell. In association with a warming climate, *S. alveolata* remained present at the majority of suitable sites in all decades. Populations that settled on suitable habitat generally persisted through time and changes in state between populated and unpopulated conditions were in the minority. This is in agreement with Cunningham et al., (1984) who suggested that any changes in *S. alveolata* distribution would be minimal through time. In addition to being highly persistent, *S. alveolata* populations have demonstrated long-term broad-scale stability in SACFOR abundance and morphology. Strongholds of reef-forming populations were present within southwest England, mid-Wales and northwest England in all decades. Long-term persistence and stability has also been documented from other regions such as Mont-Saint-Michel Bay, France, where reef-forming *S. alveolata* populations have been reported consistently for centuries (Audouin & Edwards, 1832; Galaine & Houlbert, 1916; Renaud, 1917; Dollfus, 1960; Mathieu, 1967; Le Rhun and Mathieu, 1982; Gruet, 1992; Dubois et al., 2006; Noernberg et al., 2010; Desroy et al., 2011).

Since the late 1980s, Britain has undergone several decades of warming (Hawkins et al., 2009; Firth et al., 2015a). Both a range extension and an increase in abundance *S. alveolata* might be expected in association with increasing average temperatures. But despite gradual average warming, national persistence and stability of *S. alveolata* were observed within Britain. Whilst increased occupancy within range was observed, *S. alveolata* have failed to breach hydrographic boundaries or regions of no habitat availability that set range edges or bound areas of dense populations. Extreme weather events may be partly responsible for the observed stability. For example, extremely cold winters have been reported to counteract responses to a warming climate in the short-term in other intertidal species (e.g. *Perna viridis*, Firth et al., 2011). *Sabellaria alveolata* is susceptible to cold (Gruet, 1982; Bamber & Irvine, 1997), and local extirpations have been reported following extremely cold winters (Crisp, 1964; Cunningham et al., 1984; Gruet & Baudet, 1995). From 2009 to 2010, northern Europe suffered an extremely cold winter (Cattiaux et al., 2010; Cohen et al., 2010; Ouzeau et al., 2011) that may have negatively impacted some populations on a small-scale. The impact of extreme weather events is likely to be spatially restricted. The impact of extreme cold is dependent on the duration and magnitude of the cold spell and the length of aerial exposure with populations at the extreme low shore are potentially buffered from extreme aerial conditions. For example, in previous cold winters, lethargy and mortality have been reported from the upper shore and raised populations (e.g. following the extremely cold winter of 1962/1963; Crisp, 1964; Wilson, 1971), whilst populations on the low shore were unaffected (Wilson, 1971). Similarly, following extremely stormy winters, populations in the upper shore have been physically removed, whilst those on the lower shore have thrived (Bush, pers. obs.). In such instances, no change in the presence to absence ratio or in SACFOR abundance would be observed.

The observed stability may be partially due to the nature of the methodology. SACFOR methodology inherently reports the zone of maximum abundance (Cunningham et al., 1984; Firth et al., 2015a), and consequently, small-scale decreases in abundance and morphology would not be detected. Despite the limitations of this methodology, it is clear that *S. alveolata* has not responded as predicted to increasing average temperatures. The ecology and life history strategy of *S. alveolata* are partially responsible for the persistence and stability of this species (Section 1.4.2). *Sabellaria alveolata* create solid protective tubes and, when reefs are emersed, individuals retreat downward, sealing the tube aperture with their opercular chaeta. Tubes are composed of sand and shell fragments bound by a biomineralised cement (Fournier et al., 2010; Le Cam et al., 2011) that is highly durable and able to dissipate mechanical energy (e.g. from trampling or wave action) for several years, even after death (Le Cam et al., 2011). Consequently, degrading reef structures can survive for many years with little change in morphology. Larvae are attracted to reef structures, both alive and dead (Wilson, 1968), that often facilitates gregarious settlement. In successful settlement years, rapid reef recovery can occur (e.g. at Criccieth following the winter of 1962/1963; Gubbay, 1988), making complete reef destruction unlikely (Gruet, 1986).

2.5.2. Change in distribution

In temporal comparisons, the majority of *S. alveolata* populations demonstrated persistence nationally. However, some changes in distribution were detected through time. More colonisations (i.e. increases from absent to present) were reported than extirpations (i.e. decreases from present to absent) from the 1980s to the 2000s. In contrast, from the 1980s to the 2010s, more extirpations were reported than colonisations, with a decrease in the relative proportion of presence to absence data from the 2000s to the 2010s demonstrated, reflecting some cold winters and a slight downturn in sea surface temperature. Additionally, colonisations predominantly occurred in the north of the range in temporal comparisons from the 1980s to recent decades, whilst extirpations dominated change further south. It is suggested that environmental conditions from the 1980s to the 2000s were favourable for *S. alveolata* persistence and colonisation, particularly in the north of the range, but were less so from the 2000s to the 2010s. The mid-1980s were notably colder than all subsequent years, followed by the 2000s (Wethey et al., 2011). Recent climate change has positively impacted some populations near the northern range edge, whilst negatively impacting those further south.

Cunningham et al., (1984) suggested that fluctuations in distribution would be localised, and in support of this, some spatial clustering of decadal change was observed. Consistent changes occurred at multiple sites within regions, indicative of a sub-regional rather than national scale driver of change. It is theorised that the impact of changes in environmental drivers will be site-specific, with coastline orientation and topography likely important, as has been observed in other intertidal species (e.g. Firth et al., 2015b). Whilst increases in average temperature are likely to be the dominant driver of change in the north of the range, they are not responsible for the decreases observed in southern Britain. Increased storminess has been detected across northern Europe from the 1970s (Alexandersson et al., 1998), with the early 1990s featuring some of the highest winds on record across the British Isles, particularly on southwest coasts (Alexander & Tett, 2005; Allan et al., 2009; Wang et al., 2011; Earl et al., 2013). Increased wave exposure has been implicated in localised reef destruction (Wilson, 1971; 1976; Gruet, 1982; Dias & Paula, 2001), but a degree of wave exposure is necessary to supply food (Anadón, 1981; Dias & Paula, 2001), larvae (Ayata et al., 2009), and suspended sediment for tube construction (Anadón, 1981; Gruet & Bodeur, 1995) and for the removal of waste (Anadón, 1981). Consequently, as wave exposure has increased in recent decades, some sheltered sites may have benefited, whilst exposed sites may have suffered. Wave-exposure induced post-settlement mortality has been observed in other intertidal species including algae (Taylor & Schiel, 2003) and molluscs (Naylor & McShane, 2001). There is also likely to be a seasonal element to the impact of elevated relative wave exposure as a degree of wave action may actively remove settlement stage larvae and recently settled juveniles from the substratum before they can begin tube formation, but not damage adult tubes.

Other environmental parameters may also be influencing *S. alveolata* distribution. Trampling, predation, and competition are reported to negatively impact *S. alveolata* reefs (Cunningham et al., 1984; Dubois et al., 2006; Desroy et al., 2011). Anthropogenic coastal hardening may have facilitated the step-wise colonisation of some British coastlines as several newly colonised sites within north Wales and northwest England, in the 2000s and 2010s, were of anthropogenic origin (Frost et al., 2004; Firth et al., 2015a). Increased siltation may increase the risk of smothering.

Several extirpations occurred on the south coast of the Bristol Channel, from the 1980s to the 2010s. This is known to be a highly turbid and hydrodynamically variable water body (Uncles, 2010). Surviving populations in this region suffered heavy siltation when status was assessed in 2013, and hard substrata at extirpated sites were overlayed with up to 50 cm of mud (Bush, pers. obs.). Porras et al. (1996) previously reported a loss of *S. alveolata* due to high siltation and sand accumulation in the Mediterranean Gulf of Valencia, and I theorise that smothering by fine particles may have induced extirpations at some sites in the British Isles.

2.5.3. Change in abundance

As with distribution, the majority of *S. alveolata* populations demonstrated temporal stability in abundance and incidence of reef-forming morphology nationally. However, the proportions of abundance and morphology were significantly different in the 1990s to comparable decades (i.e. 1980s, 2000s and 2010s), with the greatest proportion of encrusting, and lowest proportion of reef-forming populations. This increase in low abundance populations may have been due to a suppression of existing populations, however it may also have been due to increased colonisation by low abundance encrusting populations. A reduction in average abundance due to numerous colonisations by low encrusting populations cannot be ruled out, but more decreases in abundance at persistent sites occurred than increases from the 1980s to the 1990s, whilst more increases occurred than decreases between the 1990s and subsequent decades.

It is theorised that wave exposure and temperature have been working antagonistically to influence *S. alveolata* abundance and morphology within Britain. Increased temperatures have been reported to favour both *S. alveolata* individual and tube growth, and thus reef development (Gruet, 1982; Bamber & Irvine, 1997). Rapid recovery of reefs from high mortality has also been documented potentially due to increased reproductive output and successful recruitment (e.g. many populations negatively impacted by the extreme winter of 1962-1963 demonstrated complete recovery by the early 1980s; Crisp, 1964; Cunningham et al., 1984). In contrast, high wave exposure has been implicated in reef fragmentation, particularly of large reefs with fissures or holes (Wilson, 1974). Decreases in both size and growth rate under conditions of high wave exposure have been reported in other species (e.g. Adey (1978) in coral reef ecology; Blanchette (1997) in intertidal plant ecology). Consequently, at exposed sites, increased wave exposure is likely to favour encrusting forms of *S. alveolata.*

Decreases in abundance and morphology from the 1980s to the 1990s were observed, but increases from the 1990s to subsequent decades. Unprecedented maximum winter storminess was reported in the early 1990s around the British Isles (Alexander & Tett, 2005; Allan et al., 2009; Wang et al., 2011). The winter of 1989-90 featured some of the most damaging winds on record (e.g. windstorms Daria and Vivian) with widespread destruction across England and Wales (Earl et al., 2013). It is theorised that such storminess had a direct detrimental effect on more exposed *S. alveolata* populations. Additionally, the decrease in the proportion of high abundance *S. alveolata* populations during the 1990s may in part be the result of the prolonged cold of the 1980s resulting in both adult mortality (Gubbay, 1988), and potential failed recruitment success over a period of almost a decade (Slater, 2013). Dependent on environmental conditions (Gruet, 1982; Dias & Paula, 2001), original reef morphology (Wilson, 1974), and the success of larval recruitment, any decrease in physical reef morphology following a period of extreme cold may show a temporal lag.

2.6. Conclusions

The biogenic reef-forming species *S. alveolata* has demonstrated no change in range, and stability in abundance and the incidence of reef-forming morphology, on long temporal and broad spatial scales in the north of its range, from the 1980s to the 2010s. Overlaying this trend, a decrease in occupancy at suitable sites was demonstrated from the 2000s to the 2010s, whilst the proportion of high abundance reef-forming *S. alveolata* populations was reduced in the 1990s (associated with a potential expansion in distribution), with recovery by the 2000s. Additionally, it is suggested that changes in both distribution and abundance may be occurring on reduced spatial and temporal scales. For example, recolonisation of sites in north Wales occurred from the 1980s to the 2000s, and changes in both abundance and distribution at the range edge were often in opposition to changes within the range. Individual reefs exist in a delicate balance between stages of development with growth, stagnation and decline often occurring within a single reef, potentially controlled by physical processes (e.g. temperature, wave exposure, sediment supply) but also by biological processes (e.g. recruitment success; Gruet, 1986; Brown & Miller, 2011). It is suggested that on British coastlines, changes in other environmental variables (e.g. reported increases in wave exposure, or an increased frequency of extreme weather events), in addition to natural hydrographic barriers (e.g. exposed peninsulas or regions of soft substrata) are restricting the predicted increase in both distribution and abundance of an ecosystem engineer, in response to warming temperatures.

2.7. Acknowledgements

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2.8. Appendices

Appendix 2.1: Sources of available data on *Sabellaria alveolata* presence and abundance on British coastlines (* Data sourced through the National Biodiversity Network gateway). The number of records sourced from each data provider, and the format of the original record (SACFOR = SACFOR abundance, PA = just presence data, TYPE COMMENT = abundance data provided on alternative scale, and converted to SACFOR, COMMENT = reef morphological descriptors given allowing conversion to SACFOR) was noted.

Data Sources	**No. Records**	**Original Record Type**
All	1713	As below
Authors	350	SACFOR/PA
Cunningham et al., 1984	315	SACFOR/PA
Marine Nature Conservation Review	221	SACFOR/PA
Marclim	205	SACFOR/PA
Natural Resources Wales	179	SACFOR/TYPE COMMENT/PA
Allen et al., 1999; 2002	155	SACFOR/TYPE COMMENT/PA
South East Wales Biodiversity Records Centre	116	SACFOR/PA
Merseyside BioBank	77	COMMENT/PA
Marine Biological Association	75	SACFOR/PA
UK MarLIN Shore Thing	35	SACFOR/PA
Bamber & Irving, 1997	30	COMMENT/PA
Scottish Natural Heritage	29	SACFOR/PA
Frost et al., 2004	28	SACFOR/PA
Cumbria Biodiversity Data Centre	18	COMMENT/PA
Wilson, 1929; 1970; 1971	7	SACFOR/COMMENT/PA
Sykes, 1996	6	COMMENT/PA
North Wales Environmental Information Service	5	SACFOR/PA
Bristol Regional Environmental Data Centre	4	PA
Marine Conservation Society	4	SACFOR/PA
Marine Recorder	4	PA
Unicomarine	4	COMMENT/PA
Martin, 1993	3	COMMENT/PA
Naylor & Viles, 2000	3	PERS. COMM/PA
White., 2011	3	COMMENT/PA
Boalch, 1957	2	COMMENT/PA
Pembrokeshire Marine Species Atlas	2	PA
Allan et al, 1991	1	PA
Cutts & Hemingway, 1995	1	SACFOR/PA
Horne, 1982	1	COMMENT/PA

Appendix 2.2: Collated *Sabellaria alveolata* distribution and abundance data, including individual data point identification numbers, original site name, OSGB geographic coordinates, sampling year, available presence and abundance data, the responsible surveyor and the data source (n = 1713). Presence is reported as either present (1) or absent (0). Abundance is reported on the SACFOR scale where Superabundant (7) to Rare (2). Additional categories include just presence with no associated abundance data (10), Remains (1) and Not Seen (0). Data sources followed by an asterisk were accessed through the National Biodiversity Network gateway.

ID	**Site name**	**Eastings**	**Northings**	**Date**	**Presence**	**Abundance**	**Surveyor**	**Data Source**
1	Leiravagh Bridge (Loch Chill Eireabhaigh, Benbecula)	83000	846000	03/05/1978	1	3	Unknown	Marine Nature Conservation Review and associated benthic marine data held and managed by JNCC (subsequently referred to as MNCR- JNCC;*)
2	Tresco	88000	16000	00/00/1973	1	3	Harvey	Cunningham et al., 1984
3	Nanjizal (Lands End)	135000	23000	26/06/2002	0	0	Marclim Team	Marclim
4	Cape Cornwall	135000	32000	12/05/2002	0	0	Marclim Team	Marclim
5	Cape Cornwall	135000	32000	01/06/2003	0	0	Marclim Team	Marclim
6	Whitesand Bay (Lands End)	136000	27000	26/06/2002	0	0	Marclim Team	Marclim
7	Porth Swtan	137000	21000	12/08/2003	0	0	Marclim Team	Marclim
8	Ardnamurchan Point	142000	767000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
9	Lamorna Cove	145000	23000	27/06/2002	0	0	Marclim Team	Marclim
10	Mousehole	147000	26000	27/06/2002	0	0	Marclim Team	Marclim
11	Penzance	147000	29000	28/06/2002	0	0	Marclim Team	Marclim
12	Ardmore Point	147000	650000	00/00/1967	1	10	Norton	Cunningham et al., 1984
13	Saint Ives	152000	41000	12/05/2002	0	0	Marclim Team	Marclim
14	Saint Ives	152000	41000	15/06/2003	0	0	Marclim Team	Marclim
15	Porthleven	162000	25000	00/00/1980	0	0	Hawkins	Cunningham et al., 1984
16	Porthleven	162000	25000	00/00/1981	0	0	Hawkins	Cunningham et al., 1984
17	Porthleven	162000	25000	00/00/1982	0	0	Hawkins	Cunningham et al., 1984
18	Porthleven	162000	25000	00/00/1983	0	0	Hawkins	Cunningham et al., 1984
19	Porthleven	162000	25000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
20	Porthleven	162000	25000	11/05/2002	0	0	Marclim Team	Marclim
21	Porthleven	162000	25000	31/05/2003	0	0	Marclim Team	Marclim
22	Porthleven	162000	25000	27/05/2013	0	0	Bush	-
23	Machrihanish	163000	620000	18/08/2012	0	0	Bush	-
24	Machrihanish	163000	622000	18/08/2012	0	0	Bush	-
25	Kentra	164000	769000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
26	Arisaig	165000	786000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
27	Poldhu Cove (Mullion)	166000	19000	28/06/2002	0	0	Marclim Team	Marclim
28	Mallaig	167000	797000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
29	Loch Allort	169000	778000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
30	Lizard	170000	11000	11/05/2002	0	0	Marclim Team	Marclim
31	Lizard	170000	11000	30/05/2003	0	0	Marclim Team	Marclim
32	Lizard	170000	11000	27/05/2013	0	0	Bush	-
33	Trevellas	172000	51000	27/05/2013	0	0	Bush	-
34	Trevellas	172000	52000	00/00/1979	1	10	Williams	Cunningham et al., 1984

35	Whitesand Bay (St. Davids)	173000	226000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
36	Whitesand Bay (St. Davids)	173000	227000	05/07/2012	0	0	Bush	-
37	Martins Haven	175000	209000	28/08/2003	0	0	Marclim Team	Marclim
38	Caerfai Bay (St. Davids)	175000	224000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
39	Caerfai Bay, N (St. Davids)	175000	224000	05/07/2012	0	0	Bush	-
40	Caerfai Bay (St. Davids)	176000	224000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
41	Caerfai Bay, S (St. Davids)	176000	224000	05/07/2012	0	0	Bush	-
42	Fistral Beach	179000	62000	26/07/2002	0	0	Marclim Team	Marclim
43	Fistral Beach	179000	62000	26/05/2013	0	0	Bush	-
44	Abereiddy	179000	231000	00/00/1984	1	2	Cunningham	Cunningham et al., 1984
45	Abereiddy	179000	231000	22/08/2002	0	0	Marclim Team	Marclim
46	Abereiddy, N	179000	231000	05/07/2012	0	0	Bush	-
47	Newquay	180000	62000	11/04/2001	0	0	Hawkins	Hawkins notebooks
48	Newquay	180000	62000	11/04/2002	0	0	Marclim Team	Marclim
49	Fistral Beach, N	180000	62000	26/05/2013	0	0	Bush	-
50	Plockton	180000	834000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
51	Loch Gairloch	180000	875000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
52	Loch Gairloch	180000	876000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
53	Flushing (Falmouth)	181000	33000	28/07/2002	0	0	Marclim Team	Marclim
54	Gann Flats	181000	206000	27/04/1998 - 08/10/1998	1	10	CCW Team	Marine Intertidal Phase 1 species dataset from the Countryside Council for Wales 1996-2005 (subsequently referred to as MIP1-CCW; *)
55	Newquay	182000	63000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
56	Trevelgue Head	182000	63000	26/05/2013	0	0	Bush	-
57	Dale	182000	205000	05/10/2002	0	0	Marclim Team	Marclim
58	West Angle Bay	184000	203000	23/08/2002	0	0	Marclim Team	Marclim
59	West Angle Bay	184000	203000	27/08/2003	0	0	Marclim Team	Marclim
60	West Angle Bay (Dale)	184000	203000	06/07/2012	0	0	Bush	-
61	Newgale	184000	222000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
62	Newgale	184000	222000	05/07/2012	0	0	Bush	-
63	Loch Ewe	184000	890000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
64	West Angle Bay	185000	203000	00/00/1973	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
65	West Angle Bay	185000	203000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
66	West Angle Bay (Dale)	185000	203000	06/07/2012	0	0	Bush	-
67	Broadhaven	185000	212000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
68	Broadhaven	185000	212000	05/07/2012	0	0	Bush	-
69	Broadhaven	185000	214000	23/08/2002	0	0	Marclim Team	Marclim
70	Broadhaven	185000	214000	27/08/2003	0	0	Marclim Team	Marclim
71	Broadhaven	185000	214000	05/07/2012	0	0	Bush	-
72	Nolton Haven	185000	218000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
73	Nolton Haven	185000	218000	05/07/2012	0	0	Bush	-
74	Abercastle	185000	233000	08/08/2002	0	0	Marclim Team	Marclim
75	Littlewick Bay (Larne)	186000	206000	25/08/2002	0	0	Marclim Team	Marclim

76	Littlewick Bay (Larne)	186000	206000	25/09/2003	0	0	Marclim Team	Marclim
77	Loch Ewe	186000	881000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
78	Trevone	188000	75000	00/00/1968	1	2	Wilson	Wilson, 1968/ Cunningham et al., 1984
79	Newtrain Bay (Trevone)	188000	75000	11/04/2002	0	0	Marclim Team	Marclim
80	Trevone	188000	75000	27/05/2013	0	0	Bush	-
81	Trevone	188000	76000	27/05/2013	0	0	Bush	-
82	Freshwater West	188000	199000	00/00/1973	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
83	Freshwater West	188000	199000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
84	Freshwater West	188000	199000	06/07/2012	0	0	Bush	-
85	Port Ann (Loch Fyne)	190000	685000	00/00/1918	0	0	Chumley	Cunningham et al., 1984
86	Port Ann (Loch Fyne)	190000	685000	18/08/2012	0	0	Bush	-
87	Harbour Cove, S (Padstow)	191000	76000	27/05/2013	0	0	Bush	-
88	Harbour Cove, N (Padstow)	191000	77000	27/05/2013	0	0	Bush	-
89	Harbour Cove (Padstow)	192000	76000	00/00/1970	1	1	Wilson	Cunningham et al., 1984
90	Harbour Cove, S (Padstow)	192000	76000	27/05/2013	0	0	Bush	-
91	Sites 5 and 6	192000	203000	13/12/1994	1	10	Restricted access	Marine records from Pembrokeshire Marine Species Atlas (subsequently referred to as PemAt;*)
92	Polzeath	193000	79000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
93	Polzeath	193000	79000	27/05/2013	0	0	Bush	-
94	Castle Point to Fishguard Breakwater	194000	237000	25/04/2001	1	10	CCW Team	MIP1-CCW (*)
95	Castle Point to Fishguard Breakwater	194000	237000	16/07/2003	1	10	CCW Team	Countryside Council of Wales (subsequently referred to as CCW)
96	Castle Point to Fishguard Breakwater	195000	237000	25/04/2001	1	10	CCW Team	MIP1-CCW (*)
97	Kilbride Bay	195000	666000	18/08/2012	0	0	Bush	-
98	Port Quin Harbour	196000	80000	00/00/1970	1	3	Wilson	Wilson, 1971/Cunningham et al., 1984
99	Port Quin	196000	80000	27/05/2013	0	0	Bush	-
100	The Wash to Long Matthew Point	196000	192000	22/05/2001	1	10	CCW Team	MIP1-CCW (*)
101	St Govans Chapel	196000	192000	24/08/2002	0	0	Marclim Team	Marclim
102	Reiff	196000	914000	29/05/2002	0	0	Marclim Team	Marclim
103	Reiff	196000	914000	07/02/2003	0	0	Marclim Team	Marclim
104	Rudha Coigeach	196000	915000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
105	Alltain Duidh	198000	911000	29/05/2002	0	0	Marclim Team	Marclim
106	Dinas Head to Castle Point	199000	238000	29/04/2003	1	10	CCW Team	MIP1-CCW (*)
107	Portpatrick	199000	553000	20/07/2012	0	0	Bush et al.	-
108	Portpatrick	199000	554000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
109	Portpatrick	199000	554000	20/07/2012	0	0	Bush et al.	-
110	Dinas Head to Castle Point	200000	239000	29/04/2003	1	10	CCW Team	MIP1-CCW (*)
111	Freshwater East	201000	197000	31/07/2000	1	10	CCW Team	MIP1-CCW (*)
112	Cwmyr Eglwys, E (Newport)	201000	240000	15/05/1976	1	3	Unknown	Cunningham et al., 1984/ PemAt (*)/ MNCR-JNCC (*)
113	Cwm yr Eglwys	201000	240000	05/07/2012	1	4	Bush	-
114	Achnhaird	201000	914000	29/05/2002	0	0	Marclim Team	Marclim
115	Ailsa Craig	202000	599000	00/00/1984	0	0	Norton	Cunningham et al., 1984
116	Tregardock Beach	203000	83000	00/00/1970	1	3	Wilson	Cunningham et al., 1984

117	Tregardock Beach	203000	83000	26/05/2013	1	3	Bush	-
118	Tregardock Beach	203000	84000	26/05/2013	1	3	Bush	-
119	Kyles of Bute (Colintraive)	203000	674000	18/08/2012	0	0	Bush	-
120	Clachtoll	203000	926000	28/05/2002	0	0	Marclim Team	Marclim
121	Clachtoll	203000	927000	28/05/2002	0	0	Marclim Team	Marclim
122	Stoer	203000	928000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
123	Stoer	203000	928000	27/05/2002	0	0	Marclim Team	Marclim
124	Saint Astell	204000	51000	00/00/1954	1	10	Collis	Cunningham et al., 1984
125	Trebarwith Strand	204000	86000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
126	Trebarwith Strand	204000	86000	26/05/2013	1	2	Bush	-
127	Parrog	204000	239000	00/00/1984	1	4	Cunningham	Cunningham et al., 1984/ Marine Biological Association (DASSH Data Archive Centre academic surveys) (subsequently referred to as DASSHac; *)
128	Parrog to Cwm yr Eglwys	204000	239000	16/05/2003	1	10	CCW Team	MIP1-CCW (*)
129	Parrog	204000	239000	05/07/2012	0	0	Bush	-
130	Parrog	204000	239000	18/02/2014	0	0	Bush	-
131	Stranraer West Beach	204000	562000	20/04/2013	0	0	Logan/Logan/SNH	Scottish Natural Heritage (subsequently referred to as SNH)
132	Kyles of Bute	204000	673000	00/00/1984	0	0	Norton	Cunningham et al., 1984
133	Culkein	204000	933000	27/05/2002	0	0	Marclim Team	Marclim
134	Manorbier	205000	197000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
135	Manorbier	205000	197000	06/07/2012	0	0	Bush	-
136	Newport Sands (Ceibwr Bay toPan y Bal)	205000	241000	10/05/2001	1	10	CCW Team	MIP1-CCW (*)
137	Ceibwr Bay to Peny Bal	205000	241000	06/07/2004	1	10	CCW Team	MIP1-CCW (*)
138	Achmelvich	205000	925000	27/05/2002	0	0	Marclim Team	Marclim
139	Ardwell Bay	206000	545000	25/07/2014	0	0	Bush	-
140	Clarach	206000	931000	08/08/2002	0	0	Marclim Team	Marclim
141	Loch Strivan	207000	671000	18/08/2012	0	0	Bush	-
142	Boscastle	208000	91000	26/05/2013	1	2	Bush	-
143	Boscastle	208000	92000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
144	Priests Nose to Lydstep Point	208000	197000	06/08/1997	1	10	CCW Team	MIP1-CCW (*)
145	Loch Strivan	208000	671000	00/00/1918	0	0	Chumley	Cunningham et al., 1984
146	Loch Strivan	208000	671000	18/08/2012	0	0	Bush	-
147	Polkerris	209000	52000	29/03/2002	1	5	Marclim Team	Marclim
148	Port Logan Harbour	209000	537000	25/07/2014	0	0	Bush	-
149	Port Logan Bay	209000	538000	25/07/2014	0	0	Bush	-
150	Ceibwr Bay (Cardigan)	210000	245000	23/06/1997	1	5	Campline/CCW	MNCR-JNCC
151	Sandhead	210000	549000	00/00/2000	1	5	Hammond	Allen et al., 2002
152	Sandhead	210000	549000	24/07/2014	1	3	Bush	-
153	Olbany	210000	933000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
154	Cardigan Bay SAC	211000	245000	26/07/2002	1	5	Holt/CCW	Marine data from Countryside Council for Wales (CCW) Technical Support (Research & Monitoring) Contracts, Wales (subsequently referred to as

								CCWTech; *)
155	Logan Mills (Solway, N)	211000	543000	15/09/1989	1	3	Covey	MNCR-JNCC
156	Logan Mills (Solway, N)	211000	543000	00/00/2000	1	5	Hammond	Allen et al., 2002
157	Logan Mills (Solway, N)	211000	543000	25/07/2014	1	4	Bush	-
158	Crackington Haven, W	212000	97000	00/00/1984	0	0	Southward	Cunningham et al., 1984
159	Tripods (2m trawl)	212000	328000	27/07/2001	1	10	Bergmann/CCW	CCWTech (*)
160	Terally Point	212000	540000	00/00/2000	1	5	Hammond	Allen et al., 2002
161	Terally Point	212000	540000	25/07/2014	1	4	Bush	-
162	Loch Fyne	212000	708000	00/00/1918	0	0	Chumley	Cunningham et al., 1984
163	Crackington Haven	213000	96000	01/05/2003	0	0	Marclim Team	Marclim
164	Crackington Haven, SW	213000	96000	26/05/2013	1	4	Bush	-
165	Crackington Haven, N	213000	97000	00/00/1984	1	3	Cunningham	Cunningham et al., 1984
166	Crackington Haven, N	213000	97000	26/05/2013	1	4	Bush	-
167	Tenby	213000	200000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
168	Overhangs (Saint Catherines)	213000	200000	17/09/2008	1	10	Aquatic Survey & Monitoring Ltd	CCWTech (*)
169	Tenby	213000	200000	28/04/2013	0	0	Bush	-
170	Overhangs (Waterwynch)	213000	201000	16/09/2008	1	10	Aquatic Survey & Monitoring Ltd	CCWTech (*)
171	Cardigan Bay SAC	213000	249000	25/07/2002	1	6	Holt/CCW	CCWTech (*)
172	Crackington Haven	214000	96000	26/05/2013	1	4	Bush	-
173	Monkstone Point (Saundersfoot)	214000	203000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
174	Monkstone Point (Saundersfoot)	214000	203000	28/04/2013	1	2	Bush	-
175	Teifi Estuary to Ceibwr Bay	214000	249000	18/07/1996	1	10	CCW Team	MIP1-CCW (*)
176	East Tarbert	214000	530000	00/00/2000	1	4	Hammond	Allen et al., 2002
177	East Tarbert	214000	530000	24/07/2014	1	2	Bush	-
178	Portankill	214000	532000	00/00/2000	1	4	Hammond	Allen et al., 2002
179	Maryport Bay	214000	534000	00/00/2000	1	10	Hammond	Allen et al., 2002
180	Scourie	214000	944000	28/05/2002	0	0	Marclim Team	Marclim
181	Scourie	214000	944000	04/03/2003	0	0	Marclim Team	Marclim
182	Scourie Bay	214000	945000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
183	Monkstone Point (Saundersfoot)	215000	203000	24/08/2002	0	0	Marclim Team	Marclim
184	Overhangs (Monkstone Point)	215000	203000	18/09/2008	1	10	Aquatic Survey & Monitoring Ltd	CCWTech (*)
185	Monkstone Point (Saundersfoot)	215000	203000	28/04/2013	1	2	Nuutilla	-
186	Amroth	215000	206000	29/04/2013	0	0	Bush	-
187	Gwbert	215000	250000	00/00/2002	1	5	Marclim Team	Marclim
188	Cardigan Bay SAC	215000	251000	25/07/2002	1	4	Holt/CCW	CCWTech (*)
189	Mull of Galloway	215000	530000	00/00/2000	1	4	Hammond	Allen et al., 2002
190	Mull of Galloway	215000	530000	24/07/2014	1	2	Bush	-
191	Amroth	216000	206000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
192	Cardigan Island Sound (cave, Cardigan)	216000	251000	24/09/1996	1	7	Nichols/CCW	MNCR-JNCC
193	Aberdaron	216000	326000	13/08/2003	1	2	Marclim Team	Marclim

194	Porth or	216000	329000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
195	Porth Oer	216000	329000	11/06/2002	0	0	Marclim Team	Marclim
196	Porth Oer	216000	329000	13/08/2003	0	0	Marclim Team	Marclim
197	Porth Oer, S	216000	329000	03/07/2012	0	0	Bush	-
198	Porth Oer, N	216000	330000	03/07/2012	0	0	Bush	-
199	N Target Base (Luce Sands)	216000	554000	00/00/2000	1	4	Hammond	Allen et al., 2002
200	Great Cumbrae	216000	656000	00/00/1984	0	0	Norton	Cunningham et al., 1984
201	Aberdaron	217000	326000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
202	Aberdaron	217000	326000	03/07/2012	0	0	Bush	-
203	Woodland Bay	217000	595000	20/07/2012	0	0	Bush	-
204	Porten Cross(Largs)	217000	648000	00/00/1984	0	0	Norton	Cunningham et al., 1984
205	Porten Cross(Largs)	217000	648000	17/08/2012	0	0	Bush	-
206	Dunoon Basin	217000	676000	18/08/2012	0	0	Bush	-
207	Dunoon Basin	217000	677000	00/00/1918	0	0	Chumley	Cunningham et al., 1984
208	Millook	218000	100000	00/00/1957	1	5	M.B.A.	Wilson, 1971/Cunningham et al., 1984
209	Millook	218000	100000	00/00/1975	1	10	Burrows	Cunningham et al., 1984
210	Millook	218000	100000	00/00/1984	1	7	Cunningham	Cunningham et al., 1984
211	Millook	218000	100000	00/00/2012	1	6	Bush	-
212	Port Erin, S	218000	469000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984/ DASSHac (*)
213	Port Erin, S	218000	469000	03/08/2012	0	0	Bush	-
214	Black Rock (Widemouth Bay)	219000	101000	00/00/1986	1	6	Pawlik	DASSHac (*)
215	Black Rock (Widemouth Bay)	219000	101000	01/05/2003	0	0	Marclim Team	Marclim
216	Black Rock (Widemouth Bay)	219000	101000	25/05/2013	1	5	Bush	-
217	Widemouth Bay	219000	102000	00/00/1970	1	3	Wilson	Wilson, 1971/Cunningham et al., 1984
218	Widemouth Bay	219000	102000	01/05/2003	0	0	Marclim Team	Marclim
219	Widemouth Bay	219000	102000	25/05/2013	1	6	Bush	-
220	BudeW	219000	106000	25/05/2013	1	6	Bush	-
221	Bude	219000	107000	18/04/2003	1	6	Marclim Team	Marclim
222	Flexbury (Bude)	219000	107000	25/05/2013	1	6	Bush	-
223	Duckpool (Coombe)	219000	111000	30/05/1961-23/11/1961	1	10	Wilson	DASSHac (*)
224	Duckpool (Coombe)	219000	111000	07/02/1962-12/12/1962	1	7	Wilson	Cunningham et al., 1984/ DASSHac (*)
225	Duckpool (Coombe)	219000	111000	5/02/1963-01/12/1963	1	10	Wilson	DASSHac (*)
226	Duckpool (Coombe)	219000	111000	01/01/1964-20/12/1964	1	10	Wilson	DASSHac (*)
227	Duckpool (Coombe)	219000	111000	19/03/1965-24/11/1965	1	10	Wilson	DASSHac (*)
228	Duckpool (Coombe)	219000	111000	08/01/1966-14/12/1966	1	10	Wilson	DASSHac (*)
229	Duckpool (Coombe)	219000	111000	28/01/1967-03/12/1967	1	10	Wilson	DASSHac (*)
230	Duckpool (Coombe)	219000	111000	16/02/1968-	1	10	Wilson	DASSHac (*)

				21/11/1968				
231	Duckpool (Coombe)	219000	111000	19/01/1969-11/12/1969	1	10	Wilson	DASSHac (*)
232	Duckpool (Coombe)	219000	111000	11/03/1970-13/11/1970	1	10	Wilson	Wilson, 1971/DASSHac (*)
233	Duckpool (Coombe)	219000	111000	29/01/1971-02/12/1971	1	10	Wilson	DASSHac (*)
234	Duckpool (Coombe)	219000	111000	02/01/1972-22/12/1972	1	10	Wilson	DASSHac (*)
235	Duckpool (Coombe)	219000	111000	04/05/1973	1	10	Wilson	DASSHac (*)
236	Duckpool (Coombe)	219000	111000	00/00/1975	1	7	Wilson	Cunningham et al., 1984/ DASSHac (*)
237	Duckpool (Coombe)	219000	111000	00/00/1977	1	10	N.C.C., I.S.U.	Cunningham et al., 1984/ MNCR-JNCC
238	Duckpool (Coombe)	219000	111000	00/00/1978	1	10	Powell	DASSHac (*)
239	Duckpool (Coombe)	219000	111000	00/00/1984	1	7	Cunningham	Cunningham et al., 1984
240	Duckpool (Coombe)	219000	111000	16/04/1992	1	6	Hawkins	Hawkins notebooks
241	Duckpool (Coombe)	219000	111000	11/08/1996	1	5	Hawkins	Hawkins notebooks
242	Duckpool (Coombe)	219000	111000	10/08/1998	1	6	Hawkins	Hawkins notebooks
243	Duckpool (Coombe)	219000	111000	31/07/1999	1	6	Hawkins	Hawkins notebooks
244	Duckpool (Coombe)	219000	111000	28/08/2000	1	6	Hawkins	Hawkins notebooks
245	Duckpool (Coombe)	219000	111000	22/09/2001	1	6	Hawkins	Hawkins notebooks
246	Duckpool (Coombe)	219000	111000	15/05/2002	1	6	Marclim Team	Marclim
247	Duckpool (Coombe)	219000	111000	12/09/2003	1	10	Marclim Team	Marclim
248	Duckpool (Coombe)	219000	111000	25/05/2013	1	7	Bush	-
249	Port Erin, S	219000	469000	00/00/1976	0	0	Hawkins	Cunningham et al., 1984
250	Port Erin, N	219000	469000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
251	Port Erin, N	219000	469000	03/08/2012	0	0	Bush	-
252	Balkenna Isle (Turnberry)	219000	604000	17/08/2012	0	0	Bush	-
253	Turnberry Golf Course	219000	606000	17/08/2012	0	0	Bush	-
254	Loch Goil	219000	695000	19/08/2012	0	0	Bush	-
255	Loch Goil	219000	696000	00/00/1918	1	10	Chumley	Cunningham et al., 1984/ DASSHac (*)
256	Oldshoremore	219000	958000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
257	Bude	220000	106000	00/00/1977	1	10	N.C.C., I.S.U.	Cunningham et al., 1984
258	Bude	220000	106000	00/00/1980	1	6	Hawkins	Cunningham et al., 1984
259	Bude	220000	106000	20/04/1997	1	4	Hawkins	Hawkins notebooks
260	Bude	220000	106000	20/05/2000	1	6	Hawkins	Hawkins notebooks
261	Bude	220000	106000	16/04/2001	1	6	Hawkins	Hawkins notebooks
262	Bude	220000	106000	24/03/2012	1	7	Bush	-
263	Bude	220000	106000	25/05/2013	1	6	Bush	-
264	Marsland Mouth to Welcombe Mouth (Longpeak to Mars…	220000	117000	00/00/1992	1	10	Hobbs	MNCR-JNCC
265	Crows Nest	220000	553000	17/06/1991	1	4	Davies	MNCR-JNCC
266	N of Crows Nest and Burn	220000	553000	16/06/2007	1	6	Dalkin/SNH	SNH
267	Luce Bay, E	220000	553000	20/07/2012	1	1	Bush et al.	-
268	Luce Sands	220000	554000	20/07/2012	1	1	Bush et al.	-

269	South Inch (West Kilbride)	220000	645000	17/08/2012	0	0	Bush	-
270	Welcombe Mouth	221000	117000	30/04/2002	1	6	Marclim Team	Marclim
271	Welcombe Mouth	221000	117000	30/04/2003	1	5	Marclim Team	Marclim
272	Welcombe Mouth (Long peak to Marsland Mouth)	221000	118000	04/04/1992	1	10	King	MNCR-JNCC
273	Port Saint Mary	221000	466000	00/00/1976	0	0	Hawkins	Cunningham et al., 1984
274	Port Saint Mary	221000	466000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
275	Port Saint Mary	221000	466000	04/08/2012	0	0	Bush	-
276	Niarbyl	221000	477000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
277	Niarbyl	221000	477000	05/08/2012	0	0	Bush	-
278	Maidenhead Bay	221000	608000	17/08/2012	0	0	Bush	-
279	Speke Mill Mouth (Stoke)	222000	123000	20/04/1992	1	7	Conober	MNCR-JNCC
280	Hartland Quay	222000	124000	00/00/1977	1	10	N.C.C., I.S.U.	Cunningham et al., 1984/ MNCR-JNCC
281	Hartland Quay	222000	124000	00/00/1984	1	7	Hawkins	Cunningham et al., 1984
282	Hartland Quay	222000	124000	03/04/1993	1	10	Hawkins	Hawkins notebooks
283	Hartland Quay	222000	124000	18/04/1999	1	6	Hawkins	Hawkins notebooks
284	Hartland Quay	222000	124000	13/02/2002	1	6	Marclim Team	Marclim
285	Hartland Quay	222000	124000	19/04/2003	1	2	Marclim Team	Marclim
286	Hartland Quay	222000	124000	24/03/2012	1	3	Hawkins	Hawkins notebooks
287	Hartland Quay	222000	124000	25/05/2013	1	6	Bush	-
288	Hartland Quay	222000	125000	24/03/2012	1	6	Hawkins	Hawkins notebooks
289	Hartland Quay, N	222000	125000	26/05/2013	1	6	Bush	-
290	Mull of Sinniness	222000	551000	00/00/2000	1	4	Hammond	Allen et al., 2002
291	Porth Dafarch	223000	379000	14/06/2002	0	0	Marclim Team	Marclim
292	Fenella Beach (Peel)	223000	484000	05/08/2012	0	0	Bush	-
293	Auchenmalg Bay	223000	551000	00/00/1984	1	6	Cunningham	Cunningham et al., 1984/ DASSH (*)
294	Cock Inn	223000	551000	15/09/1989	1	2	Johnston	MNCR-JNCC
295	Auchenmalg Bay	223000	551000	00/00/2000	1	6	Hammond	Allen et al., 2002
296	Cock Inn	223000	551000	18/06/2007	1	7	DalkinSNH	SNH
297	Auchenmalg Bay, SE	223000	551000	20/07/2012	1	6	Bush et al.	-
298	Cock Inn	223000	551000	10/07/2012	1	10	SNH Team	SNH
299	Shipload Bay (Titchberry)	224000	127000	15/09/1992	1	3	King	MNCR-JNCC
300	Hells Mouth	224000	328000	03/07/2012	0	0	Bush	-
301	Poyllvaaish	224000	467000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
302	Peel	224000	484000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
303	Glenalmar House	224000	551000	17/06/2007	1	7	DalkinSNH	SNH
304	Glenalmar House	224000	551000	07/08/2012	1	10	SNH Team	SNH
305	Croy Shore	224000	612000	20/07/2012	0	0	Bush	-
306	Gare Loch	224000	686000	00/00/1918	0	0	Chumley	Cunningham et al., 1984
307	Gare Loch	224000	686000	19/08/2012	0	0	Bush	-
308	West Looe	225000	52000	02/05/2002	0	0	Marclim Team	Marclim
309	Looe	225000	52000	28/04/2003	0	0	Marclim Team	Marclim
310	Aberporth	225000	251000	00/00/1984	1	7	Cunningham	Cunningham et al., 1984

311	Traeth Penbryn to Craigy Gwbert	225000	251000	04/06/1996	1	10	CCW Team	MIP1-CCW (*)
312	Aberporth, E	225000	251000	22/06/1997	1	6	Nichols/CCW	MNCR-JNCC
313	Aberporth	225000	251000	21/08/2002	1	6	Marclim Team	Marclim
314	Aberporth	225000	251000	03/09/2004	1	5	CCW Team	CCW
315	Aberporth	225000	251000	00/00/2005	1	6	Marclim Team	Marclim
316	Aberporth	225000	251000	00/00/2006	1	5	Marclim Team	Marclim
317	Aberporth	225000	251000	16/05/2007	1	10	Hebog Ltd	CCWTech (*)
318	Aberporth	225000	251000	07/05/2008	1	10	Aquatic Survey & Monitoring Ltd	CCWTech (*)
319	Aberporth	225000	251000	05/07/2012	1	5	Bush	-
320	Aberporth	225000	251000	18/02/2014	1	5	Bush	-
321	Trearddur Bay	225000	378000	00/00/1980	0	0	Hawkins	Cunningham et al., 1984
322	Trearddur Bay	225000	378000	00/00/1981	0	0	Hawkins	Cunningham et al., 1984
323	Trearddur Bay	225000	378000	00/00/1982	0	0	Hawkins	Cunningham et al., 1984
324	Trearddur Bay	225000	378000	00/00/1983	0	0	Hawkins	Cunningham et al., 1984
325	Trearddur Bay	225000	378000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
326	Trearddur Bay	225000	378000	02/08/2012	0	0	Bush	-
327	Trearddur Bay	225000	379000	24/07/2012	0	0	Bush	-
328	Craignarget, E (Solway, N)	225000	550000	13/07/2012	1	10	SNH Team	SNH
329	Craignarget, E (Solway, N)	225000	551000	10/07/2012	1	10	SNH Team	SNH
330	Dunure (Ayr, S)	225000	615000	00/00/1984	0	0	Norton	Cunningham et al., 1984
331	Dunure (Ayr, S)	225000	615000	20/07/2012	0	0	Bush	-
332	Dunure (Ayr, S)	225000	616000	20/07/2012	0	0	Bush	-
333	Aberporth	226000	251000	21/08/2002	1	6	Marclim Team	Marclim
334	Garheugh Port (Solway, N)	226000	549000	11/07/2012	1	10	SNH Team	SNH
335	Garheugh Port, NW	226000	550000	20/06/2007	1	6	Dalkin/SNH	SNH
336	Garheugh Port, NW	226000	550000	11/07/2012	1	10	SNH Team	SNH
337	Tresaith, Treath Penbryn (Aberporth)	227000	251000	16/05/1996	1	10	CCW Team	MIP1-CCW (*)
338	Tresaith, Treath Penbryn (Aberporth)	227000	251000	21/06/1997	1	3	Dipper	MNCR-JNCC
339	Tresaith	227000	251000	03/09/2004	1	5	CCW Team	CCW
340	Hells Mouth	227000	327000	00/00/1983	0	0	Hawkins	Cunningham et al., 1984
341	Porth Dinllaen	227000	341000	11/06/2002	0	0	Marclim Team	Marclim
342	Porth Dinllaen	227000	341000	13/04/2013	1	2	Bush	-
343	RoseneathPoint	227000	680000	19/08/2012	0	0	Bush	-
344	Porth Neigwll	228000	324000	12/06/2002	0	0	Marclim Team	Marclim
345	Porth Neigwll	228000	324000	14/08/2003	0	0	Marclim Team	Marclim
346	Penrhyn Bodeilas to Penrhyn Nefyn	229000	341000	18/05/2004	1	10	CCW Team	MIP1-CCW (*)
347	Llangrannog	230000	254000	05/07/2012	1	4	Bush	-
348	Glen Wyllin	230000	490000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
349	House S. of Rd to Changue	230000	546000	19/06/2007	1	6	Dalkin/SNH	SNH
350	Deils Dyke (Ayr)	230000	619000	17/08/2012	0	0	Bush	-
351	Clovelly	231000	124000	22/09/2002	1	10	Marclim Team	Marclim
352	Clovelly Pier	231000	124000	26/05/2013	1	4	Bush	-

353	Llangranog, Clarach to Aberystwyth Harbour Mouth	231000	254000	00/00/1984	1	10	Hawkins	Cunningham et al., 1984/ DASSH (*)
354	Llangrannog	231000	254000	05/07/2012	1	4	Bush	-
355	Llangrannog	231000	254000	18/02/2014	1	5	Bush	-
356	NE Ynys Lochtyn	231000	255000	12/06/1995	1	2	Hope/Murray	MNCR-JNCC
357	Abersoch	231000	328000	00/00/2003	0	0	Marclim Team	Marclim
358	Abersoch	231000	328000	00/00/2004	0	0	Marclim Team	Marclim
359	Abersoch Lifeboat Station	231000	328000	00/00/2009	1	3	Marclim Team	Marclim
360	Abersoch	231000	328000	00/00/2010	0	0	Marclim Team	Marclim
361	Abersoch Lifeboat Station	231000	328000	00/00/2011	0	0	Marclim Team	Marclim
362	Abersoch Lifeboat Station	231000	328000	00/00/2012	0	0	Marclim Team	Marclim
363	Abersoch Lifeboat Station	231000	328000	00/00/2013	0	0	Marclim Team	Marclim
364	Abersoch	231000	328000	00/00/2013	0	0	Marclim Team	Marclim
365	Rhosneigr	231000	372000	00/00/1983	0	0	Smith& Gault	Cunningham et al., 1984
366	Rhosneigr	231000	372000	14/06/2002	0	0	Marclim Team	Marclim
367	Rhosneigr	231000	372000	00/00/2005	0	0	Marclim Team	Marclim
368	Rhosneigr	231000	372000	00/00/2006	1	2	Marclim Team	Marclim
369	Rhosneigr	231000	372000	00/00/2007	0	0	Marclim Team	Marclim
370	Rhosneigr	231000	372000	00/00/2008	1	5	Marclim Team	Marclim
371	Rhosneigr	231000	372000	00/00/2009	1	2	Marclim Team	Marclim
372	Rhosneigr	231000	372000	00/00/2010	0	0	Marclim Team	Marclim
373	Rhosneigr	231000	372000	00/00/2011	0	0	Marclim Team	Marclim
374	Rhosneigr	231000	372000	02/08/2012	0	0	Bush	-
375	Rhosneigr	231000	372000	00/00/2012	0	0	Marclim Team	Marclim
376	Rhosneigr	231000	372000	13/04/2013	0	0	Bush	-
377	Ardmore Point	231000	678000	00/00/1984	0	0	Norton	Cunningham et al., 1984
378	Bass Rock (Downderry)	232000	53000	27/07/2002	0	0	Marclim Team	Marclim
379	Clovelly	232000	124000	00/00/1983	1	5	Ackers	Cunningham et al., 1984
380	Clovelly	232000	124000	26/05/2013	1	4	Bush	-
381	Cei Newydd to Traeth Penbryn	232000	255000	17/07/1996	1	10	CCW Team	MIP1-CCW (*)
382	Philip and Mary	232000	545000	18/06/2007	1	6	Dalkin/SNH	SNH
383	Philip and Mary	232000	545000	11/07/2012	1	10	SNH Team	SNH
384	Black Rocks (Troon)	232000	628000	17/08/2012	0	0	Bush	-
385	Llanbedrog (Pwllheli)	233000	331000	01/07/1995	1	3	Uttley	MNCR-JNCC
386	Llanbedrog (Pwllheli)	233000	331000	06/06/1996	1	10	CCW Team	MIP1-CCW (*)
387	Llanbedrog	233000	331000	14/08/2003	0	0	Marclim Team	Marclim
388	Porth Cwyfan (Rhosneigr)	233000	368000	31/07/1996	1	3	Brazier/CCW	MNCR-JNCC
389	Aberffraw	233000	368000	13/04/2013	0	0	Bush	-
390	Cemlyn Bay	233000	393000	14/06/2002	0	0	Marclim Team	Marclim
391	Cemlyn Bay	233000	393000	24/07/2012	0	0	Bush	-
392	Carreg y Defaid	234000	332000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
393	Carreg y Defaid	234000	332000	03/07/2012	0	0	Bush	-
394	Bucks Mills	235000	123000	00/00/1984	1	5	Hawkins	Cunningham et al., 1984

395	Bucks Mills	235000	123000	24/04/1993	1	6	Campline/CCW	MNCR-JNCC
396	Bucks Mills	235000	123000	25/05/2013	1	6	Bush	-
397	Cwmtudu Headland	235000	257000	00/00/1982	1	6	Bamber	Cunningham et al., 1984/ DASSH (*)
398	Cwmtudu Headland	235000	257000	21/06/1997	1	2	Cooke/Nichols/CCW	MNCR-JNCC
399	Cwmtudu Headland	235000	257000	05/07/2012	1	5	Bush	-
400	Cwmtudu Headland	235000	257000	18/02/2014	1	5	Bush	-
401	Traeth Aberffraw to Dinas Lwyd	236000	365000	11/06/1999	1	10	CCW Team	MIP1-CCW (*)
402	Back Bay	236000	539000	00/00/2000	1	4	Hammond	Allen et al., 2002
403	Monreith Bay	236000	540000	00/00/2000	1	5	Hammond	Allen et al., 2002
404	Trefor	237000	347000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
405	Trefor	237000	347000	14/04/2013	0	0	Bush	-
406	Cemaes Bay (Llanbadrig)	237000	394000	15/09/2002	0	0	Marclim Team	Marclim
407	Cemaes Bay (Llanbadrig)	237000	394000	24/07/2012	0	0	Bush	-
408	Peppercombe	238000	124000	08/05/1993	1	6	Campline/CCW	MNCR-JNCC
409	Target Rocks, Carreg Wall to g…	238000	260000	12/06/1995	1	4	Rostron/Holt/CCW	MNCR-JNCC
410	NewQuay	238000	260000	28/06/2002	1	6	Ager	Marine Biological Association (DASSH Data Archive Centre volunteer sightings records) (subsequently referred to as DASSHvol*)
411	Target Rocks, Carreg Wall to g…	238000	260000	01/05/2013	1	5	Bush	-
412	Llanddwyn Island	238000	362000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
413	Llanddwyn Island	238000	362000	02/08/2012	0	0	Bush	-
414	Worms Head	239000	186000	18/09/2001	1	10	CCW Team	South East Wales Biodiversity Records Centre (subsequently referred to as SEWBRC)
415	Worms Head	239000	186000	02/06/2004	1	10	CCW Team	SEWBRC
416	Worms Head	239000	186000	15/03/2013	1	5	Bush	-
417	Worms Head	239000	187000	00/00/1973	1	10	Nelson-Smith	SEWBRC
418	Worms Head	239000	187000	00/10/1978	1	10	Freytag	SEWBRC
419	Worms Head	239000	187000	18/09/2001	1	10	CCW Team	SEWBRC
420	Worms Head	239000	187000	15/03/2013	1	5	Bush	-
421	Greencliff (Abbotsham)	240000	127000	15/11/1993	1	6	Campline/CCW	MNCR-JNCC
422	Greencliff (Abbotsham)	240000	127000	27/09/2007	1	10	Jollands	2005-Ongoing United Kingdom MarLIN Shore Thing timed search results (subsequently referred to as MarLIN; *)
423	Greencliff (Abbotsham)	240000	127000	17/09/2008	1	10	Jollands	MarLIN (*)
424	Greencliff (Abbotsham)	240000	127000	14/07/2010-14/09/2010	1	10	Crouch	MarLIN (*)
425	Greencliff (Abbotsham)	240000	127000	14/06/2011	1	10	Crouch	MarLIN (*)
426	Pembrey	240000	199000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
427	Cei Bach	240000	259000	01/09/2004	1	10	Institute of Estuarine and Coastal Studies (IECS)/CCW	CCWTech (*)
428	Cei Bach	240000	259000	18/05/2007	1	10	CCW Team	CCWTech (*)
429	Cei Bach	240000	259000	07/05/2009	1	10	CCW Team	CCWTech (*)
430	Cei Bach	240000	259000	26/04/2010	1	10	CCW Team	CCWTech (*)

431	Cei Bach	240000	260000	01/09/2004	1	5	IECS/CCW	CCWTech (*)
432	Cei Bach	240000	260000	17-18/05/2007	1	10	Jones/CCW	CCWTech (*)
433	Cei Bach	240000	260000	05/05/2008	1	10	CCW Team	CCWTech (*)
434	Cei Bach	240000	260000	07/05/2009	1	10	CCW Team	CCWTech (*)
435	Cei Bach	240000	260000	26/04/2010	1	10	CCW Team	CCWTech (*)
436	Whitsand Bay (Millbrook)	241000	50000	00/00/1927	1	6	Wilson	Wilson, 1929
437	Abbotsham	241000	127000	06/07/2008	1	10	Jollands	MarLIN (*)
438	Abbotsham	241000	127000	25/06/2009-18/09/2009	1	10	Jollands	MarLIN (*)
439	Abbotsham	241000	127000	14/06/2011	1	10	Hughes	MarLIN (*)
440	Abbotsham	241000	127000	18/09/2013	1	10	Jollands/Phillips	MarLIN (*)
441	Aberdesach, SW (Trefor)	241000	350000	29/06/1995	1	2	Murray	MNCR-JNCC
442	Aberdesach	241000	350000	14/04/2013	0	0	Bush	-
443	Whitsand Bay (Millbrook)	242000	49000	00/00/1929	1	10	Wilson	Wilson, 1929/ Cunningham et al., 1984
444	Whitsand Bay (Millbrook)	242000	49000	00/00/1957	1	5	M.B.A.	Cunningham et al., 1984
445	Whitsand Bay (Millbrook)	242000	49000	00/00/1970	0	0	Wilson	Cunningham et al., 1984
446	Westward Ho	242000	129000	00/00/1977	1	10	N.C.C., I.S.U.	Cunningham et al., 1984
447	Westward Ho	242000	129000	00/00/1984	1	5	Hawkins	Cunningham et al., 1984
448	Westward Ho	242000	129000	19/05/1988	1	5	Frid	MNCR-JNCC
449	Westward Ho, W	242000	129000	25/05/2013	1	3	Bush	-
450	Downend (Croyde, Taw Torridge Estuary)	242000	138000	19/05/1988	1	10	Unknown	MNCR-JNCC
451	Tears Point to Port Eynon Point	242000	186000	06/09/2001	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
452	Tears Point to Port Eynon Point	242000	186000	06/07/2004	1	10	CCW Team	SEWBRC
453	Craig Ddu (Aberaeron)	242000	260000	02/09/2004	1	5	IECS/CCW	CCWTech (*)
454	Craig Ddu (Aberaeron)	242000	261000	02/09/2004	1	5	IECS/CCW	CCWTech (*)
455	Bulls Bay	242000	394000	13/06/2002	0	0	Marclim Team	Marclim
456	Bulls Bay	242000	394000	13/04/2013	0	0	Bush	-
457	Cawsands South Reef (Devil's Point to Penlee Point)	243000	50000	15/09/1993	1	2	Tyrrel	MNCR-JNCC
458	Westward Ho	243000	129000	25/05/2013	1	2	Bush	-
459	Downend (Croyde, S)	243000	138000	00/00/1977	1	10	N.C.C., I.S.U.	Cunningham et al., 1984/ MNCR-JNCC
460	Downend (Croyde, S)	243000	138000	00/00/1978	1	5	Hawkins	Cunningham et al., 1984
461	Downend (Croyde, S)	243000	138000	00/00/1983	1	4	Hawkins	Cunningham et al., 1984
462	Downend (Croyde, S)	243000	138000	24/05/2013	1	6	Bush	-
463	Croyde	243000	139000	16/06/1977	1	10	N.C.C., I.S.U.	Cunningham et al., 1984/ MNCR-JNCC
464	Croyde	243000	139000	18/06/2004	1	10	Unknown	DASSHvol(*)
465	Croyde	243000	139000	24/05/2013	1	6	Bush	-
466	Paviland Cliff	243000	185000	00/00/1973	1	10	Nelson-Smith/ N.C.C., I.S.U	Cunningham et al., 1984/ SEWBRC
467	Paviland Cliff	243000	185000	00/10/1978	1	10	Freytag	SEWBRC
468	Paviland Cliff	243000	185000	13/03/2013	1	3	Bush	-
469	Tears Point to Port Eynon Point	243000	186000	06/08/2001	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC

470	Tears Point to Port Eynon Point	243000	186000	06/07/2004	1	10	CCW Team	SEWBRC
471	Tears Point to Port Eynon Point	243000	261000	13/05/1996	1	10	CCW Team	MIP1-CCW (*)
472	SW of Gilfach yr Halen (Aberaeron)	243000	261000	09/04/1997	1	6	Nichols/CCW	MNCR-JNCC
473	SW of Gilfach yr Halen (Aberaeron)	243000	261000	02/09/2004	1	10	IECS/CCW	CCWTech (*)
474	Penychain (Pwllheli)	243000	335000	01/07/1995	1	2	Brazier/CCW	MNCR-JNCC
475	Porth Fechan and Rhosneigr (W of Afon Wen)	243000	335000	31/07/1996	1	3	CCW Team	CCW
476	Porth Fechan and Rhosneigr (W of Afon Wen)	243000	335000	05/07/2004	1	10	CCW Team	CCW
477	Porth Fechan and Rhosneigr (W of Afon Wen)	243000	335000	06/08/2005	1	10	IECS/CCW	CCWTech (*)
478	Traeth Afon Wen	243000	336000	02/07/1996	1	10	CCW Team	MIP1-CCW (*)
479	Cawsand Bay	244000	51000	00/00/1957	1	5	M.B.A.	Cunningham et al., 1984
480	Cawsand Bay	244000	51000	00/00/1984	0	0	Burrows	Cunningham et al., 1984
481	Barricane Beach, S (Morte Point to Woolacombe)	244000	145000	00/00/1992	1	10	Unknown	MNCR-JNCC
482	Barricane Beach, S (Morte Point to Woolacombe)	244000	145000	00/00/1995	1	10	Unknown	MNCR-JNCC (NBN website)
483	Tears Point to Port Eynon Point	244000	185000	06/08/2001	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
484	Tears Point to Port Eynon Point	244000	185000	06/07/2004	1	10	CCW Team	SEWBRC
485	Craig Ddu (Aberaeron)	244000	261000	02/09/2004	1	5	IECS/CCW	CCWTech (*)
486	Aberaeron, S	244000	262000	09/04/1997	1	4	Nichols/CCW	MNCR-JNCC
487	Craig Ddu (Aberaeron)	244000	262000	02/09/2004	1	5	IECS/CCW	CCWTech (*)
488	Afon Wen	244000	336000	03/07/2012	1	5	Bush	-
489	Afon Wen	244000	337000	00/00/1964	1	3	Crisp/N.C.C.	Cunningham et al., 1984/ DASSH (*)
490	Afon Wen	244000	337000	00/00/1984	1	6	Rees/N.C.C	Cunningham et al., 1984/DASSH (*)
491	Afon Wen	244000	337000	03/07/2012	0	0	Bush	-
492	Skerray	244000	958000	26/05/2002	0	0	Marclim Team	Marclim
493	West Crow Ridge (Braunton)	245000	132000	15/05/1988	1	4	Little	MNCR-JNCC
494	Woolacombe	245000	143000	00/00/1983	1	3	Hawkins	Cunningham et al., 1984
495	Woolacombe	245000	143000	18/11/2001	1	2	Hawkins	Hawkins notebooks
496	Barricane Beach (Woolacombe, N)	245000	144000	08/10/1994	1	3	Cooke/Campline	MNCR-JNCC
497	Rockham Bay (Bull Point to Morte Point)	245000	146000	19/03/1992	1	10	Unknown	MNCR-JNCC
498	Overton	245000	184000	00/00/1973	1	10	N.C.C., I.S.U.	Cunningham et al., 1984
499	Overton	245000	184000	13/03/2013	1	3	Bush	-
500	Aberaeron	245000	263000	00/00/1964	1	6	Crisp/N.C.C.	Cunningham et al., 1984/ DASSH (*)
501	Aberaeron	245000	263000	09/04/1997	1	4	Nichols/CCW	MNCR-JNCC
502	Aberaeron	245000	263000	07/08/2002	0	0	Marclim Team	Marclim
503	Aberaeron	245000	263000	02/09/2004	1	10	IECS/CCW	CCWTech (*)
504	Aberaeron	245000	263000	15/05/2007	1	10	CCW Team	CCWTech (*)
505	Aberaeron	245000	263000	06/05/2008	1	10	CCW Team	CCWTech (*)
506	Aberaeron	245000	263000	06/05/2009	1	10	CCW Team	CCWTech (*)
507	Aberaeron	245000	263000	29/04/2010	1	10	CCW Team	CCWTech (*)
508	Aberaeron	245000	263000	00/00/2010	1	5	Marclim Team	Marclim

509	Aberaeron	245000	263000	00/00/2011	1	5	Marclim Team	Marclim
510	Aberaeron	245000	263000	05/07/2012	1	5	Bush	-
511	Aberaeron	245000	263000	17/02/2014	1	5	Bush	-
512	E of Discharge (Amlwch)	245000	393000	14/02/2003	1	2	Brazier/CCW	CCWTech (*)
513	E of Discharge (Amlwch)	245000	393000	13/04/2013	1	2	Bush	-
514	Ramsey	245000	493000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
515	Rispond	245000	965000	05/03/2003	0	0	Marclim Team	Marclim
516	Overton	246000	184000	00/00/1973	1	10	Nelson-Smith/ N.C.C., I.S.U	SEWBRC
517	Overton	246000	184000	00/10/1978	1	10	Freytag	SEWBRC
518	Tears Point to Port Eynon Point	246000	184000	06/08/2001	1	10	CCW Team	SEWBRC
519	Overton	246000	184000	06/07/2004	1	10	CCW Team	SEWBRC
520	Overton	246000	184000	13/03/2013	1	4	Bush	-
521	Aberarth	246000	263000	02/09/2004	1	5	IECS/CCW	CCWTech (*)
522	Aberarth	246000	263000	17/02/2014	1	6	Bush	-
523	Afon Wen to Criccieth	246000	337000	05/07/1996	1	10	CCW Team	MIP1-CCW (*)
524	Criccieth	246000	337000	05/07/2004	1	4	CCW Team	CCW
525	Lee Bay, W (Woolacombe)	247000	146000	25/09/2007	1	10	Jollands	MarLIN (*)
526	Lee Bay, W (Woolacombe)	247000	146000	07/07/2008	1	10	Crouch	MarLIN (*)
527	Lee Bay, W (Woolacombe)	247000	146000	13/07/2010-08/10/2010	1	10	Crouch	MarLIN (*)
528	Lee Bay, W (Woolacombe)	247000	146000	01/07/2011	1	5	Hughes	MarLIN (*)
529	Lee Bay, W (Woolacombe)	247000	146000	24/05/2013	1	4	Bush	-
530	Port Eynon	247000	184000	00/10/1978	1	10	Freytag	SEWBRC
531	Port Eynon	247000	184000	28/09/2000	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
532	Tears Point to Port Eynon Point	247000	184000	06/08/2001	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
533	Port Eynon	247000	184000	06/07/2004	1	10	CCW Team	SEWBRC
534	Port Eynon	247000	184000	02/07/2011	1	10	Hughes	MarLIN (*)
535	Port Eynon	247000	184000	13/03/2013	1	6	Bush	-
536	Port Eynon	247000	185000	00/00/1984	1	6	Hawkins	Cunningham et al., 1984
537	Aberarth (Aberaeron)	247000	263000	02/09/2004	1	5	IECS/CCW	CCWTech (*)
538	Aberarth	247000	263000	17/02/2014	1	6	Bush	-
539	Aberarth (Aberaeron)	247000	264000	02/09/2004	1	5	IECS/CCW	CCWTech (*)
540	Aberarth	247000	264000	17/02/2014	1	6	Bush	-
541	Criccieth	247000	336000	05/07/2004	1	5	CCW Team	CCW
542	Criccieth	247000	337000	13/09/2002	1	10	CCW Team	CCW
543	Criccieth	247000	337000	05/07/2004	1	4	CCW Team	CCW
544	Afon Dwyfor , W of Transect 9	247000	337000	09/07/2009	1	3	Aquatic Survey & Monitoring Ltd	CCWTech (*)
545	Afon Dwyfor	247000	337000	09/07/2009	1	10	CCW Team	CCWTech (*)
546	Afon Dwyfor , W of Transect 9	247000	337000	09/07/2009	1	2	Aquatic Survey & Monitoring Ltd	CCWTech (*)
547	Criccieth	247000	337000	03/07/2012	1	5	Bush	-
548	Porth Eilian	247000	392000	13/09/2002	0	0	Marclim Team	Marclim

549	PortyerrockBay	247000	539000	00/00/2000	1	4	Hammond	Allen et al., 2002
550	Lee Bay (Woolacombe)	248000	146000	00/00/1983	1	5	Hawkins	Cunningham et al., 1984
551	Lee Bay, E (Woolacombe)	248000	146000	24/05/2013	1	4	Bush	-
552	Oxwich Point	248000	185000	00/10/1978	1	10	Freytag	SEWBRC
553	Port Eynon Bay to Oxwich Point	248000	185000	28/09/2000	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
554	Aberarth (Aberaeron)	248000	264000	09/04/1997	1	7	Woolford	MNCR-JNCC
555	Aberarth (Aberaeron)	248000	264000	30/06/2013	1	5	Bush	-
556	Llangrannog (Aberarth)	248000	264000	30/06/2013	1	5	Bush	-
557	Aberarth (Aberaeron)	248000	264000	17/02/2014	1	6	Bush	-
558	Criccieth, W (Tremadog)	248000	337000	01/07/1995	1	4	Northen	MNCR-JNCC
559	W of Criccieth (Tremadog)	248000	337000	05/07/2004	1	10	IECS/CCW	CCWTech (*)
560	Criccieth	248000	337000	05/07/2004	1	6	CCW Team	CCW
561	Dulas Bay	248000	388000	24/07/2012	0	0	Bush	-
562	Dulas Bay	248000	389000	00/00/1984	0	0	Burrows	Cunningham et al., 1984
563	Dulas Bay	248000	389000	03/08/2012	0	0	Bush	-
564	Point Lynas	248000	392000	13/06/2002	0	0	Marclim Team	Marclim
565	Lynas Point, E (Dulas Bay)	248000	393000	25/07/1997	1	2	Brazier/Spence/CCW	MNCR-JNCC
566	Lynas Point (Dulas Bay)	248000	393000	13/04/2013	1	2	Bush	-
567	Renney Rocks (Heybrook Bay)	249000	48000	08/05/2002	0	0	Marclim Team	Marclim
568	Renney Rocks (Heybrook Bay)	249000	49000	00/00/1984	0	0	Burrows	Cunningham et al., 1984
569	Plymouth, W	249000	50000	00/00/1984	0	0	Southward	Cunningham et al., 1984
570	Criccieth	249000	337000	00/00/1950	1	5	Knight-Jones	Cunningham et al., 1984/ DASSHac (*)
571	Criccieth	249000	337000	00/00/1964	1	3	Crisp/N.C.C.	Cunningham et al., 1984/ DASSH (*)
572	Criccieth	249000	337000	00/00/1984	1	6	Cunningham/Rees	Cunningham et al., 1984/ DASSH (*)
573	Afon Wen to Criccieth	249000	337000	05/07/1996	1	10	CCW Team	MIP1-CCW (*)
574	Criccieth Castle (Criccieth)	249000	337000	11/06/2002	0	0	Marclim Team	Marclim
575	Criccieth Castle (Criccieth)	249000	337000	15/08/2003	0	0	Marclim Team	Marclim
576	Criccieth Castle (Criccieth)	249000	337000	05/07/2004	1	10	IECS/CCW	CCWTech (*)
577	Criccieth Castle (Criccieth)	249000	337000	00/00/2005	0	0	Marclim Team	Marclim
578	Criccieth Castle (Criccieth)	249000	337000	00/00/2006	0	0	Marclim Team	Marclim
579	Criccieth Castle (Criccieth)	249000	337000	00/00/2007	0	0	Marclim Team	Marclim
580	Criccieth Castle (Criccieth)	249000	337000	00/00/2008	0	0	Marclim Team	Marclim
581	Criccieth Castle (Criccieth)	249000	337000	00/00/2009	1	5	Marclim Team	Marclim
582	Criccieth Castle (Criccieth)	249000	337000	00/00/2010	1	6	Marclim Team	Marclim
583	Criccieth Castle (Criccieth)	249000	337000	00/00/2011	0	0	Marclim Team	Marclim
584	Criccieth Castle (Criccieth)	249000	337000	00/00/2012	0	0	Marclim Team	Marclim
585	Criccieth Castle (Criccieth)	249000	337000	08/08/2013	1	6	Bush	-
586	Porth yr Aber (Penysarn)	249000	390000	16/06/2014	1	3	Bush	-
587	Combe Martin	250000	147000	00/00/1977	1	3	Cunningham	Cunningham et al., 1984
588	Wild Pear Beach (CombeMartin)	250000	147000	00/00/1984	1	10	Cunningham	Cunningham et al., 1984
589	Oxwich Point	250000	184000	00/00/1973	1	10	Nelson-Smith	SEWBRC
590	Oxwich Point	250000	184000	00/10/1978	1	10	Freytag	SEWBRC
591	Oxwich	250000	184000	13/03/2013	1	3	Bush	-

592	Oxwich	250000	185000	00/00/1973	1	10	N.C.C., I.S.U.	Cunningham et al., 1984
593	Oxwich	250000	185000	00/00/1984	1	4	Hawkins	Cunningham et al., 1984
594	Oxwich	250000	185000	13/03/2013	1	6	Bush	-
595	Oxwich	250000	186000	13/03/2013	1	6	Bush	-
596	S of Llanon (Aberaeron)	250000	266000	09/04/1997	1	7	Holt/CCW	MNCR-JNCC
597	S of Llanon (Aberaeron)	250000	266000	28/04/2003	1	6	CCW Team	CCW
598	Criccieth Castle, E (Criccieth)	250000	337000	01/07/1995	1	4	Gilkes	MNCR-JNCC
599	Criccieth Castle, E (Criccieth)	250000	337000	05/07/1996	1	10	CCW Team	CCW
600	Criccieth Castle, E (Criccieth)	250000	337000	18/09/1997	1	10	CCW Team	CCW
601	Criccieth Castle, E (Criccieth)	250000	337000	08/08/2013	1	6	Bush	-
602	Criccieth, E (Criccieth)	250000	338000	00/00/2003	1	6	Marclim Team	Marclim
603	Criccieth, E (Criccieth)	250000	338000	00/00/2004	1	6	Marclim Team	Marclim
604	Criccieth, E (Criccieth)	250000	338000	00/00/2006	1	6	Marclim Team	Marclim
605	Criccieth, E (Criccieth)	250000	338000	00/00/2007	1	6	Marclim Team	Marclim
606	Criccieth, E (Criccieth)	250000	338000	00/00/2008	1	6	Marclim Team	Marclim
607	Criccieth, E (Criccieth)	250000	338000	00/00/2009	1	6	Marclim Team	Marclim
608	Criccieth, E (Criccieth)	250000	338000	00/00/2010	1	6	Marclim Team	Marclim
609	Criccieth, E (Criccieth)	250000	338000	00/00/2011	0	0	Marclim Team	Marclim
610	Criccieth, E (Criccieth)	250000	338000	00/00/2012	1	6	Marclim Team	Marclim
611	Criccieth, E (Criccieth)	250000	338000	00/00/2013	1	6	Bush	-
612	Ilfracombe	251000	147000	00/00/1984	1	5	Crothers	Cunningham et al., 1984
613	Ilfracombe	251000	147000	24/05/2013	0	0	Bush	-
614	Oxwich Bay, W	251000	185000	00/00/1973	1	10	Nelson-Smith	SEWBRC
615	Oxwich Bay, W	251000	185000	00/10/1978	1	10	Freytag	SEWBRC
616	Oxwich Bay, W	251000	185000	29/08/2011	1	10	Hughes	MarLIN (*)
617	Moelfre	251000	385000	13/06/2002	0	0	Marclim Team	Marclim
618	Moelfre	251000	385000	10/09/2013	0	0	Bush	-
619	Moelfre	251000	386000	00/00/1984	0	0	Burrows	Cunningham et al., 1984
620	Moelfre	251000	386000	03/08/2012	0	0	Bush	-
621	WemburyBay	252000	48000	00/00/1957	1	5	M.B.A.	Cunningham et al., 1984
622	Llanrhystud (Aberystwyth)	252000	269000	00/00/1984	1	6	Cunningham	Cunningham et al., 1984/ DASSH (*)
623	Llanrhystud (Aberystwyth)	252000	269000	08/04/1997	1	4	Nichols/CCW	MNCR-JNCC
624	Carreg Tipw to Aberarth	252000	269000	28/04/2003	1	10	CCW Team	MIP1-CCW (*)
625	Llanrhystud (Aberystwyth)	252000	269000	04/07/2012	1	6	Bush	-
626	Criccieth to North Bank of Afon Glaslyn	252000	337000	18/09/1997	1	10	CCW Team	CCW
627	Plas Newydd	252000	369000	14/03/2014	1	3	Bush	-
628	Cellar (Wembury)	253000	47000	10/04/2001	1	2	Hawkins	Hawkins notebooks
629	Cellar (Wembury)	253000	47000	11/09/2002	0	0	Marclim Team	Marclim
630	Cellar (Wembury)	253000	47000	18/09/2003	0	0	Marclim Team	Marclim
631	Hele Bay	253000	147000	24/05/2013	1	5	Bush	-
632	Hele Bay	253000	148000	00/00/1984	1	5	Crothers	Cunningham et al., 1984
633	Hele Bay	253000	148000	24/05/2013	1	5	Bush	-
634	Carreg Tipw (Aberystwyth)	253000	270000	08/04/1997	1	6	Holt/CCW	MNCR-JNCC

635	Shirecombe	254000	187000	00/00/1973	1	10	Nelson-Smith/ N.C.C., I.S.U	Cunningham et al., 1984/ SEWBRC
636	Shirecombe	254000	187000	00/10/1978	1	10	Freytag	SEWBRC
637	Shirecombe	254000	187000	03/06/2004	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
638	Southgate	254000	187000	13/03/2013	1	6	Bush	-
639	Southgate	254000	187000	19/02/2014	1	5	Bush	-
640	Shell Island (Mochras)	254000	326000	04/04/1997	1	7	Holt/CCW	MNCR-JNCC
641	Menai	254000	371000	13/08/2003	0	0	Marclim Team	Marclim
642	Menai	254000	371000	24/07/2012	0	0	Bush	-
643	LimesladeBay	255000	186000	22/04/2004	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
644	LimesladeBay	255000	186000	14/03/2013	1	6	Bush	-
645	Deep Slade	255000	186000	19/02/2014	1	5	Bush	-
646	Shirecombe to Graves End	255000	187000	22/04/2004	1	10	CCW Team	MIP1-CCW (*)
647	Caswell	255000	187000	13/03/2013	1	4	Bush	-
648	Caswell	255000	187000	19/02/2014	1	5	Bush	-
649	NW of Llanddeiniol (Aberystwyth)	255000	274000	08/04/1997	1	7	Brazier/CCW	MNCR-JNCC
650	Blaenplwyf, W (Aberystwyth)	255000	275000	08/04/1997	1	6	Woolford	MNCR-JNCC
651	Tonfanau	255000	303000	00/00/1984	1	5	Hawkins	Cunningham et al., 1984
652	Shell Island (Mochras)	255000	326000	06/07/2004	1	5	CCW Team	CCW
653	Shell Island (Mochras)	255000	326000	10/08/2005	1	10	IECS/CCW	CCWTech (*)
654	Shell Island (Mochras)	255000	326000	04/07/2012	1	6	Bush	-
655	Shell Island (Mochras)	255000	327000	06/07/2004	1	6	CCW Team	CCW
656	Shell Island (Mochras)	255000	327000	04/07/2012	1	6	Bush	-
657	Mossyard Bay	255000	551000	00/00/1984	1	6	Cunningham	Cunningham et al., 1984/ DASSH (*)
658	Garvellan Rocks (Mossyard Bay)	255000	551000	00/00/2000	1	4	Hammond	Allen et al., 2002
659	Garvellan Rocks (Mossyard Bay, Newton)	255000	551000	01/11/2011	1	10	Hughes	MarLIN (*)
660	Mossyard Bay	255000	551000	20/07/2012	1	5	Bush et al.	-
661	Mossyard Bay	255000	551000	10/06/2013	1	10	Logan/Logan/Crouch/ SNH	SNH
662	Sandy Bay (Combe Martin)	256000	147000	00/00/1984	1	3	Cunningham	Cunningham et al., 1984
663	Deep Slade (Pwll Du)	256000	186000	1970 to 1980	1	3	CCW Team	SEWBRC
664	Deep Slade	256000	186000	00/00/1973	1	10	N.C.C., I.S.U.	Cunningham et al., 1984
665	Deep Slade	256000	186000	19/08/1978	1	3	Unknown	MNCR-JNCC
666	Deep Slade	256000	186000	1970 to 1980	1	3	CCW Team	SEWBRC
667	Shirecombe to Graves End	256000	186000	22/04/2004	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
668	Deep Slade	256000	186000	14/03/2013	1	5	Bush	-
669	Deep Slade	256000	186000	19/02/2014	1	5	Bush	-
670	Allt Wen to Morfa Bychan	256000	277000	14/05/2003	1	10	CCW Team	MIP1-CCW (*)
671	Friog	256000	304000	06/07/2004	1	5	CCW Team	CCW
672	Tonfanau	256000	304000	06/07/2004	1	10	IECS	CCWTech (*)
673	Tonfanau	256000	304000	09/08/2005	1	10	IECS/CCW	CCWTech (*)

674	Cae Du (Tywyn)	256000	305000	05/04/1997	1	10	IECS/CCW	CCWTech (*)/MIP1-CCW (*)
675	Friog	256000	305000	06/07/2004	1	5	CCW Team	CCW
676	Tonfanau	256000	305000	09/08/2005	1	10	IECS/CCW	CCWTech (*)
677	Llangelynin beach (Barmouth Bay)	256000	306000	06/04/1997	1	4	Nichols/CCW	MNCR-JNCC
678	Friog	256000	306000	06/07/2004	1	6	CCW Team	CCW
679	Cae Du (LlangelyninBeach, BarmouthBay)	256000	306000	09/08/2005	1	10	IECS/CCW	CCWTech (*)
680	Cae-Du	256000	307000	06/07/2004	1	10	IECS	CCWTech (*)
681	Shell Island (Mochras)	256000	327000	00/00/1978	1	10	N.C.C., I.S.U.	Cunningham et al., 1984/ DASSH (*)
682	Shell Island (Mochras)	256000	327000	00/00/1984	1	7	Hawkins	Cunningham et al., 1984/ DASSH (*)/ North Wales Environmental Information Service (subsequently referred to as NWEIS)
683	Shell Island (Mochras)	256000	327000	06/07/2004	1	5	CCW Team	CCW
684	Shell Island (Mochras)	256000	327000	04/07/2012	1	6	Bush	-
685	Shell Island (Mochras)	256000	328000	06/07/2004	1	4	CCW Team	CCW
686	Llandanwg	256000	328000	10/08/2005	1	10	IECS/CCW	CCWTech (*)
687	Llandanwg	256000	328000	06/07/2009	1	3	Aquatic Survey & Monitoring Ltd	CCWTech (*)
688	Llandanwg	256000	328000	06/07/2009	1	3	Aquatic Survey & Monitoring Ltd	CCWTech (*)
689	Llandanwg	256000	328000	06/07/2009	1	10	Aquatic Survey & Monitoring Ltd	CCWTech (*)
690	Llandanwg	256000	328000	04/07/2012	1	6	Bush	-
691	Llandanwg (Pen Llŷn ar Sarnau)	256000	329000	06/07/2004	1	5	CCW Team	CCW
692	Murray Isles (Islands of Fleet, Solway, N)	256000	549000	00/00/1978	1	10	Knight-Jones/SNH	SNH
693	Murray Isles (Islands of Fleet, Solway, N)	256000	549000	00/00/2000	1	4	Hammond	Allen et al., 2002
694	Cat Craig, Dunrosness Beach, Dumfrieshire	256000	553000	20/07/2013	0	0	Logan/Logan/SNH	SNH
695	Deep Slade	257000	147000	24/05/2013	1	4	Bush	-
696	PwllDu	257000	186000	00/00/1973	1	10	Nelson-Smith/ N.C.C., I.S.U	Cunningham et al., 1984/ SEWBRC
697	PwllDu	257000	186000	00/10/1978	1	10	Freytag	SEWBRC
698	Shirecombe to Graves End	257000	186000	22/04/2004	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
699	Allt Wen to Morfa Bychan	257000	278000	14/05/2003	1	10	CCW Team	MIP1-CCW (*)
700	Tanybwlch, S (Aberystwyth)	257000	279000	10/04/1997	1	4	Nichols/Holt/CCW	MNCR-JNCC
701	Clarach to Aberystwyth harbourmouth	257000	281000	14/05/2003	1	10	CCW Team	MIP1-CCW (*)
702	Castle Rocks (Aberystwyth)	257000	281000	04/09/2005	1	6	Porter/Ward	Marine Conservation Society (Seasearch Marine Surveys) (subsequently referred ro as Seasearch*)
703	Castle Rocks (Aberystwyth)	257000	281000	08/06/2006	1	5	Rushbrook	Seasearch(*)
704	Castle Rocks, Aberystwyth, Ceredigion	257000	281000	11/05/2008	1	10	Bowen	Seasearch(*)
705	Aberystwyth	257000	281000	04/07/2012	1	5	Bush	-
706	Aber Dysynni to Aberdyfi	257000	301000	07/04/1997	1	10	CCW Team	CCW

707	Cae Du (Tywyn, N)	257000	307000	06/07/2004	1	6	CCW Team	CCW
708	Friog (Barmouth Bay)	257000	308000	07/07/2004	1	10	IECS/CCW	CCWTech (*)
709	Friog	257000	309000	00/07/2004	1	5	CCW Team	CCW
710	Llandanwg (Pen Llŷn ar Sarnau)	257000	329000	00/00/1978	1	5	Jones	Cunningham et al., 1984/ DASSH (*)
711	Llandanwg	257000	329000	00/00/1984	1	5	Hawkins	Cunningham et al., 1984/ DASSH (*)
712	Llandanwg (Pen Llŷn ar Sarnau)	257000	329000	04/04/1997	1	10	CCW Team	CCW
713	Llandanwg (Pen Llŷn ar Sarnau)	257000	329000	06/07/2004	1	5	CCW Team	CCW
714	Islands of Fleet (Solway, N)	257000	549000	00/00/1978	1	5	Knight-Jones	Cunningham et al., 1984/ DASSH (*)
715	Ardwall Isle (Islands of Fleet, Solway, N)	257000	549000	00/00/2000	1	4	Hammond	Allen et al., 2002
716	Carrick	257000	550000	30/05/2013	1	10	Logan/Logan/SNH	SNH
717	Caswell	258000	187000	19/04/2004	1	10	CCW Team	SEWBRC
718	Caswell	258000	187000	13/03/2013	1	5	Bush	-
719	Aberystwyth	258000	282000	00/00/1984	1	6	Cunningham	Cunningham et al., 1984/ DASSH (*)
720	Castle Rocks, N (Aberystwyth)	258000	282000	10/04/1997	1	6	Woolford	MNCR-JNCC
721	Aberystwyth	258000	282000	07/08/2002	1	6	Marclim Team	Marclim
722	Clarach to Aberystwyth harbourmouth	258000	282000	14/05/2003	1	10	CCW Team	MIP1-CCW (*)
723	Castle Rocks, N (Aberystwyth)	258000	282000	00/00/2005	1	5	Marclim Team	Marclim
724	Castle Rocks, N (Aberystwyth)	258000	282000	00/00/2006	1	3	Marclim Team	Marclim
725	Castle Rocks, N (Aberystwyth)	258000	282000	00/00/2010	1	6	Marclim Team	Marclim
726	Castle Rocks, N (Aberystwyth)	258000	282000	00/00/2011	1	4	Marclim Team	Marclim
727	Castle Rocks, N (Aberystwyth)	258000	282000	04/07/2012	1	5	Bush	-
728	Castle Rocks, N (Aberystwyth)	258000	282000	00/00/2013	1	6	Marclim Team	Marclim
729	Clarach Bay (Aberystwyth)	258000	284000	11/04/1997	1	6	Holt/CCW	MNCR-JNCC
730	Clarach Bay (Aberystwyth)	258000	284000	31/08/2004	1	5	CCW Team	CCW
731	Sarn Cynfelyn (Aberystwyth)	258000	285000	07/04/1997	1	6	Brazier/CCW	MNCR-JNCC
732	Clarach Bay/Sarn Cynfelyn (Aberystwyth)	258000	285000	31/08/2004	1	6	CCW Team	CCW
733	Friog	258000	309000	07/07/2004	1	10	IECS	CCWTech (*)
734	Llwyngwril (Barmouth Bay)	258000	310000	05/04/1997	1	6	CCW Team	CCW
735	Friog	258000	310000	07/07/2004	1	6	CCW Team	CCW
736	Llwyngwril (Barmouth Bay)	258000	310000	04/07/2012	1	6	Bush	-
737	Unknown (Abersoch)	258000	382000	13/08/2003	0	0	Marclim Team	Marclim
738	Ardwall Isle (Islands of Fleet, Solway, N)	258000	548000	00/00/1978	1	10	Knight-Jones/SNH	SNH
739	Barlocco Isle (Islands of Fleet, Solway, N)	258000	548000	00/00/2000	1	4	Hammond	Allen et al., 2002
740	Caswell	259000	187000	00/00/1973	1	10	N.C.C., I.S.U.	Cunningham et al., 1984
741	Borth	259000	286000	08/04/1997	1	10	CCW Team	MIP1-CCW (*)
742	Borth	259000	286000	31/08/2004	1	6	CCW Team	CCW
743	Borth	259000	287000	31/08/2004	1	6	CCW Team	CCW
744	Borth	259000	288000	08/04/1997	1	10	CCW Team	MIP1-CCW (*)
745	Borth	259000	288000	31/08/2004	1	4	CCW Team	CCW
746	Llwyngwril Beach, N (Barmouth Bay)	259000	310000	05/04/1997	1	7	Nichols/CCW	MNCR-JNCC
747	Friog	259000	310000	00/07/2004	1	6	CCW Team	CCW

748	Llwyngwril (Barmouth Bay)	259000	310000	04/07/2012	1	7	Bush	-
749	Llwyngwril	259000	311000	00/00/1982	1	7	Kendall	Cunningham et al., 1984/ DASSH (*)
750	Llwyngwril	259000	311000	00/00/1984	1	7	Hawkins	Cunningham et al., 1984/ DASSH (*)/NWEIS
751	Friog	259000	311000	00/07/2004	1	6	CCW Team	CCW
752	Llwyngwril (Barmouth Bay)	259000	311000	04/07/2012	1	6	Bush	-
753	NW of Meggerland Point (Kirkandrews Bay)	259000	547000	18/09/1989	1	4	Johnston	MNCR-JNCC
754	Kirkandrews Bay	259000	547000	00/00/2000	1	4	Hammond	Allen et al., 2002
755	Mothecome	260000	47000	23/10/2002	1	6	Marclim Team	Marclim
756	Graves End to Langland Bay	260000	186000	19/04/2004	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
757	Graves End to Langland Bay	260000	187000	19/04/2004	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
758	Borth	260000	288000	00/00/1935	1	7	Knight-Jones	Cunningham et al., 1984/ DASSHac (*)
759	Borth	260000	288000	00/00/1984	1	6	Hawkins	Cunningham et al., 1984/ DASSH (*)
760	Upper Borth (Aberdyfi)	260000	288000	07/04/1997	1	6	Holt/CCW	MNCR-JNCC
761	Borth	260000	288000	08/08/2002	1	6	Marclim Team	Marclim
762	Borth	260000	288000	00/00/2004	0	0	CCW Team	CCW
763	Borth	260000	288000	13/04/2006	1	10	Fair	DASSHvol(*)
764	Borth	260000	288000	04/07/2012	1	6	Bush	-
765	Dyfi estuary (Cardigan)	260000	294000	00/00/1982	1	5	Kendall	Cunningham et al., 1984
766	Friog	260000	311000	00/07/2004	1	6	CCW Team	CCW
767	Friog (Barmouth Bay)	260000	311000	08/08/2005	1	10	IECS/CCW	CCWTech (*)
768	Barmouth	260000	314000	04/07/2012	0	0	Bush	-
769	Barmouth	260000	315000	00/00/1984	1	4	Hawkins	Cunningham et al., 1984/ DASSH (*)
770	Barmouth	260000	315000	04/07/2012	0	0	Bush	-
771	Mothecombe Beach	261000	46000	02/08/2003	1	10	Ager	DASSHvol(*)
772	Mothecombe Beach	261000	46000	24/05/2005	1	10	Oakley	DASSHvol(*)
773	Mothecombe Beach (Erme Mouth)	261000	47000	00/00/1929	1	10	Wilson	Cunningham et al., 1984
774	Erme Mouth (Mothecombe)	261000	47000	00/00/1968	0	0	Wilson	Wilson, 1970
775	Erme Mouth (Mothecombe)	261000	47000	00/00/1970	0	0	Wilson	Cunningham et al., 1984
776	Erme Mouth (Mothecombe)	261000	47000	23/10/2002	1	6	Marclim Team	Marclim
777	Graves End to Langland Bay	261000	187000	19/04/2004	1	10	CCW Team	SEWBRC
778	Fryars Bay (Beaumaris)	261000	377000	12/06/2014	1	3	Bush	-
779	Limeslade	262000	186000	14/03/2013	1	6	Bush	-
780	LimesladeBay	262000	186000	19/02/2014	1	6	Bush	-
781	Limeslade Bay/TheMumbles/BraceletBay (Swansea)	262000	187000	00/00/1973	1	10	N.C.C., I.S.U.	Cunningham et al., 1984
782	Limeslade Bay/TheMumbles/BraceletBay (Swansea)	262000	187000	00/00/1984	1	4	Hawkins	Cunningham et al., 1984
783	Langland Bay to Mumbles Head	262000	187000	23/07/2001	1	10	CCW Team	SEWBRC
784	Limeslade Bay/TheMumbles/BraceletBay (Swansea)	262000	187000	03/06/2004	1	10	CCW Team	SEWBRC

785	Bracelet Bay/The Mumbles (Swansea)	262000	187000	23/10/2006	1	10	Oakley	MarLIN (*)
786	Limeslade Bay/TheMumbles/BraceletBay (Swansea)	262000	187000	28/05/2013	1	6	Bush	-
787	Limeslade Bay/TheMumbles/BraceletBay (Swansea)	262000	187000	19/02/2014	1	6	Bush	-
788	Norton to Afon Tawe (Swansea Bay)	262000	189000	24/07/2001	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
789	Norton to Afon Tawe (Swansea Bay)	262000	189000	11/09/2003	1	10	CCW Team	SEWBRC
790	Norton to Afon Tawe (Swansea Bay)	262000	190000	24/07/2001	1	10	CCW Team	SEWBRC
791	Norton to Afon Tawe (Swansea Bay)	262000	190000	11/09/2003	1	10	CCW Team	SEWBRC
792	Penmon Priory to Black Rock (Menai Strait)	262000	379000	02/08/1992	1	10	CCW Team	CCWTech (*)/MNCR-JNCC
793	Brighouse Bay	262000	544000	16/07/2013	0	0	Coombey/SNH	SNH
794	Bracelet Bay (Swansea)	263000	187000	17/08/1978	1	3	Unknown/N.C.C., I.S.U.	Cunningham et al., 1984/ MNCR-JNCC
795	Bracelet Bay (Swansea)	263000	187000	00/00/1984	1	7	Knight-Jones	Cunningham et al., 1984
796	Langland Bay to Mumbles Head	263000	187000	23/07/2001	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
797	Survey 122	263000	187000	23/10/2006	1	10	Oakley	SEWBRC
798	Bracelet Bay (Swansea)	263000	187000	17/06/2011-16/08/2011	1	10	Hughes	MarLIN (*)
799	Bracelet Bay (Swansea)	263000	187000	14/03/2013	1	5	Bush	-
800	Bracelet Bay (Swansea)	263000	187000	19/02/2014	1	5	Bush	-
801	Penmon	263000	380000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
802	Penmon	263000	380000	04/08/2012	0	0	Bush	-
803	Penmon, S	263000	380000	14/04/2013	0	0	Bush	-
804	Penmon Point, W (Menai Strait, N)	263000	381000	21/07/1997	1	2	Brazier/CCW	MNCR-JNCC
805	Penmon, N	263000	381000	04/07/2012	0	0	Bush	-
806	Penmon, W	263000	381000	14/04/2013	0	0	Bush	-
807	Brighouse Bay (Solway, N)	263000	545000	15/06/1991	1	2	Covey	MNCR-JNCC
808	Norton to Afon Tawe (Swansea Bay)	264000	191000	24/07/2001	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
809	Norton to Afon Tawe (Swansea Bay)	264000	191000	11/09/2003	1	10	CCW Team	SEWBRC
810	Puffin Island, S (Menai Strait, N)	264000	381000	22/07/1997	1	3	Brazier/Nichols/CCW	MNCR-JNCC
811	Penmon, N	264000	381000	13/06/2002	0	0	Marclim Team	Marclim
812	Penmon, N	264000	381000	12/08/2003	0	0	Marclim/Frost et al.	Frost et al., 2004
813	Fauldbog Bay	264000	544000	00/00/2000	1	4	Hammond	Allen et al., 2002
814	Bantham (Thurlestone)	265000	43000	28/06/2002	1	5	Marclim Team	Marclim
815	Langland Bay to Mumbles Head	265000	191000	24/07/2001	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
816	Norton to Afon Tawe (Swansea Bay)	265000	191000	11/09/2003	1	10	CCW Team	SEWBRC
817	Swansea Bay	265000	191000	19/02/2014	1	6	Calloway	-
818	Meikle Ross (Kirkcudbright Bay)	265000	543000	17/09/1989	1	3	Davies	MNCR-JNCC
819	Meikle Ross (Kirkcudbright Bay)	265000	543000	00/00/2000	1	4	Hammond	Allen et al., 2002
820	Warren Point (Thurlestone)	266000	42000	00/00/1980	0	0	Hawkins	Cunningham et al., 1984
821	Warren Point (Thurlestone)	266000	42000	00/00/1981	0	0	Hawkins	Cunningham et al., 1984

822	Warren Point (Thurlestone)	266000	42000	00/00/1982	0	0	Hawkins	Cunningham et al., 1984
823	Warren Point (Thurlestone)	266000	42000	00/00/1983	0	0	Hawkins	Cunningham et al., 1984
824	Warren Point (Thurlestone)	266000	42000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
825	Thurlestone	266000	42000	16/05/2002	0	0	Marclim Team	Marclim
826	Norton to Afon Tawe (Swansea Bay)	266000	191000	24/07/2001	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
827	Norton to Afon Tawe (Swansea Bay)	266000	191000	11/09/2003	1	10	CCW Team	SEWBRC
828	Clashnessie	266000	964000	27/05/2002	0	0	Marclim Team	Marclim
829	Hope Cove	267000	39000	00/00/1980	0	0	Hawkins	Cunningham et al., 1984
830	Hope Cove	267000	39000	00/00/1981	0	0	Hawkins	Cunningham et al., 1984
831	Hope Cove	267000	39000	00/00/1982	0	0	Hawkins	Cunningham et al., 1984
832	Hope Cove	267000	39000	00/00/1983	0	0	Hawkins	Cunningham et al., 1984
833	Hope Cove	267000	39000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
834	Hope Cove	267000	39000	10/05/2002	0	0	Marclim Team	Marclim
835	Thurlestone	267000	41000	00/00/1980	0	0	Hawkins	Cunningham et al., 1984
836	Thurlestone	267000	41000	00/00/1981	0	0	Hawkins	Cunningham et al., 1984
837	Thurlestone	267000	41000	00/00/1982	0	0	Hawkins	Cunningham et al., 1984
838	Thurlestone	267000	41000	00/00/1983	0	0	Hawkins	Cunningham et al., 1984
839	Thurlestone	267000	41000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
840	Afon Tawe to Baglan Bay	267000	191000	29/10/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
841	Balmae Haen	267000	544000	00/00/2000	1	4	Hammond	Allen et al., 2002
842	Torrs Point, N (Kirkcudbright Bay)	267000	545000	19/09/1989	1	3	Davies	MNCR-JNCC
843	Torrs Point, N (Kirkcudbright Bay)	267000	545000	00/00/2000	1	4	Hammond	Allen et al., 2002
844	Lee Bay (Lynton)	268000	149000	24/05/2013	0	0	Bush	-
845	Lee Bay (Lynton)	269000	149000	00/00/1932	1	5	Wilson	Cunningham et al., 1984
846	Lee Bay (Lynton)	269000	149000	24/05/2013	1	2	Bush	-
847	Afon Tawe to Baglan Bay	269000	191000	29/10/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
848	Swansea Bay	269000	191000	19/02/2014	1	6	Calloway	-
849	Penaenmawr	269000	376000	12/06/2002	0	0	Marclim Team	Marclim
850	Howell Bay	269000	543000	00/00/2000	1	4	Hammond	Allen et al., 2002
851	Lynmouth, W (Lynton)	271000	150000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
852	Lynmouth, W (Lynton)	271000	150000	24/05/2013	0	0	Bush	-
853	Witford Point and Aberavon Sands	271000	191000	12/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
854	Mullock Bay	271000	543000	00/00/2000	1	5	Hammond	Allen et al., 2002
855	Farr	271000	963000	26/05/2002	0	0	Marclim Team	Marclim
856	Lynmouth	272000	149000	24/05/2013	0	0	Bush	-
857	Lynmouth (Lynton)	272000	150000	24/05/2013	0	0	Bush	-
858	White Port	272000	543000	00/00/2000	1	4	Hammond	Allen et al., 2002
859	North Sands (Salcombe)	273000	38000	00/00/1980	0	0	Hawkins	Cunningham et al., 1984
860	North Sands (Salcombe)	273000	38000	00/00/1981	0	0	Hawkins	Cunningham et al., 1984
861	North Sands (Salcombe)	273000	38000	00/00/1982	0	0	Hawkins	Cunningham et al., 1984
862	North Sands (Salcombe)	273000	38000	00/00/1983	0	0	Hawkins	Cunningham et al., 1984
863	North Sands (Salcombe)	273000	38000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
864	Salcombe	273000	38000	12/04/2002	0	0	Marclim Team	Marclim

865	Lynmouth	273000	149000	24/05/2013	0	0	Bush	-
866	Lynmouth, E (Lynton)	273000	150000	24/05/2013	0	0	Bush	-
867	Sheep Bught Rock	273000	543000	00/00/2000	1	4	Hammond	Allen et al., 2002
868	Lower Blackhead (Lynmouth)	274000	149000	24/05/2013	0	0	Bush	-
869	Lower Blackhead (Lynmouth)	274000	150000	11/07/1976	1	10	N.C.C., I.S.U.	Cunningham et al., 1984/ MNCR-JNCC
870	Witford Point and Aberavon Sands	274000	186000	12/09/2003	1	10	CCW Team	SEWBRC
871	Port Talbot Harbour	274000	187000	30/09/2003	1	10	CCW Team	SEWBRC
872	Port Talbot Harbour	274000	187000	04/08/2013	1	10	Bush	-
873	Afon Afan (Witford Point and Aberavon Sands)	274000	188000	12/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
874	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2003	0	0	Marclim Team	Marclim
875	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2004	0	0	Marclim Team	Marclim
876	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2005	0	0	Marclim Team	Marclim
877	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2006	1	2	Marclim Team	Marclim
878	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2007	0	0	Marclim Team	Marclim
879	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2008	0	0	Marclim Team	Marclim
880	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2009	0	0	Marclim Team	Marclim
881	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2010	0	0	Marclim Team	Marclim
882	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2011	0	0	Marclim Team	Marclim
883	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2012	0	0	Marclim Team	Marclim
884	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2013	0	0	Marclim Team	Marclim
885	Abbey Head	274000	543000	00/00/2000	1	4	Hammond	Allen et al., 2002
886	Abbey Burn Foot	274000	544000	00/00/1984	1	6	Cunningham	Cunningham et al., 1984/ DASSH (*)
887	Abbey Burn Foot	274000	544000	17/09/1989	1	2	Johnston/Mills	MNCR-JNCC
888	Abbey Burn Foot	274000	544000	00/00/2000	1	4	Hammond	Allen et al., 2002
889	Margam Sands	275000	187000	10/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
890	Port Talbot Harbour	275000	188000	30/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
891	Port Talbot Harbour	275000	188000	01/08/2013	1	10	Bush	-
892	Llandudno (Great Ormes Head, W)	275000	383000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
893	Llandudno (Great Ormes Head, W)	275000	383000	22/07/1997	1	2	Brazier/Nichols/CCW	MNCR-JNCC
894	Llandudno (Great Ormes Head, W)	275000	383000	2003-4	0	0	Frost et al.,	Frost et al., 2004
895	Llandudno (Great Ormes Head, W)	275000	383000	23/07/2012	0	0	Bush et al.	-
896	Port Mary	275000	545000	29/10/1978	1	5	Hammond/Hammond	Cumbria Biodiversity Data Centre (subsequently referred to as CBDC)
897	Port Mary	275000	545000	00/00/2000	1	4	Hammond	Allen et al., 2002
898	Margam Sands	276000	185000	10/09/2003	1	10	CCW Team	SEWBRC
899	Prawle	277000	35000	14/02/2002	0	0	Marclim Team	Marclim
900	Orroland Heugh	277000	545000	00/00/2000	1	4	Hammond	Allen et al., 2002
901	Langerstone Point (East Prawle)	278000	35000	25/07/2002	0	0	Marclim Team	Marclim
902	Sker Point (Kenfig)	278000	179000	00/00/1957	1	7	Purchon	Cunningham et al., 1984
903	Sker Point (Kenfig)	278000	179000	00/00/1973	1	3	Boyden	Cunningham et al., 1984
904	Sker Point (Kenfig)	278000	179000	29/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
905	Sker Point (Kenfig)	278000	179000	03/06/2004	1	10	CCW Team	SEWBRC

906	No site name available	278000	179000	15/06/2007-25/10/2007	1	10	Oakley	MarLIN (*)
907	Sker Point (Kenfig)	278000	179000	06/06/2008	1	10	Oakley	SEWBRC/MarLIN (*)
908	Kenfig Sands	278000	180000	10/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
909	Kenfig Sands	278000	181000	10/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
910	Great Ormes Head, E	278000	383000	02/07/2012	1	2	Bush et al.	-
911	Gorah Rocks (Devon)	279000	36000	04/07/2008	1	10	Crouch	MarLIN (*)
912	Rest Bay	279000	178000	29/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
913	Sker Point (Kenfig)	279000	179000	27/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
914	Barlocco Bay	279000	546000	00/00/2000	1	4	Hammond	Allen et al., 2002
915	Castle Muir Point	279000	547000	00/00/2000	1	4	Hammond	Allen et al., 2002
916	Lannacombe Beach, E (Harris Beach, Little Slead)	280000	37000	06/01/1992	1	10	Unknown	MNCR-JNCC
917	Site 481 (Porthcawl)	280000	171000	27/04/1988	1	10	Mettam	MNCR-JNCC
918	Hutchwns Point (Porthcawl)	280000	176000	00/00/1984	1	7	Cunningham	Cunningham et al., 1984
919	Porthcawl	280000	176000	27/04/1988	1	10	Mettam	Marine Biological Association (DASSH Data Archive Centre Statutory Agency and commercial marine surveys) (subsequently referred to as DASSHcom*)
920	Hutchwns Point (Porthcawl)	280000	176000	27/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
921	Hutchwns Point (Porthcawl)	280000	176000	14/03/2013	1	6	Bush	-
922	Little Ormes Head, W	280000	382000	00/00/2012	1	2	Bush et al.	-
923	Rascarrel Bay (Auchencairn, Solway, N)	280000	548000	19/09/1989	1	4	Covey	MNCR-JNCC
924	Rascarrel Bay (Auchencairn, Solway, N)	280000	548000	00/00/2000	1	4	Hammond	Allen et al., 2002
925	Porthcawl	281000	176000	14/03/2013	1	6	Bush	-
926	Little Ormes Head	281000	382000	23/07/1997	1	3	Brazier/Spence/CCW	MNCR-JNCC
927	Little Ormes Head	281000	382000	00/00/2004	0	0	Marclim Team	Marclim
928	Little Ormes Head	281000	382000	00/00/2005	0	0	Marclim Team	Marclim
929	Little Ormes Head	281000	382000	00/00/2006	0	0	Marclim Team	Marclim
930	Little Ormes Head	281000	382000	00/00/2007	1	5	Marclim Team	Marclim
931	Little Ormes Head	281000	382000	00/00/2008	0	0	Marclim Team	Marclim
932	Little Ormes Head	281000	382000	00/00/2009	0	0	Marclim Team	Marclim
933	Little Ormes Head	281000	382000	00/00/2010	0	0	Marclim Team	Marclim
934	Little Ormes Head	281000	382000	00/00/2011	0	0	Marclim Team	Marclim
935	Little Ormes Head	281000	382000	00/00/2012	1	2	Marclim Team	Marclim
936	Little Ormes Head	281000	382000	00/00/2013	1	5	Marclim Team	Marclim
937	Limpet Rocks (Torcross)	282000	41000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
938	Fairy Rock (Bristol Channel, N)	282000	175000	02/07/1979	1	10	Unknown	MNCR-JNCC
939	Hutchwns Point (Porthcawl)	282000	176000	08/09/1971	1	6	Ager	SEWBRC
940	Hutchwns Point (Porthcawl)	282000	176000	27/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
941	Hutchwns Point (Porthcawl)	282000	176000	14/03/2013	1	6	Bush	-
942	Groyne (Penrhyn Bay)	282000	381000	23/07/2012	1	4	Bush et al.	-
943	Little Ormes Head, E	282000	382000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
944	Little Ormes Head, E	282000	382000	2003-4	0	0	Frost et al.,	Frost et al., 2004
945	Adams Chair	282000	548000	00/00/2000	1	4	Hammond	Allen et al., 2002

946	Balcary Point (Inner Solway)	282000	549000	00/00/1973	1	4	Perkins	Perkins, 1973/Allen et al., 2002
947	Balcary Point (Inner Solway)	282000	549000	15/08/1991	1	5	Emblow	MNCR-JNCC
948	Balcary Point (Inner Solway)	282000	549000	00/00/1994	0	0	IECS	Allen et al., 2002
949	Start Point (Looe)	283000	37000	00/00/1983	0	0	Hawkins	Cunningham et al., 1984
950	Start Point (Looe)	283000	37000	02/05/2002	0	0	Marclim Team	Marclim
951	Hutchwns Point (Porthcawl)	283000	176000	27/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
952	Hutchwns Point (Porthcawl)	283000	176000	16/07/2007	1	10	Oakley	MarLIN (*)
953	No site name available	283000	176000	16/07/2007	1	10	Oakley	MarLIN (*)
954	Newton Point (Porthcawl)	283000	176000	19/06/2008	1	10	Oakley	SEWBRC/MarLIN (*)
955	HestanIsland	283000	549000	00/00/2000	1	10	Hammond	Allen et al., 2002
956	Dunraven Bay	284000	173000	28/09/2003	1	10	CCW Team	CCW
957	Tusker Rock	284000	173000	05/07/2004	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
958	Dunraven Bay	284000	173000	01/08/2010	1	6	White	White, 2011.
959	Dunraven Bay	284000	173000	31/01/2011	1	10	White	White, 2011.
960	Tusker Rock	284000	174000	05/07/2004	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
961	Hutchwns Point to Traeth yr Afon	284000	176000	27/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
962	Rhos on Sea	284000	380000	23/07/2012	1	5	Bush et al.	-
963	Rhos Point (Rhos on Sea, Penrhyn Bay)	284000	381000	00/00/1923	1	10	Wilson	DASSHac (*)
964	Rhos Point (Rhos on Sea, Penrhyn Bay)	284000	381000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
965	Rhos Point (Rhos on Sea, Penrhyn Bay)	284000	381000	2003-4	0	0	Frost et al.,	Frost et al., 2004
966	Rhos Point (Rhos on Sea, Penrhyn Bay)	284000	381000	31/12/2004	0	0	CCW Team	CCW
967	Almorness Point	284000	551000	00/00/2000	1	10	Hammond	Allen et al., 2002
968	Porlock	285000	148000	00/00/1976	1	5	Boyden	Cunningham et al., 1984
969	Gore Point (Porlock)	285000	148000	00/00/1984	1	3	Crothers	Cunningham et al., 1984
970	Tusker Rock, SE	285000	172000	16/09/2002	1	7	Northen/CCW	CCWTech (*)
971	Afon Ogwr to Black Rocks	285000	175000	28/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
972	Hutchwns Point to Traeth yr Afon	285000	176000	27/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
973	Solway, N (Dumfries and Galloway)	285000	552000	19/06/2013	1	10	Coombey/SNH	SNH
974	Porlock	286000	147000	23/05/2013	1	5	Bush	-
975	Porlock Weir	286000	148000	00/00/1984	1	6	Jensen	Cunningham et al., 1984
976	Porlock	286000	148000	23/05/2013	0	0	Bush	-
977	Black Rocks (Dunraven Bay)	286000	174000	28/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
978	Black Rocks (Dunraven Bay)	286000	174000	26 Mar 2005	1	6	Ager	DASSHvol(*)
979	Black Rocks (Dunraven Bay)	286000	174000	16 Aug 2008	1	6	Oakley/Slade Farm	MarLIN (*)
980	Black Rocks (Dunraven Bay)	286000	174000	01/10/2012	1	6	Bush	-
981	Afon Ogwr to Black Rocks	286000	175000	28/09/2003	1	10	CCW Team	SEWBRC
982	Colwyn Bay	286000	378000	23/07/2012	1	1	Bush et al.	-
983	Colwyn Bay	286000	379000	23/07/2012	1	1	Bush et al.	-
984	Balintore	286000	875000	23/05/2002	0	0	Marclim Team	Marclim
985	Porlock Bay	287000	147000	00/00/1984	1	1	Crothers	Cunningham et al., 1984
986	Dunraven Bay	287000	173000	28/09/2003	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
987	Dunraven Bay	287000	173000	18/02/2014	1	6	Bush	-
988	Dunraven Bay	287000	174000	28/09/2003	1	10	CCW Team	MIP1-CCW (*)

989	Dunraven Bay	287000	174000	31/10/2012	1	7	Bush	-
990	Colwyn Bay	287000	378000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
991	Colwyn Bay	287000	378000	2003-4	1	2	Frost et al.,	Frost et al., 2004
992	Port O Warren Bay	287000	553000	00/00/1973	1	6	Williams/Perkins	CBDC
993	Port O Warren Bay	287000	553000	00/00/1992	0	0	JNCC	Marine Recorder
994	Port O Warren Bay	287000	553000	20/07/2012	1	6	Bush et al.	-
995	Port Skerra	287000	966000	06/03/2003	0	0	Marclim Team	Marclim
996	Dancing Beggars (Stoke, Fleming)	288000	48000	26/02/1994	1	2	Campline/CCW	MNCR-JNCC
997	Porlock Bay	288000	148000	23/05/2013	1	4	Bush	-
998	Temples Bay	288000	172000	00/00/1997	1	7	Taylor & Viles, 2000	Naylor & Viles, 2000
999	Dunraven Bay	288000	172000	28/09/2003	1	6	CCW Team	SEWBRC
1000	Dunraven Bay	288000	172000	31/10/2012	1	6	Bush	-
1001	Dunraven Bay	288000	172000	25/05/2013	1	6	Bush	-
1002	Temples Bay	288000	172000	18/02/2014	1	6	Bush	-
1003	Dunraven Bay	288000	173000	00/00/1976	1	6	Boyden	Cunningham et al., 1984
1004	Dunraven Bay	288000	173000	00/00/1984	1	7	Cunningham	Cunningham et al., 1984/ DASSHac (*)
1005	Southerndown	288000	173000	00/00/1997	1	7	Taylor & Viles, 2000	Naylor & Viles, 2000
1006	Dunraven Bay	288000	173000	28/09/2003	1	10	CCW Team	MIP1-CCW (*)
1007	Dunraven Bay	288000	173000	31/01/2011	1	10	White	White, 2011.
1008	Dunraven Bay	288000	173000	18/02/2014	1	6	Bush	-
1009	Port O Warren Bay	288000	553000	00/00/1984	1	5	Cunningham	Cunningham et al., 1984/ DASSH (*)
1010	Port O Warren Bay	288000	553000	20/07/2012	1	6	Bush et al.	-
1011	Saltern Cove (Goodrington)	289000	58000	14/09/1992	1	7	Campline/CCW	MNCR-JNCC
1012	Goodrington, S	289000	58000	08/03/1993	1	3	Campline/CCW	MNCR-JNCC
1013	Shell Cove (Middle Stone to Elberry Cove)	289000	58000	07/03/1993	1	2	Camplin	MNCR-JNCC
1014	Goodrington Beach	289000	58000	21/08/2004	1	5	Ager	DASSHvol(*)
1015	Goodrington Sands	289000	59000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
1016	Goodrington Sands, Reef	289000	59000	26/10/1992	1	5	Campline/CCW	MNCR-JNCC
1017	Goodrington Sands	289000	59000	11/09/2006	1	10	Evans	MarLIN (*)
1018	Goodrington Sands	289000	59000	04/07/2007	1	10	Hatton-Brown	DASSHvol(*)
1019	No site name available	289000	59000	14/09/2007	1	10	Crouch	MarLIN (*)
1020	Goodrington Sands, Reef	289000	59000	21/08/2004-25/11/2003	1	5	Ager	DASSHvol(*)
1021	Roundham Head, S (Paignton)	289000	60000	13/10/1992	1	5	Campline/CCW	MNCR-JNCC
1022	Fairy Cove, Roundham Head (Livermead Sands to Good	289000	60000	26/11/1992	1	4	Gilbert	MNCR-JNCC
1023	Paignton Harbour	289000	60000	25/03/1993	1	3	Proctor	MNCR-JNCC
1024	Hollicombe Rocks (Torbay)	289000	61000	27/09/1992	1	6	Robinson	MNCR-JNCC
1025	Hollicombe Rocks (Torbay)	289000	61000	27/09/1992	1	3	Campline/CCW	MNCR-JNCC (NBN website)
1026	Hurlstone Point (Bristol Channel S)	289000	149000	14/06/1978	1	10	Unknown	MNCR-JNCC
1027	Traeth Bach to Nash Point	289000	171000	04/06/2004	1	10	CCW Team	SEWBRC
1028	Trwyn y Witch to Traeth Bach	289000	172000	00/00/2002	1	10	CCW Team	CCW

1029	Trwyn y Witch to Traeth Bach	289000	172000	05/07/2004	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
1030	Oil Cove (Paignton)	290000	62000	21/02/1993	1	7	Campline/CCW	MNCR-JNCC
1031	Oil Cove (Paignton)	290000	62000	21/02/1993	1	5	Proctor	MNCR-JNCC
1032	Livermead Head Caves	290000	62000	21/02/1993	1	3	Gilbert	MNCR-JNCC
1033	Corbyns Head (Torbay)	290000	63000	26/09/1992	1	5	Campline/CCW	MNCR-JNCC
1034	Torbay	290000	63000	10/04/2002	1	5	Marclim Team	Marclim
1035	Traeth Bach to Nash Point	290000	169000	04/06/2004	1	10	CCW Team	SEWBRC
1036	Scabbacombe Sands (Brixham)	291000	52000	15/03/1994	1	3	Gilbert/CCW	MNCR-JNCC
1037	Torquay	291000	63000	00/00/1910	1	5	Elwes	Wilson, 1971/Cunningham et al., 1984
1038	Nash Point (Bristol Channel, N)	291000	167000	03/07/1979	1	7	Maggs	MNCR-JNCC
1039	Nash Point (Bristol Channel, N)	291000	167000	00/00/1997	1	5	Naylor & Viles, 2000	Naylor & Viles, 2000
1040	Marcross	291000	167000	14/03/2013	1	5	Bush	-
1041	Marcross	291000	168000	00/00/1976	1	6	Boyden	Cunningham et al., 1984
1042	Marcross	291000	168000	04/06/2004	1	10	CCW Team	SEWBRC
1043	Llanddulas	291000	378000	12/02/2008-30/07/2008	1	6	Capper/Hickin/Brazier/Wyn/Prieto/CCW	NWEIS
1044	Llanddulas	291000	378000	12/02/2008-30/07/2008	1	6	Capper/Hickin/Brazier/Wyn/Prieto/CCW	NWEIS
1045	Llanddulas	291000	378000	12/02/2008-30/07/2008	1	1	Capper/Hickin/Brazier/Wyn/Prieto/CCW	NWEIS
1046	Llanddulas	291000	378000	00/00/2010	0	0	Marclim Team	Marclim
1047	Llanddulas	291000	378000	29/07/2012	1	6	Bush	-
1048	Llanddulas	291000	378000	23/07/2012	1	6	Bush et al.	-
1049	Llanddulas	291000	378000	07/04/2012	1	6	Bush et al.	-
1050	Llanddulas	291000	378000	05/04/2013	1	6	Bush	-
1051	Llanddulas	291000	378000	06/04/2014	1	6	Bush	-
1052	Llanddulas	291000	378000	29/07/2014	1	7	Bush	-
1053	Tarbat Ness	291000	884000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
1054	Scabbacombe Sands (Brixham)	292000	51000	15/03/1994	1	3	Glendinning	MNCR-JNCC
1055	Cod Rocks, Scabbacombe (Brixham)	292000	52000	27/04/1994	1	4	Cooke	MNCR-JNCC
1056	Man Sands (Brixham)	292000	53000	14/03/1994	1	3	Glendinning	MNCR-JNCC
1057	Oddicombe Beach (Torquay)	292000	65000	11/04/1994	1	3	Gilbert/CCW	MNCR-JNCC
1058	Watcombe Cove (North Bay) (The Ness to Watcombe He	292000	67000	14/08/1992	1	10	Unknown	MNCR-JNCC
1059	Watcombe Cove	292000	67000	11/04/1994	1	5	Burton/CCW	MNCR-JNCC
1060	Maidencombe	292000	68000	28/07/1992	1	6	Gilbert/CCW	MNCR-JNCC
1061	Nash Point to Tresilian Bay	292000	167000	04/06/2004	1	10	CCW Team	SEWBRC
1062	St Marys Bay (Brixham)	293000	54000	05/05/1993	1	3	Campline/CCW	MNCR-JNCC
1063	Brixham	293000	55000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
1064	St Marys Bay, N (Brixham)	293000	55000	06/05/1993	1	3	Strong/Campline/CCW	MNCR-JNCC
1065	Brixham	293000	56000	10/04/2002	0	0	Marclim Team	Marclim
1066	St Donats Point and West (Bristol Channel, N)	293000	167000	03/07/1979	1	7	Rostron	MNCR-JNCC
1067	St Donats Point and West	293000	167000	04/06/2004	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC

1068	Teignmouth Beach, Rocks	294000	73000	12/03/1994	1	4	Glendinning	MNCR-JNCC
1069	Reynards Cave, Tresilian (Bristol Channel, N)	294000	167000	03/07/1979	1	3	Dipper	MNCR-JNCC
1070	Reynards Cave	294000	167000	04/06/2004	1	10	CCW Team	SEWBRC
1071	Saint Bees Head	294000	512000	00/00/1954	1	10	Allen et al.	Allen et al., 2002
1072	Saint Bees Head	294000	512000	00/00/1989	1	4	MNCR	Allen et al., 2002
1073	Fleswick Bay, S	294000	512000	08/04/1989	1	4	Hiscock	MNCR-JNCC/ Merseyside BioBank(subsequently referred to as MBB)
1074	Saint Bees Head	294000	512000	00/00/1991	1	4	NWW	Allen et al., 2002
1075	Saint Bees Head(Tomlin)	294000	512000	05/07/2000	1	3	Hammond	CBDC/ MBB
1076	Saint Bees Head	294000	515000	04/07/2000	1	3	Lancaster	Allen et al., 2002
1077	Hopes Nose (Torquay)	295000	63000	24/04/2010	1	2	Sterland	Seasearch(*)
1078	Sprey Point (Teignmouth)	295000	73000	12/03/1994	1	5	Burton/CCW	MNCR-JNCC
1079	Man Sands (Sharkham Point to Scabbacombe Head)	295000	73000	14/03/1994	1	2	Glendinning	MNCR-JNCC
1080	Greenaleigh Point, W (Minehead)	295000	148000	05/07/1979	1	5	Rostron	MNCR-JNCC
1081	Llantwit Major	295000	167000	00/00/1957	1	10	Purchon	Cunningham et al., 1984
1082	Llantwit Major	295000	167000	15/05/1976	1	10	Mettam	SEWBRC
1083	Llantwit Major	295000	167000	00/00/1984	1	3	Cunningham	Cunningham et al., 1984
1084	Llantwit Major	295000	167000	01/07/2004	1	10	CCW Team	SEWBRC
1085	Llantwit Major	295000	167000	14/03/2013	1	5	Bush	-
1086	Saint Bees	295000	511000	00/00/1984	1	3	Widdop	Cunningham et al., 1984
1087	South Head, SE	295000	511000	08/04/1989	1	3	Davies	MNCR-JNCC/ MBB
1088	Saint Bees	295000	511000	00/00/1991	0	0	Allan et al.	Allan et al. 1991
1089	Saint Bees	295000	511000	07/12/2003	1	6	Frost et al.,	Frost et al., 2004
1090	Saint Bees, NE	295000	511000	21/07/2012	1	6	Bush et al.	-
1091	Fresco	295000	965000	25/05/2002	0	0	Marclim Team	Marclim
1092	Fresgoe	295000	965000	06/03/2003	0	0	Marclim Team	Marclim
1093	Fresco, W	295000	966000	25/05/2002	0	0	Marclim Team	Marclim
1094	Corytons Cove (Dawlish)	296000	76000	00/00/1984	1	6	Cunningham	Cunningham et al., 1984
1095	Corytons Cove (Dawlish)	296000	76000	16/06/1992	1	4	Campline/CCW	MNCR-JNCC
1096	Tresilian Bay to Limpert Bay	296000	167000	01/07/2004	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
1097	Saint Bees, S	296000	509000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1098	Saint Bees, SW	296000	510000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1099	Saint Bees, SW	296000	510000	21/07/2012	1	7	Bush et al.	-
1100	Grab samples F	296000	549000	01/07/2004	1	5	SNH Team	SNH
1101	Grab samples F	296000	549000	01-31/07/2006	1	5	SNH Team	SNH
1102	Transect 1 (Solway Firth)	296000	554000	23/09/1999	1	3	Dixon	Marine Nature Conservation Review (MNCR) and associated benthic marine data held and managed by English Nature (subsequently referred to as MNCR-EN, *)
1103	Transect 2 (Solway Firth)	296000	554000	23/09/1999	1	3	Hunt	MNCR-EN
1104	Langstone Reef (Dawlish)	297000	78000	16/06/1992	1	7	Burton/Gilbert/CCW	MNCR-JNCC

1105	Minehead	297000	147000	00/00/1976	1	5	Boyden	Cunningham et al., 1984
1106	Minehead	297000	147000	00/00/1984	1	5	Crothers	Cunningham et al., 1984
1107	Minehead, W	297000	147000	00/00/1984	1	5	Crothers	Cunningham et al., 1984
1108	Minehead	297000	147000	07/10/2002	1	5	Marclim Team	Marclim
1109	Minehead	297000	147000	23/05/2013	0	0	Bush	-
1110	Tresilian Bay to Limpert Bay	297000	166000	01/07/2004	1	10	CCW Team	SEWBRC
1111	Coulderton (Saint Bees)	297000	508000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1112	Saint Bees, S	297000	510000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1113	CunningPoint	297000	522000	07/07/2000	1	3	Hammond	CBDC/ MBB
1114	Southerness Point, Cunning Point (Solway, N)	297000	554000	00/00/1964	1	10	Williams/Perkins	CBDC
1115	Southerness (Solway, N)	297000	554000	00/00/1973	1	10	Perkins	Perkins, 1973/Allen et al., 2002
1116	Southerness (Solway, N)	297000	554000	00/00/1984	1	4	Cunningham	Cunningham et al., 1984/ DASSH (*)
1117	Southerness Point (Solway, N)	297000	554000	13/08/1991	1	3	Eno	MNCR-JNCC
1118	Southerness (Solway, N)	297000	554000	00/00/1994	1	4	Cutts & Hemingway	Allen et al., 2002
1119	Southerness Lighthouse (Solway, N)	297000	554000	22/09/1999	1	4	Dixon	MNCR-EN
1120	Transect 3 (Solway Firth)	297000	554000	23/09/1999	1	3	Dixon	MNCR-EN
1121	Southernness Point (Solway, N)	297000	554000	00/00/2000	1	4	Hammond	Allen et al., 2002
1122	Southernness Point (Solway, N)	297000	554000	20/07/2012	1	5	Bush et al.	-
1123	Exe estuary	298000	82000	00/00/1978	1	10	Powell	DASSH (*)
1124	Site 223 (Upper Bristol Channel)	298000	147000	14/04/1988	1	10	Mettam	MNCR-JNCC
1125	Nethertown (Saint Bees)	298000	506000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1126	Nethertown	298000	507000	00/00/1984	1	6	Widdop	Cunningham et al., 1984/ DASSH (*)/MBB
1127	Nethertown	298000	507000	30/11/1994	1	6	Hammond	CBDC/ MBB
1128	Nethertown	298000	507000	00/00/1995	1	7	Cutts & Hemingway	Cutts & Hemingway, 1995
1129	Nethertown	298000	507000	07/07/2000	1	6	Lancaster	CBDC/ MBB
1130	Nethertown (Saint Bees)	298000	507000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1131	Nethertown	298000	507000	20/03/2004	1	6	Frost et al.,	Frost et al., 2004
1132	Nethertown	298000	507000	21/07/2012	1	6	Bush et al.	-
1133	Coulderton (Saint Bees)	298000	508000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1134	Harrington	298000	525000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
1135	Moss Bay (Harrington)	298000	525000	21/07/2012	1	5	Bush et al.	-
1136	MossBay	298000	526000	00/00/1952	1	6	Hammond	Allen et al., 2002
1137	MossBay	298000	526000	06/07/2000	1	5	Lancaster	CBDC/ MBB
1138	MossBay	298000	526000	21/07/2012	1	6	Bush et al.	-
1139	Grab samples G	298000	553000	01/07/2004	1	5	SNH Team	SNH
1140	Grab samples G	298000	553000	01-31/07/2007	1	5	SNH Team	SNH
1141	Black Craigs and Gillfoot Bay (Solway)	298000	554000	22/09/1999	1	3	Hunt	MNCR-EN
1142	Gillfoot Bay (Southerness, Solway, N)	298000	554000	20/07/2012	1	3	Bush et al.	-
1143	Tresilian Bay to Limpert Bay	299000	166000	01/07/2004	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
1144	Rhyl	299000	381000	23/07/2012	0	0	Bush et al.	-
1145	Nethertown (Saint Bees)	299000	506000	01/03/2002	1	7	Allen et al.	Allen et al., 2002

1146	Nethertown (Saint Bees)	299000	507000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1147	Northside	299000	530000	16/09/1984	1	5	Hammond/Hammond	CBDC/ MBB
1148	Siddick Point, S (Parton Bay)	299000	530000	13/06/1991	1	4	Hartnoll	MNCR-JNCC/ MBB
1149	Siddick Scar	299000	531000	00/00/1999	1	5	Lancaster	Allen et al., 2002
1150	Siddick Scar	299000	531000	05/07/2000	1	5	Lancaster	CBDC/ MBB
1151	Siddick (Seaton)	299000	531000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1152	Siddick (Lam)	299000	532000	01/04/1971	1	2	Perkins/Abbott	CBDC/ MBB
1153	N of North Side (Parton Bay)	299000	533000	15/07/1991	1	3	Hawkins	MNCR-JNCC/ MBB
1154	Carse Scar (Nith Estuary)	299000	559000	00/00/1984	0	0	Henderson	Cunningham et al., 1984
1155	Carse Scar (Nith Estuary)	299000	559000	20/07/2012	0	0	Bush	-
1156	Tresilian Bay to Limpert Bay	300000	166000	02/07/2004-05/08/2004	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
1157	Sellafield	300000	504000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1158	Sellafield	300000	504000	21/07/2012	1	6	Bush et al.	-
1159	Siddick Scar	300000	531000	21/07/2012	1	6	Bush et al.	-
1160	Saint Helens (Seaton)	300000	532000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1161	Flimby	300000	533000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1162	Nith estuary (Solway, N)	300000	564000	00/00/1984	0	0	Henderson	Cunningham et al., 1984
1163	Exmouth, E	301000	79000	00/00/1964	1	5	Crisp	Cunningham et al., 1984
1164	Mear Rocks (Exmouth)	301000	79000	00/00/1970	1	6	Wilson	Cunningham et al., 1984
1165	Mear Rocks (Exmouth)	301000	79000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
1166	Mear Rocks (Exmouth)	301000	79000	09/11/1991	1	2	Burton/CCW	MNCR-JNCC
1167	Bristol Channel	301000	163000	01/08/1972	1	10	Warwick	Bristol Regional Environmental Records Centre (subsequently referred to as BRERC)
1168	Limpert Bay (Aberthaw)	301000	165000	00/00/1957	1	10	Purchon	Cunningham et al., 1984
1169	Limpert Bay (Aberthaw)	301000	165000	00/00/1976	1	7	Boyden	Cunningham et al., 1984
1170	Limpert Bay (Aberthaw)	301000	165000	14/03/2013	1	6	Bush	-
1171	Limpert Bay (Aberthaw)	301000	166000	02/08/2004	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
1172	Limpert Bay (Aberthaw)	301000	166000	14/03/2013	1	5	Bush	-
1173	Sellafield	301000	503000	00/00/1984	1	4	Widdop	DASSH (*)/ MBB/Cunningham et al., 1984
1174	Sellafield	301000	503000	05/08/2000	1	4	Lancaster	CBDC/ MBB
1175	Sellafield	301000	503000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1176	Sellafield	301000	503000	20/03/2004	1	7	Frost et al.,	Frost et al., 2004
1177	Sellafield	301000	503000	21/07/2012	1	6	Bush et al.	-
1178	Sellafield	301000	504000	01/03/2002	1	10	Allen et al.	Allen et al., 2002
1179	Saint Helens	301000	533000	16/09/1984	1	5	Hammond/Hammond	CBDC/MBB
1180	Flimby	301000	533000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1181	Flimby Scar	301000	534000	00/00/1938	1	6	Hammond	Allen et al., 2002
1182	Flimby Scar	301000	534000	00/00/2000	1	5	Hammond	Allen et al., 2002
1183	Exemouth (Orcombe Point)	302000	79000	00/00/1980	1	10	Boalch	Cunningham et al., 1984
1184	Orcombe Point (Exmouth)	302000	79000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
1185	Limpert Bay (Aberthaw)	302000	165000	02/08/2004	1	10	CCW Team	MIP1-CCW (*)
1186	Flimby central (Parton Bay)	302000	533000	30/05/1991	1	3	Russell	MNCR-JNCC

1187	Risehow Scar	302000	535000	00/00/1991	1	6	MNCR	Allen et al., 2002
1188	Risehow Scar	302000	535000	00/00/2000	0	0	Hammond	Allen et al., 2002
1189	Maryport, South Pier (Parton Bay)	302000	536000	00/00/2000	1	5	Hammond	Allen et al., 2002
1190	Helmsdale	302000	915000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
1191	Helmsdale	302000	915000	23/05/2002	0	0	Marclim Team	Marclim
1192	Blue Anchor	303000	143000	06/10/2002	1	5	Marclim Team	Marclim
1193	Blue Anchor	303000	143000	24/05/2013	1	5	Bush	-
1194	Blue Anchor	303000	144000	00/00/1941	1	3	Bassindale	Cunningham et al., 1984
1195	Blue Anchor	303000	144000	00/00/1976	1	6	Boyden	Cunningham et al., 1984
1196	Blue Anchor	303000	144000	00/00/1978	1	6	Horne	Horne, 1978
1197	Blue Anchor	303000	144000	00/00/1984	1	6	Crothers	Cunningham et al., 1984
1198	Blue Anchor	303000	144000	24/05/2013	1	5	Bush	-
1199	Site 226 (Upper Bristol Channel)	303000	145000	14/04/1988	1	10	Mettam	MNCR-JNCC
1200	Site 525 (Upper Bristol Channel)	303000	163000	28/04/1988	1	10	Mettam	MNCR-JNCC
1201	Barns Scar (Drigg)	303000	498000	01/08/2000	1	5	Lancaster	Allen et al., 2002
1202	Barns Scar (Drigg)	303000	498000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1203	Whitriggs Scar (Seascale)	303000	500000	07/04/1989	1	7	Hiscock	MNCR-JNCC
1204	Seascale	303000	500000	20/03/2004	1	6	Frost et al.,	Frost et al., 2004
1205	Seascale	303000	500000	21/07/2012	1	7	Bush et al.	-
1206	Seascale	303000	501000	07/10/1915	1	10	Wilson	Wilson, 1929
1207	Seascale	303000	501000	00/00/1984	1	3	Widdop	Cunningham et al., 1984/ DASSH (*)
1208	Seascale	303000	501000	21/07/2012	1	7	Bush et al.	-
1209	Maryport, S (Parton Bay)	303000	536000	29/05/1991	1	6	Hartnoll	MNCR-JNCC
1210	Maryport, North Pier (Parton Bay)	303000	536000	00/00/2000	1	5	Hammond	Allen et al., 2002
1211	Maryport, N (Parton Bay)	303000	537000	28/05/1991	1	6	Hawkins	MNCR-JNCC/ MBB
1212	Museum Scar (Maryport, Parton Bay)	303000	537000	00/00/2000	1	5	Hammond	Allen et al., 2002
1213	Maryport (Parton Bay)	303000	537000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1214	Maryport, N (Parton Bay)	303000	537000	21/07/2012	1	6	Bush et al.	-
1215	Seabrows Scar (Maryport, Parton Bay)	303000	538000	00/00/2000	1	5	Hammond	Allen et al., 2002
1216	Bank End Scar, S (Maryport, Parton Bay)	303000	538000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1217	Seabrows Scar (Maryport, Parton Bay)	303000	538000	21/07/2012	1	6	Bush et al.	-
1218	Otter Cove and Ledges (Littleham Cove to Straight Point)	304000	79000	05/05/1993	1	10	Unknown	Marine Recorder
1219	Otter Cove and Ledges (Littleham Cove to Straight Point)	304000	79000	00/00/1994	1	10	Unknown	Marine Recorder
1220	Breaksea Point to Watch House Point	304000	165000	03/08/2004	1	10	CCW Team	SEWBRC
1221	Drigg	304000	498000	00/00/1984	1	6	Widdop	Cunningham et al., 1984/ DASSH (*)/ MBB
1222	Barns Scar (Drigg)	304000	498000	02/08/2000	1	5	Hammond	CBDC/ MBB
1223	Barns Scar (Drigg)	304000	498000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1224	Drigg	304000	498000	20/03/2004	1	6	Frost et al.,	Frost et al., 2004
1225	Drigg, Mid Shore	304000	498000	21/07/2012	1	6	Bush et al.	-
1226	Bank End Scar (Maryport, Parton Bay)	304000	538000	00/00/1938	1	5	Hammond	Allen et al., 2002

1227	Bank End Scar (Maryport, Parton Bay)	304000	538000	00/00/1953	1	5	Hammond	Allen et al., 2002
1228	Bank End Scar (Maryport, Parton Bay)	304000	538000	04/07/2000	1	6	Tullie House Marine records	CBDC/ MBB
1229	Bank End Scar (Maryport, Parton Bay)	304000	538000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1230	Bank End Scar (Maryport, Parton Bay)	304000	538000	21/07/2012	1	6	Bush et al.	-
1231	Bank End Scar (Maryport, Parton Bay)	304000	539000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1232	Crosscanonby (Allonby Bay)	304000	539000	21/07/2012	1	6	Bush et al.	-
1233	Site 252 (Upper Bristol Channel)	305000	147000	15/04/1988	1	10	Mettam	MNCR-JNCC
1234	Watch House Point to Rhoose Point	305000	165000	16/09/2004	1	10	CCW Team	SEWBRC
1235	Prestatyn groyne	305000	383000	23/07/2012	1	4	Bush et al.	-
1236	Brown Rigg, NW (Allonby Bay)	305000	539000	09/08/1991	1	5	Ward	MNCR-JNCC/ MBB
1237	Maryport Golf Course (Allonby Bay)	305000	539000	00/00/2000	1	6	Hammond	Allen et al., 2002
1238	Brownrigg, Crosscanonby (Allonby Bay)	305000	539000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1239	Crosscanonby (Allonby Bay)	305000	539000	21/07/2012	1	6	Bush et al.	-
1240	Crosscanonby (Allonby Bay)	305000	540000	00/00/1984	1	7	Cunningham	Cunningham et al., 1984/ DASSH (*)/ MBB
1241	Crosscanonby (Allonby Bay)	305000	540000	00/00/2000	1	6	Allen et al.	Allen et al., 2002
1242	Crosscanonby (Allonby Bay)	305000	540000	21/07/2012	1	7	Bush et al.	-
1243	Dubmill Point, N (Mawbray)	305000	546000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1244	Ellisons Scar (Mawbray Bank, Mawbray)	305000	547000	00/00/2000	1	6	Hammond	Allen et al., 2002
1245	Ellisons Scar (Mawbray Bank, Mawbray)	305000	547000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1246	Ellisons Scar (Mawbray Bank, Mawbray)	305000	547000	21/07/2012	1	6	Bush et al.	-
1247	Watchet	306000	143000	24/05/2013	0	0	Bush	-
1248	Prestatyn groyne	306000	384000	23/07/2012	1	4	Bush et al.	-
1249	Crosscanonby Scar (Allonby Bay)	306000	539000	00/00/2000	1	6	Hammond	Allen et al., 2002
1250	Crosscanonby (Allonby Bay)	306000	539000	21/07/2012	1	6	Bush et al.	-
1251	Saltpans, Crosscanonby (Allonby Bay)	306000	540000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1252	Saltpans, N, Crosscanonby (Allonby Bay)	306000	541000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1253	Dubmill Scar (Mawbray)	306000	544000	01/03/2002	1	5	Allen et al.	Allen et al., 2002
1254	Dubmill Point (Mawbray)	306000	545000	01/03/2002	1	5	Allen et al.	Allen et al., 2002
1255	Dubmill Point (Mawbray)	306000	545000	21/07/2012	1	6	Bush et al.	-
1256	Dubmill Point, N (Mawbray)	306000	546000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1257	Dubmill Point, N (Mawbray)	306000	546000	21/07/2012	1	5	Bush et al.	-
1258	Mawbray Scar (Mawbray)	306000	547000	00/00/1998	1	6	Lancaster	Allen et al., 2002
1259	Mawbray Scar (Mawbray)	306000	547000	00/00/1999	1	4	Lancaster	Allen et al., 2002
1260	Mawbray Scar (Mawbray)	306000	547000	02/08/2000	1	4	Lancaster	Allen et al., 2002
1261	Mawbray Scar (Mawbray)	306000	547000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1262	Ellisons Scar (Mawbray Bank, Mawbray)	306000	547000	21/07/2012	1	6	Bush et al.	-
1263	Grab samples C	306000	549000	01/07/2004	1	5	SNH Team	SNH
1264	Grab samples C	306000	549000	01-31/07/2005	1	5	SNH Team	SNH
1265	Budleigh Salterton	307000	81000	05/09/2002	0	0	Marclim Team	Marclim
1266	Otterton Ledge (Black Head to Otterton Ledge)	307000	81800	14/09/1992	1	10	Unknown	MNCR-JNCC

1267	Otterton Ledge (Black Head to Otterton Ledge)	307000	81800	05/09/2002	1	10	Marclim Team	Marclim
1268	Watchet	307000	143000	00/00/1976	1	3	Boyden	Cunningham et al., 1984
1269	Watchet	307000	143000	24/05/2013	0	0	Bush	-
1270	Site 179 (Upper Bristol Channel)	307000	149000	12/04/1988	1	10	Mettam	MNCR-JNCC
1271	Rhoose Point to Bullcliff Rocks	307000	165000	15/09/2004	1	10	CCW Team	SEWBRC
1272	Annaside Bank	307000	487000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1273	Coastguard Lookout (Selker Bay, Annaside Bank)	307000	488000	06/04/1989	1	5	Covey	MNCR-JNCC/ MBB
1274	Selker Bay (Annaside Bank)	307000	488000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1275	Tarn Point	307000	489000	03/08/2000	1	6	Hammond	CBDC/ MBB
1276	Tarn Bay	307000	489000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1277	Tarn Bay	307000	489000	22/07/2012	1	6	Bush et al.	-
1278	Tarn Bay	307000	490000	00/00/1984	1	7	Widdop	Cunningham et al., 1984/ DASSH (*)/MBB
1279	Ravenglass (Tarn Bay)	307000	490000	13/07/1991	1	5	Green/Covey	MNCR-JNCC/ MBB
1280	Tarn Bay, N	307000	490000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1281	Tarn Bay	307000	490000	20/03/2004	1	6	Frost et al.,	Frost et al., 2004
1282	Tarn Bay	307000	490000	22/07/2012	1	6	Bush et al.	-
1283	River Esk (Saltcoats, SW)	307000	495000	29/07/1999	1	6	Woombs	MNCR-EN/ MBB
1284	Allonby Bay	307000	541000	00/00/1970	1	6	Perkins	Cunningham et al., 1984
1285	Allonby Bay	307000	541000	00/00/1970	1	10	N.C.C.	DASSH (*)/MBB
1286	Allonby Bay	307000	541000	00/00/1974	1	6	Perkins	Cunningham et al., 1984
1287	Allonby Bay	307000	541000	00/00/1974	1	10	N.C.C.	DASSH (*)/MBB
1288	Allonby Bay	307000	541000	00/00/1978	1	5	Perkins	Cunningham et al., 1984
1289	Allonby Bay	307000	541000	00/00/1978	1	10	N.C.C.	DASSH (*)/MBB
1290	Blue Dial (Allonby Bay)	307000	541000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1291	Allonby Bay	307000	541000	21/07/2012	1	6	Bush et al.	-
1292	Allonby Bay	307000	542000	00/00/1970	1	6	Perkins	Allen et al., 2002
1293	Allonby Bay	307000	542000	00/00/1974	1	6	Perkins	Allen et al., 2002
1294	Allonby Bay	307000	542000	00/00/2000	1	6	Hammond	Allen et al., 2002
1295	Allonby (Allonby Bay)	307000	542000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1296	Allonby Bay	307000	542000	21/07/2012	1	6	Bush et al.	-
1297	North Lodge Scar (Allonby Bay)	307000	543000	00/00/1950	1	6	Hammond	Allen et al., 2002
1298	North Lodge Scar (Allonby Bay)	307000	543000	00/00/2000	1	5	Hammond	Allen et al., 2002
1299	Allonby, N (Allonby Bay)	307000	543000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1300	North Lodge Scar (Allonby Bay)	307000	543000	21/07/2012	1	6	Bush et al.	-
1301	Dubmill Scar (Mawbray)	307000	544000	01/03/2002	1	5	Allen et al.	Allen et al., 2002
1302	Dubmill Scar	307000	545000	00/00/1984	1	4	Cunningham	Cunningham et al., 1984/ DASSH (*)/MBB
1303	Dubmill Scar	307000	545000	10/08/1991	1	5	Ward	MNCR-JNCC/ MBB
1304	Dubmill Scar	307000	545000	00/00/1999	1	3	Allen et al.	Allen et al., 1999
1305	Dubmill Point (Mawbray)	307000	545000	03/07/2000	1	6	Tullie House Marine records	CBDC/ MBB
1306	Dubmill Point (Mawbray)	307000	545000	01/03/2002	1	5	Allen et al.	Allen et al., 2002

1307	Dubmill Scar	307000	545000	21/07/2012	1	6	Bush et al.	-
1308	Dubmill Point, N (Mawbray)	307000	546000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1309	Mawbray Bank (Mawbray)	307000	547000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1310	Mawbray Scar (Mawbray)	307000	547000	21/07/2012	1	6	Bush et al.	-
1311	Stinking Crag (Mawbray)	307000	548000	01/03/2002	1	4	Allen et al.	Allen et al., 2002
1312	Lowhagstock Crag, S (Beckfoot)	307000	549000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1313	Beckfoot	307000	549000	21/07/2012	1	4	Bush et al.	-
1314	Beckfoot	307000	550000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
1315	Lowhagstock Crag, N (Beckfoot)	307000	550000	01/03/2002	1	5	Allen et al.	Allen et al., 2002
1316	Beckfoot	307000	550000	21/07/2012	1	4	Bush et al.	-
1317	Grab samples C	307000	551000	01/07/2004	1	6	SNH Team	SNH
1318	Poolness Beach (Budleigh)	308000	83000	05/10/1994	1	7	Gilbert/CCW	MNCR-JNCC
1319	Brandy Head/Poolness Beach (Crab Ledge to Black Head, Otterton)	308000	83000	05/10/1994	1	3	Campline/CCW	MNCR-JNCC
1320	Site 333 (Upper Bristol Channel)	308000	155000	17/04/1988	1	10	Mettam	MNCR-JNCC
1321	Site 444 (Upper Bristol Channel)	308000	161000	26/04/1988	1	10	Mettam	MNCR-JNCC
1322	Annaside Bank	308000	485000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1323	Annaside Bank	308000	486000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1324	Annaside Bank	308000	486000	20/03/2004	1	6	Frost et al.,	Frost et al., 2004
1325	Annaside Bank	308000	486000	22/07/2012	1	6	Bush et al.	-
1326	Annaside Bank	308000	487000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1327	Beckfoot	308000	549000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1328	Crab Ledge (Otterton)	309000	84000	07/09/1994	1	6	Campline/CCW	MNCR-JNCC
1329	Smallstones Point (Otterton)	309000	84000	26/06/1994	1	6	Rostron	MNCR-JNCC
1330	Smallstones Point to Crab Ledge (Otterton)	309000	84000	07/09/1994	1	6	Campline/CCW	MNCR-JNCC
1331	Smallstones Point to Crab Ledge (Otterton)	309000	84000	20/06/2007	1	3	Evans	MarLIN (*)
1332	Ladram Bay (Otterton)	309000	85000	07/03/1992	1	3	Campline/CCW	MNCR-JNCC
1333	Hern Rock Bay (Otterton)	309000	85000	27/04/1994	1	7	Burton/CCW	MNCR-JNCC
1334	Doniford	309000	143000	00/00/1984	1	6	Crothers	Cunningham et al., 1984
1335	Hurlestone Point (Doniford)	309000	143000	07/10/2002	0	0	Marclim Team	Marclim
1336	Site 255 (Upper Bristol Channel)	309000	145000	15/04/1988	1	10	Mettam	MNCR-JNCC
1337	Annaside Bank	309000	484000	00/00/1984	1	6	Cunningham	Cunningham et al., 1984/ DASSH (*)/ MBB
1338	Gutterby Spa	309000	484000	06/04/1989	1	6	Smith	MNCR-JNCC/ MBB
1339	Gutterby Spa	309000	484000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1340	Annaside Bank	309000	484000	22/07/2012	1	6	Bush et al.	-
1341	St Audries Bay (Doniford)	310000	143000	00/00/1984	1	6	Crothers	Cunningham et al., 1984
1342	St Audries Bay (Doniford)	310000	143000	24/05/2013	1	5	Bush	-
1343	Site 276 (Upper Bristol Channel)	310000	146000	16/04/1988	1	10	Mettam	MNCR-JNCC
1344	Site 181 (Upper Bristol Channel)	310000	149000	12/04/1988	1	10	Mettam	MNCR-JNCC
1345	Site 329 (Upper Bristol Channel)	310000	152000	17/04/1988	1	10	Mettam	MNCR-JNCC
1346	Cold Knap Point to Barry Dock	310000	165000	14/09/2004	1	10	CCW Team	MIP1-CCW (*)

1347	Gutterby, S	310000	482000	01/03/2002	1	4	Allen et al.	Allen et al., 2002
1348	Gutterby	310000	483000	01/03/2002	1	4	Allen et al.	Allen et al., 2002
1349	Gutterby Spa (Annaside Bank)	310000	484000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1350	Silloth	310000	553000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
1351	Silloth	310000	553000	21/07/2012	0	0	Bush et al.	-
1352	Rough Scar	310000	563000	00/00/2000	1	10	Hammond	Allen et al., 2002
1353	Site 530 (Upper Bristol Channel)	311000	163000	28/04/1988	1	10	Mettam	MNCR-JNCC
1354	Site 29 (Upper Bristol Channel)	311000	164000	07/04/1988	1	10	Mettam	MNCR-JNCC
1355	Barry Island	311000	165000	14/03/2013	1	6	Bush	-
1356	Gutterby, S	311000	481000	01/03/2002	1	4	Allen et al.	Allen et al., 2002
1357	Gutterby, S	311000	482000	01/03/2002	1	4	Allen et al.	Allen et al., 2002
1358	Sidmouth (Jacobs Ladder)	312000	86000	00/00/1980	1	10	Boalch	Cunningham et al., 1984
1359	Sidmouth	312000	86000	14/01/1998	1	4	Hawkins	Hawkins notebooks
1360	Sidmouth	312000	86000	05/09/2002	1	6	Marclim Team	Marclim
1361	Chit Rocks (Sidmouth)	312000	87000	02/09/1992	1	3	Burton/CCW	MNCR-JNCC
1362	Site 257 (Upper Bristol Channel)	312000	145000	15/04/1988	1	10	Mettam	MNCR-JNCC
1363	Brewing Scar	312000	563000	00/00/1987	1	10	Allen et al.	Allen et al., 2002
1364	Priestdale Bank (Solway, N)	312000	564000	26/09/1994	1	6	Cutts/SNH	SNH
1365	Barry	313000	166000	00/00/1957	1	10	Purchon	Cunningham et al., 1984
1366	Barry	313000	166000	14/03/2013	1	5	Bush	-
1367	Barry Dock to Sully Island	313000	167000	10/09/2002	1	10	CCW Team	SEWBRC
1368	Kilve	314000	144000	00/00/1941	1	6	Bassindale	Cunningham et al., 1984
1369	Kilve	314000	144000	00/00/1976	1	6	Boyden	Cunningham et al., 1984
1370	Kilve	314000	144000	24/05/2013	0	0	Bush	-
1371	Barry Dock to Sully Island	314000	167000	27/08/2002	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
1372	Brow Scar	314000	559000	00/00/2000	1	4	Hammond	Allen et al., 2002
1373	Hook Ebb (Sidmouth)	315000	87000	23/08/1994	1	3	Campline/CCW	MNCR-JNCC
1374	Hook Ebb (Beer Head to Chit Rocks, Sidmouth)	315000	87000	23/08/1994	1	3	Burton/Campline/CCW	MNCR-JNCC
1375	Site 326 (Upper Bristol Channel)	315000	152000	17/04/1988	1	10	Mettam	MNCR-JNCC
1376	Site 338 (Upper Bristol Channel)	315000	155000	17/04/1988	1	10	Mettam	MNCR-JNCC
1377	Site 69 (Upper Bristol Channel)	315000	160000	08/04/1988	1	10	Mettam	MNCR-JNCC
1378	Barry Dock to Sully Island	315000	167000	10/09/2002	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
1379	Site 325 (Upper Bristol Channel)	316000	152000	17/04/1988	1	10	Mettam	MNCR-JNCC
1380	Sully Island	316000	166000	00/00/1957	1	10	Purchon	Cunningham et al., 1984
1381	Sully Island	316000	166000	00/00/1964	0	0	Crisp	Cunningham et al., 1984
1382	Sully Island	316000	166000	00/00/1973	1	3	Boyden	Cunningham et al., 1984
1383	Barry Dock to Sully Island	316000	166000	10/09/2002	1	10	CCW Team	SEWBRC
1384	Barry Dock to Sully Island	316000	166000	10/09/2002	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
1385	Sully Island	316000	166000	14/03/2013	1	5	Bush	-
1386	Sully Island	316000	166000	10/09/2002-12/11/2004	1	10	CCW Team	CCW
1387	Sully Island	316000	167000	24/10/1976	1	6	Mettam	SEWBRC

1388	Sully Island	316000	167000	24/10/1976	1	10	Mettam	SEWBRC
1389	Earnse Bay (Walney Island)	316000	469000	00/00/2002	1	4	Allen et al.	Allen et al., 2002
1390	Weston Ebb (Weston)	317000	87000	24/08/1994	1	5	Burton/Campline/CCW	MNCR-JNCC
1391	Weston Ebb (Beer Head to Chit Rocks, Weston)	317000	87000	24/08/1994	1	5	Burton/Campline/CCW	MNCR-JNCC
1392	Bent Haw Scar (Walney Island)	317000	466000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1393	Tummer Hill Scar (Walney Island)	317000	467000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1394	Earnse Bay (Walney Island)	317000	469000	16/02/2012	1	10	Wildlife Trusts Marine Shoresearch	MBB
1395	Earnse Bay (Walney Island)	317000	469000	16/02/2012	1	10	Wildlife Trusts Marine Shoresearch	MBB
1396	MurkleBay	317000	969000	25/05/2002	0	0	Marclim Team	Marclim
1397	Site 438 (Upper Bristol Channel)	318000	161000	26/04/1988	1	10	Mettam	MNCR-JNCC
1398	Lavernock Point	318000	167000	00/00/1976	1	5	Boyden	Cunningham et al., 1984
1399	Lavernock Point	318000	167000	00/00/1984	1	6	Cunningham	Cunningham et al., 1984
1400	Sully Island to Lavernock Point	318000	167000	10/09/2002	1	10	CCW Team	SEWBRC
1401	Lavernock Point	318000	167000	14/03/2013	1	6	Bush	-
1402	Lavernock Point to Cardiff Bay	318000	168000	27/08/2002	1	10	CCW Team	SEWBRC
1403	Lavernock Point to Cardiff Bay	318000	170000	27/08/2002	1	10	CCW Team	SEWBRC
1404	Hilbre Island	318000	387000	00/00/1919	1	6	Herdmann/University Marine Biological Station, Millport	Cunningham et al., 1984/ DASSHac (*)/MBB
1405	Hilbre Island	318000	387000	00/00/1940	0	0	MacMillan	Cunningham et al., 1984
1406	Hilbre Island	318000	387000	00/00/1979	1	2	Craggs	Cunningham et al., 1984/ DASSH (*)/ MBB
1407	Hilbre Island	318000	387000	00/00/1984	0	0	Craggs	Cunningham et al., 1984
1408	Hilbre Island	318000	387000	07/03/2004	1	6	Frost et al.,	Frost et al., 2004
1409	Hilbre Island	318000	387000	17/07/2005	1	6	Felton	MBB
1410	Hilbre Island	318000	387000	08/03/2006	1	10	Felton	MBB
1411	HilbreIsland, SW	318000	387000	23/07/2012	1	6	Bush et al.	-
1412	North Bay (Hilbre Island)	318000	388000	07/03/2004	1	6	Frost et al.,	Frost et al., 2004
1413	North Bay (Hilbre Island)	318000	388000	24/07/2012	1	6	Bush et al.	-
1414	Cross Dyke Scar (Walney Island)	318000	464000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1415	Bent Haw Scar (Walney Island)	318000	466000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1416	Branscombe Ebb	319000	87000	00/00/1964	1	5	Crisp	Cunningham et al., 1984
1417	Branscombe Ebb	319000	87000	00/00/1980	1	5	Hawkins	Cunningham et al., 1984
1418	Branscombe Ebb	319000	87000	25/08/1994	1	6	Burton/CCW	MNCR-JNCC
1419	Hinckley Point	319000	146000	26-30/07/1993	1	5	Martin	Martin, 1993
1420	Hinckley Point	319000	146000	26-30/07/1993	1	5	Martin	Sykes, 1996
1421	Hinckley Point	319000	146000	26-30/07/1993	1	5	Sykes	Sykes, 1996
1422	Lavernock Point to Cardiff Bay	319000	171000	27/08/2002	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC
1423	Lavernock Point to Cardiff Bay	319000	171000	27/04/2002	1	10	CCW Team	MIP1-CCW (*)/ SEWBRC

1424	South End Scar (Walney Island)	319000	462000	30/08/2007	1	6	Worsfold	Worsfold, Unicomarine
1425	South End Scar (Walney Island)	319000	462000	18/09/2007	1	6	Worsfold	Worsfold, Unicomarine
1426	Cross Dyke Scar (Walney Island)	319000	463000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1427	South End Scar (Walney Island)	319000	463000	18/09/2007	1	6	Worsfold	Worsfold, Unicomarine
1428	Cross Dyke Scar (Walney Island)	319000	464000	01/03/2002	1	6	Allen et al.	Allen et al., 2002
1429	Cross Dyke Scar (Walney Island)	319000	464000	22/07/2012	1	6	Bush et al.	-
1430	Branscombe	320000	87000	00/00/1964	1	5	Crisp	Cunningham et al., 1984
1431	Hinckley Point	320000	146000	00/00/1984	1	5	Bamber & Coughlan	Bamber & Irving, 1997
1432	Hinckley Point	320000	146000	00/00/1985	1	5	Bamber & Coughlan	Bamber & Irving, 1997
1433	Hinckley Point	320000	146000	00/02/1986	1	5	Bamber & Coughlan	Bamber & Irving, 1997
1434	Hinckley Point	320000	146000	00/04/1986	1	5	Bamber & Coughlan	Bamber & Irving, 1997
1435	Hinckley Point	320000	146000	00/06/1986	1	5	Bamber & Coughlan	Bamber & Irving, 1997
1436	Hinckley Point	320000	146000	00/07/1986	1	5	Bamber & Coughlan	Bamber & Irving, 1997
1437	Hinckley Point	320000	146000	00/08/1990	1	5	Bamber & Irving	Bamber & Irving, 1997
1438	Hinckley Point	320000	146000	00/09/1990	1	5	Bamber & Irving	Bamber & Irving, 1997
1439	Hinckley Point	320000	146000	00/10/1991	1	5	Bamber & Irving	Bamber & Irving, 1997
1440	Hinckley Point	320000	146000	00/12/1991	1	5	Bamber & Irving	Bamber & Irving, 1997
1441	Hinckley Point	320000	146000	21/01/1992	1	5	Bamber & Irving	Bamber & Irving, 1997
1442	Hinckley Point	320000	146000	18-19/02/1992	1	5	Bamber & Irving	Bamber & Irving, 1997
1443	Hinckley Point	320000	146000	00/11/1992	1	5	Bamber & Irving	Bamber & Irving, 1997
1444	Hinckley Point	320000	146000	00/12/1992	1	5	Bamber & Irving	Bamber & Irving, 1997
1445	Hinckley Point	320000	146000	00/03/1993	1	5	Bamber & Irving	Bamber & Irving, 1997
1446	Hinckley Point	320000	146000	26-30/07/1993	1	6	Martin	Martin, 1993
1447	Hinckley Point	320000	146000	26-30/07/1993	1	6	Martin	Sykes, 1996
1448	Hinckley Point	320000	146000	26-30/07/1993	1	6	Sykes	Sykes, 1996
1449	Site 64 (Upper Bristol Channel)	320000	163000	08/04/1988	1	10	Mettam	MNCR-JNCC
1450	Site 63 (Severn Estuary)	320000	164000	08/04/1988	1	10	Mettam	MNCR-JNCC
1451	Site 61 (Severn Estuary)	320000	167000	08/04/1988	1	10	Mettam	MNCR-JNCC
1452	Walney Island, S	320000	461000	22/07/2012	0	0	Bush et al.	-
1453	South End Scar (Walney Island)	320000	462000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1454	South End (Walney Island)	320000	463000	22/07/2012	1	6	Bush et al.	-
1455	Hinckley Point	321000	146000	00/00/1976	1	5	Boyden	Cunningham et al., 1984
1456	Hinckley Point	321000	146000	00/00/1982	1	4	Bamber	Cunningham et al., 1984
1457	Hinckley Point	321000	146000	00/00/1984	1	6	Bamber & Coughlan	Bamber & Irving, 1997
1458	Hinckley Point	321000	146000	00/00/1985	1	6	Bamber & Coughlan	Bamber & Irving, 1997
1459	Hinckley Point	321000	146000	00/02/1986	1	6	Bamber & Coughlan	Bamber & Irving, 1997
1460	Hinckley Point	321000	146000	00/04/1986	1	6	Bamber & Coughlan	Bamber & Irving, 1997
1461	Hinckley Point	321000	146000	00/06/1986	1	6	Bamber & Coughlan	Bamber & Irving, 1997
1462	Hinckley Point	321000	146000	00/07/1986	1	6	Bamber & Coughlan	Bamber & Irving, 1997
1463	Hinckley Point	321000	146000	00/08/1990	1	6	Bamber & Irving	Bamber & Irving, 1997

1464	Hinckley Point	321000	146000	00/09/1990	1	6	Bamber & Irving	Bamber & Irving, 1997
1465	Hinckley Point	321000	146000	00/10/1991	1	10	Bamber & Irving	Bamber & Irving, 1997
1466	Hinckley Point	321000	146000	00/12/1991	1	10	Bamber & Irving	Bamber & Irving, 1997
1467	Hinckley Point	321000	146000	21/01/1992	1	10	Bamber & Irving	Bamber & Irving, 1997
1468	Hinckley Point	321000	146000	18-19/02/1992	1	10	Bamber & Irving	Bamber & Irving, 1997
1469	Hinckley Point	321000	146000	00/11/1992	1	10	Bamber & Irving	Bamber & Irving, 1997
1470	Hinckley Point	321000	146000	00/12/1992	1	10	Bamber & Irving	Bamber & Irving, 1997
1471	Hinckley Point	321000	146000	00/03/1993	1	10	Bamber & Irving	Bamber & Irving, 1997
1472	Hinckley Point	321000	146000	26-30/07/1993	1	6	Martin	Martin, 1993
1473	Hinckley Point	321000	146000	00/00/1994	1	6	Martin	Sykes, 1996
1474	Hinckley Point	321000	146000	00/08/1996	1	6	Sykes	Sykes, 1996
1475	Site 289 (Upper Bristol Channel)	321000	147000	16/04/1988	1	10	Mettam	MNCR-JNCC
1476	Site 162 (Severn Estuary)	321000	161000	12/04/1988	1	10	Mettam	MNCR-JNCC
1477	Walney Island, S	321000	461000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
1478	Walney Island, S	321000	461000	00/00/1998	0	0	Worsfold	Worsfold, Unicomarine
1479	Hilpsford Scar (Walney Island, S)	321000	461000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1480	Hilpsford Scar (Walney Island, S)	321000	461000	19/03/2004	0	0	Frost et al.,	Frost et al., 2004
1481	Hilpsford Scar (Walney Island, S)	321000	461000	22/07/2012	0	0	Bush et al.	-
1482	Beer Head	322000	87000	00/00/1984	1	6	Hawkins	Cunningham et al., 1984
1483	Beer	322000	88000	00/00/1957	1	6	Boalch	Cunningham et al., 1984
1484	Beer	322000	88000	00/00/1970	1	6	Wilson	Wilson, 1971/Cunningham et al., 1984
1485	Beer	322000	88000	00/00/1977	1	6	N.C.C., I.S.U.	Cunningham et al., 1984/ MNCR-JNCC
1486	Big Ledge(Beer)	322000	88000	24/06/1994	1	3	Burton/Gilbert/CCW	MNCR-JNCC
1487	Site name protected	322000	160000	12/08/1995	1	10	Restricted access	BRERC
1488	Ynys Echni, Flat Holm (The Wolves and Monkstone Rock)	322000	164000	27/08/2002	1	10	CCW Team	SEWBRC
1489	Ynys Echni, Flat Holm (The Wolves and Monkstone Rock)	322000	165000	27/08/2002	1	10	CCW Team	SEWBRC
1490	Pickle Scar, N (Piel Channel, Morecombe Bay)	322000	464000	15/09/1998	1	5	Lumb	MNCR-EN/ MBB
1491	NW of Number 2 buoy, Piel Channel (Morecombe Bay)	322000	464000	17/09/1998	1	2	Woombs	MNCR-EN/MBB
1492	E of Pickle Scar Beacon, Piel Channel (Morecombe B	322000	464000	15/09/1998	1	4	Fletcher	MNCR-EN/MBB
1493	Head Scar Beacon, Piel Channel (Morecombe Bay)	322000	464000	15/09/1998	1	4	Brazier/CCW	MNCR-EN/MBB
1494	Head Scar (Piel Channel, Morecombe Bay)	322000	465000	26/09/1999	1	2	Haley	MNCR-EN/ MBB
1495	Head Scar (Barrow, Morecombe Bay)	322000	465000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1496	Beer	323000	88000	00/00/1954	1	6	Boalch	Boalch, 1957
1497	Beer	323000	88000	00/00/1955	1	6	Boalch	Boalch, 1957
1498	Beer	323000	88000	00/00/1957	1	6	Boalch	Wilson, 1971

1499	Beer	323000	88000	00/00/1970	1	6	Wilson	Wilson, 1971
1500	Beer	323000	88000	03/09/1992	1	4	King	MNCR-JNCC
1501	Seaton Hole	323000	89000	22/06/1994	1	2	Gilbert/CCW	MNCR-JNCC
1502	Gore Point (Stolford)	323000	146000	07/10/2002	0	0	Marclim Team	Marclim
1503	Unknown	323000	160000	00/00/1900	1	10	Unknown	BRERC
1504	Unknown	323000	160000	12/08/1995	1	10	Unknown	BRERC
1505	SE Point (Walney Island)	323000	461000	01/03/2002	1	4	Allen et al.	Allen et al., 2002
1506	Piel Island (Barrow, Morecombe Bay)	323000	463000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1507	Site 313 (Severn Estuary)	324000	165000	17/04/1988	1	10	Mettam	MNCR-JNCC
1508	Site 311 (Severn Estuary)	324000	168000	17/04/1988	1	10	Mettam	MNCR-JNCC
1509	Site 310 (Severn Estuary)	324000	170000	17/04/1988	1	10	Mettam	MNCR-JNCC
1510	Site 309 (Severn Estuary)	324000	171000	17/04/1988	1	10	Mettam	MNCR-JNCC
1511	Site 129 (Severn Estuary)	324000	173000	11/04/1988	1	10	Mettam	MNCR-JNCC
1512	Leasowe BW, W of Lighthouse (Wirral Foreshore)	324000	391000	00/00/2003	1	2	Frost et al.,	Frost et al., 2004
1513	Leasowe BW, W of Lighthouse (Wirral Foreshore)	324000	391000	24/07/2012	1	3	Bush et al.	-
1514	East Scar Buoy, N (Piel Channel, Morecombe Bay)	324000	462000	16/09/1999	1	2	Woombs	MNCR-EN/ MBB
1515	Piel East Buoy (Piel Channel, Morecombe Bay)	324000	463000	16/09/1999	1	3	Fletcher	MNCR-EN/ MBB
1516	SE of Castle Buoy (Morecombe Bay)	324000	463000	17/09/1999	1	2	Fletcher	MNCR-EN/ MBB
1517	Piel West Buoy, Pile Channel (Morecombe Bay)	324000	463000	17/09/1999	1	2	Fletcher	MNCR-EN/ MBB
1518	E of Ridge Buoy, Piel Channel (Morecombe Bay)	324000	463000	16/09/1999	1	3	Fletcher	MNCR-EN/ MBB
1519	Long Barrow Scar (Walney Island)	324000	464000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1520	Seaton	325000	89000	25/04/2002	0	0	Marclim Team	Marclim
1521	Sennen Cove (Seaton)	325000	89000	01/06/2003	0	0	Marclim Team	Marclim
1522	Leasowe Lighthouse (Wirral Foreshore)	325000	391000	24/07/2012	0	0	Bush et al.	-
1523	Elbow to Point of Comfort Scars (Morecombe Bay)	325000	463000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1524	Barren Point Scar (Foulney Island)	325000	464000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1525	Sparrowbush Ledge (Seaton)	326000	89000	22/09/1994	1	3	Lovett	MNCR-JNCC
1526	Sparrowbush Ledge (Seaton)	326000	89000	28/06/2002	1	10	Marclim Team	Marclim
1527	Site 378 (Severn Estuary)	326000	161000	19/04/1988	1	10	Mettam	MNCR-JNCC
1528	Site 376 (Severn Estuary)	326000	164000	19/04/1988	1	10	Mettam	MNCR-JNCC
1529	Site 373 (Severn Estuary)	326000	168000	19/04/1988	1	10	Mettam	MNCR-JNCC
1530	Site 130 (Severn Estuary)	326000	173000	11/04/1988	1	10	Mettam	MNCR-JNCC
1531	Site 308 (Severn Estuary)	326000	176000	17/04/1988	1	10	Mettam	MNCR-JNCC
1532	Leasowe BW, Mid (Wirral Foreshore)	326000	392000	00/00/2003	1	5	Frost et al.,	Frost et al., 2004
1533	Leasowe BW, Mid (Wirral Foreshore)	326000	392000	24/07/2012	1	5	Bush et al.	-
1534	High Bottom (Walney Island)	326000	464000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1535	Ulverston Sands	326000	467000	01/03/2002	0	0	Allen et al.	Allen et al., 2002

1536	Culverhole Point (Lyme Regis)	327000	89000	25/06/1994	1	6	Little	MNCR-JNCC
1537	Site 269 (Upper Bristol Channel)	327000	155000	16/04/1988	1	10	Mettam	MNCR-JNCC
1538	Site 385 (Severn Estuary)	327000	168000	19/04/1988	1	10	Mettam	MNCR-JNCC
1539	Site 131 (Severn Estuary)	327000	173000	11/04/1988	1	10	Mettam	MNCR-JNCC
1540	Leasowe BW, East (Wirral Foreshore)	327000	392000	24/07/2012	1	1	Bush et al.	-
1541	Site 380 (Severn Estuary)	328000	162000	19/04/1988	1	10	Mettam	MNCR-JNCC
1542	Kings Parade, W (Wirral Foreshore)	328000	393000	24/07/2012	1	5	Bush et al.	-
1543	Ulverston Sands	328000	471000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1544	Kirkcaldy (Fife)	328000	691000	00/00/1983	0	0	Williamson/FRPB	Cunningham et al., 1984
1545	Site 400 (Severn Estuary)	329000	170000	20/04/1988	1	10	Mettam	MNCR-JNCC
1546	Kings Parade, E (Wirral Foreshore)	329000	394000	00/00/2003	1	5	Frost et al.,	Frost et al., 2004
1547	Kings Parade, E (Wirral Foreshore)	329000	394000	24/07/2012	1	5	Bush et al.	-
1548	Birnbeck (Weston Super Mare)	330000	162000	00/00/1941	1	6	Bassindale	Cunningham et al., 1984
1549	Birnbeck (Weston Super Mare)	330000	162000	00/00/1984	1	4	Cunningham	Cunningham et al., 1984
1550	Birnbeck (Weston Super Mare)	330000	162000	28/05/2013	1	4	Bush	-
1551	Site 456 (Severn Estuary)	330000	165000	26/04/1988	1	10	Mettam	MNCR-JNCC
1552	Site 399 (Severn Estuary)	330000	170000	20/04/1988	1	10	Mettam	MNCR-JNCC
1553	N Brighton Lighthouse, W (Wirral Foreshore)	330000	394000	00/00/2003	0	0	Frost et al.,	Frost et al., 2004
1554	N Brighton Lighthouse, W (Wirral Foreshore)	330000	394000	24/07/2012	1	5	Bush et al.	-
1555	Blackpool Sea Wall	330000	432000	04/02/2012	1	2	Wildlife Trusts Marine Shoresearch	MBB
1556	Rossal Point (Fleetwood)	330000	447000	22/07/2012	1	4	Bush et al.	-
1557	Humble Point, E (Lyme Regis)	331000	90000	20/09/1994	1	5	Lovett	MNCR-JNCC
1558	Pinhay East (Beer Head to Burton Bradstock)	331000	90000	23/06/1994	1	3	Little	MNCR-JNCC
1559	Sand Point (Kewstoke)	331000	165000	00/00/1984	1	4	Cunningham	Cunningham et al., 1984
1560	Sand Point (Kewstoke)	331000	165000	28/05/2013	0	0	Bush	-
1561	Mersey, Mid Groyne	331000	392000	24/07/2012	0	0	Bush et al.	-
1562	Seaward Groyne (Mersey)	331000	393000	24/07/2012	1	4	Bush et al.	-
1563	N Brighton Lighthouse, E (Wirral Foreshore)	331000	394000	00/00/2003	1	5	Frost et al.,	Frost et al., 2004
1564	N Brighton Lighthouse, E (Wirral Foreshore)	331000	394000	24/07/2012	1	5	Bush et al.	-
1565	St Annes Pier	331000	428000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
1566	St Annes Pier	331000	428000	18/03/2004	0	0	Frost et al.,	Frost et al., 2004
1567	St Annes Pier	331000	428000	21/07/2012	0	0	Bush et al.	-
1568	Rossal Point (Fleetwood)	331000	447000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
1569	Rossal Point (Fleetwood)	331000	447000	18/03/2004	1	4	Frost et al.,	Frost et al., 2004
1570	Rossal Point (Fleetwood)	331000	447000	22/07/2012	0	0	Bush et al.	-
1571	WadheadScar	331000	474000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
1572	WadheadScar	331000	475000	19/03/2004	0	0	Frost et al.,	Frost et al., 2004
1573	Pinhay, W (Lyme Regis)	332000	90000	23/06/1994	1	7	Little	MNCR-JNCC

1574	Seven Rock Point	332000	90000	23/06/1994	1	2	Burton/CCW	MNCR-JNCC
1575	Lyme Regis	332000	90000	30/01/2002	0	0	Marclim Team	Marclim
1576	Lyme Regis	332000	90000	15/07/2003	1	4	Marclim Team	Marclim
1577	Site 538 (Severn Estuary)	332000	168000	28/04/1988	1	10	Mettam	MNCR-JNCC
1578	Site 398 (Severn Estuary)	332000	170000	20/04/1988	1	10	Mettam	MNCR-JNCC
1579	Mersey, River Groyne	332000	391000	24/07/2012	0	0	Bush et al.	-
1580	Lyme Regis	333000	91000	00/00/1964	0	0	Crisp	Cunningham et al., 1984
1581	Monmouth Beach (Lyme Regis)	333000	91000	00/00/1981	1	5	Hawthorn	Cunningham et al., 1984
1582	Lyme Regis	333000	91000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
1583	Devonshire Head (Lyme Regis)	333000	91000	27/05/1994	1	7	Rostron	MNCR-JNCC
1584	Devonshire Head (Lyme Regis)	333000	91000	30/04/2011-14/10/2011	1	10	Hughes	MarLIN (*)
1585	Middle Hope Cove (Kewstoke)	333000	166000	00/00/1984	1	4	Cunningham	Cunningham et al., 1984
1586	Middle Hope Cove (Kewstoke)	333000	166000	28/05/2013	1	5	Bush	-
1587	Gills Bay	333000	972000	24/05/2002	0	0	Marclim Team	Marclim
1588	Broad Ledges (Lyme Regis)	334000	92000	28/03/1994	1	3	Campline/CCW	MNCR-JNCC
1589	Broad Ledges (Lyme Regis)	334000	92000	27/05/1994	1	3	Campline/CCW	MNCR-JNCC
1590	Lyme Regis	334000	92000	09/06/1997	1	6	Hawkins	Hawkins notebooks
1591	Lyme Regis	334000	92000	15/04/1999	1	6	Hawkins	Hawkins notebooks
1592	Lyme Regis	334000	92000	15/06/2000	1	6	Hawkins	Hawkins notebooks
1593	Lyme Regis	334000	92000	26/04/2001	1	6	Hawkins	Hawkins notebooks
1594	Lyme Regis	334000	92000	25/04/2002	1	5	Marclim Team	Marclim
1595	Lyme Regis	334000	92000	01/06/2003	1	6	Marclim Team	Marclim
1596	Lyme Regis	334000	92000	08/05/2012	1	6	Hawkins	Hawkins notebooks
1597	Severn Estuary	334000	176000	00/00/1988	1	10	Mettam	DASSHcom(*)
1598	Bar Ledges (Lyme Regis)	335000	92000	26/05/1994	1	2	Little	MNCR-JNCC
1599	Charmouth	335000	92000	15/10/2008	1	10	Whiteley/Bridgwater College	MarLIN (*)
1600	Site 461 (Severn Estuary)	335000	167000	26/04/1988	1	10	Mettam	MNCR-JNCC
1601	Knott End On Sea (Fleetwood)	335000	449000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1602	Charmouth, N	336000	92000	09/08/1994	1	3	Strawbridge	MNCR-JNCC
1603	Site 376 and Site 412 (Severn Estuary)	336000	180000	19/04/1988	1	10	Mettam	MNCR-JNCC
1604	Site 26 (Severn Estuary)N	336000	181000	01/07/1980	1	10	Jones	MNCR-JNCC
1605	Lytham Pier	336000	426000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
1606	Lytham Pier	336000	426000	18/03/2004	0	0	Frost et al.,	Frost et al., 2004
1607	Lytham Pier	336000	426000	22/07/2012	0	0	Bush et al.	-
1608	Black Rocks (Clevedon)	338000	170000	23/05/2013	1	6	Bush	-
1609	North Head (Wick)	338000	950000	25/05/2002	0	0	Marclim Team	Marclim
1610	Foot Skear (Heysham Sands)	339000	462000	25/09/1999	1	6	Tullie House Marine records	CBDC/ MBB
1611	Knot End (Heysham Sands)	339000	462000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1612	Foot Skear (Heysham Sands)	339000	462000	00/00/2003	1	10	Frost et al.,	Frost et al., 2004
1613	Heysham Flats	339000	462000	30/08/2011	1	10	Haines	MBB

1614	Foot Skear (Heysham Sands)	339000	462000	14/08/2012	1	7	Bush	-
1615	Foot Skear (Heysham Sands)	339000	462000	28/08/2013	1	7	Bush	-
1616	Humphrey Head	339000	473000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
1617	Humphrey Head	339000	473000	19/03/2004	0	0	Frost et al.,	Frost et al., 2004
1618	Clevedon Village	340000	171000	23/05/2013	0	0	Bush	-
1619	Clevedon	340000	172000	00/00/1976	1	5	Boyden	Cunningham et al., 1984
1620	Clevedon	340000	172000	00/00/1984	1	3	Cunningham	Cunningham et al., 1984
1621	Clevedon	340000	172000	23/05/2013	0	0	Bush	-
1622	Foot Skear (Heysham Sands)	340000	460000	00/00/1959	1	3	Jones/N.C.C	Cunningham et al., 1984/DASSHac (*)/ MBB
1623	Foot Skear (Heysham Sands)	340000	460000	00/00/1960	1	4	Jones	Cunningham et al., 1984/DASSHac (*)/MBB
1624	Foot Skear (Heysham Sands)	340000	460000	00/00/1961	1	2	Jones	Cunningham et al., 1984/DASSHac (*)/ MBB
1625	Heysham Village	340000	460000	00/00/1984	0	0	Jones	Cunningham et al., 1984
1626	Heysham Village	340000	460000	21/03/2004	0	0	Frost et al.,	Frost et al., 2004
1627	Heysham Power Station	340000	460000	00/00/2012	1	5	Bush	-
1628	Foot Skear (Heysham Sands)	340000	461000	00/00/2012	1	6	Bush	-
1629	Foot Skear (Heysham Sands)	340000	461000	07/02/2012	1	4	Wildlife Trusts Marine Shoresearch	MBB
1630	Foot Skear (Heysham Sands)	340000	462000	00/00/1997	1	6	Allen et al.	Allen et al., 2002
1631	Foot Skear (Heysham Sands)	340000	462000	25/09/1999	1	6	Haley	MNCR-EN/ MBB
1632	Foot Skear (Heysham Sands)	340000	462000	01/03/2002	1	7	Allen et al.	Allen et al., 2002
1633	Heysham Flats	340000	462000	27/09/2011	1	10	Haines	MBB
1634	Heysham Flats	340000	462000	27/09/2011	1	10	Haines	MBB
1635	Heysham Flats	340000	462000	27/09/2011	1	10	Haines	MBB
1636	Heysham Flats	340000	462000	27/09/2011	1	10	Haines	MBB
1637	Heysham Flats	340000	462000	27/09/2011	1	10	Haines	MBB
1638	Heysham Flats	340000	462000	27/09/2011	1	10	Haines	MBB
1639	Heysham Flats	340000	462000	30/08/2011	1	10	Haines	MBB
1640	Heysham Flats	340000	462000	30/08/2011	1	10	Haines	MBB
1641	Heysham Flats	340000	462000	30/08/2011	1	10	Haines	MBB
1642	Heysham Flats	340000	462000	30/08/2011	1	10	Haines	MBB
1643	Heysham Flats	340000	462000	30/08/2011	1	10	Haines	MBB
1644	Heysham Flats	340000	462000	30/08/2011	1	10	Haines	MBB
1645	Heysham Flats	340000	462000	27/09/2011	1	10	Haines	MBB
1646	Heysham Flats	340000	462000	27/09/2011	1	10	Haines	MBB
1647	Heysham Flats	340000	462000	27/09/2011	1	10	Haines	MBB
1648	Heysham Flats	340000	462000	27/09/2011	1	10	Haines	MBB
1649	Heysham Flats	340000	462000	30/08/2011	1	10	Haines	MBB
1650	Foot Skear (Heysham Sands)	340000	462000	14/08/2012	1	6	Bush	-
1651	Foot Skear (Heysham Sands)	340000	462000	28/08/2013	1	6	Bush	-
1652	Foot Skear, N (Heysham Sands)	340000	463000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1653	Cockenzie (Edinburgh)	340000	675000	00/00/1983	0	0	Williamson/FRPB	Cunningham et al., 1984
1654	Foot Skear Inshore (Heysham Sands)	341000	462000	14/08/2012	0	0	Bush	-
1655	Foot Skear Inshore (Heysham Sands)	341000	462000	28/08/2013	0	0	Bush	-

1656	Foot Skear Inshore (Heysham Sands)	341000	463000	28/11/1997	1	5	Haley	MNCR-EN/ MBB
1657	Foot Skear Inshore (Heysham Sands)	341000	463000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1658	Foot Skear Inshore (Heysham Sands)	341000	463000	14/08/2012	1	5	Bush	-
1659	Foot Skear Inshore (Heysham Sands)	341000	463000	28/08/2013	0	0	Bush	-
1660	Plover Scar (Mouth of the River Lune)	342000	454000	00/00/2002	0	0	Allen et al.	Allen et al., 2002
1661	Holme Island (Grange)	342000	478000	00/00/1984	0	0	Cunningham	Cunningham et al., 1984
1662	Holme Island (Grange)	342000	478000	19/03/2004	0	0	Frost et al.,	Frost et al., 2004
1663	Portishead	343000	175000	23/05/2013	1	6	Bush	-
1664	Portishead	344000	176000	23/05/2013	0	0	Bush	-
1665	Morecambe Scar, N	344000	465000	01/03/2002	0	0	Allen et al.	Allen et al., 2002
1666	West Bay (Bridport)	345000	90000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
1667	West Bay	345000	90000	25/04/2002	0	0	Marclim Team	Marclim
1668	Portishead	346000	177000	00/00/1924	1	5	Matthews	Cunningham et al., 1984
1669	Portishead	346000	177000	00/00/1939	0	0	Purchon	Wilson, 1971/Cunningham et al., 1984
1670	Portishead	346000	177000	00/00/1941	0	0	Bassindale	Cunningham et al., 1984, Wilson, 1971
1671	Portishead	346000	177000	00/00/1974	1	6	Boyden	Cunningham et al., 1984
1672	Portishead	346000	177000	00/00/1984	1	3	Wilson/Cunningham	Wilson, 1971/Cunningham et al., 1984
1673	Portishead	346000	177000	23/05/2013	0	0	Bush	-
1674	Saint Andrews	350000	717000	00/00/1984	0	0	Todd	Cunningham et al., 1984
1675	Cullen	350000	867000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
1676	English Stones (Severn Estuary)	351000	186000	23/07/1997	1	7	Hiscock	MNCR-JNCC
1677	N Berwick	351000	686000	00/00/1983	0	0	Williamson/FRPB	Cunningham et al., 1984
1678	Chapel Rock (Severn Estuary, ST)	354000	189000	22/07/1997	1	2	Northen	MNCR-JNCC
1679	Aust Rocks (Severn Estuary, ST)	356000	190000	21/07/1997	1	6	Pollack	MNCR-JNCC
1680	Portland Bill	367000	68000	00/00/1980	0	0	Hawkins	Cunningham et al., 1984
1681	Portland Bill	367000	68000	00/00/1981	0	0	Hawkins	Cunningham et al., 1984
1682	Portland Bill	367000	68000	00/00/1982	0	0	Hawkins	Cunningham et al., 1984
1683	Portland Bill	367000	68000	00/00/1983	0	0	Hawkins	Cunningham et al., 1984
1684	Portland	367000	68000	26/07/2002	0	0	Marclim Team	Marclim
1685	Clay Ope Cave	368000	72000	05/11/2002	0	0	Marclim Team	Marclim
1686	Dunbar	368000	678000	00/00/1983	0	0	Williamson/FRPB	Cunningham et al., 1984
1687	Osmington	371000	81000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
1688	Barns Ness (Eyemouth)	372000	677000	00/00/1983	0	0	Williamson/FRPB	Cunningham et al., 1984
1689	Osmington Mills	373000	81000	26/04/2002	0	0	Marclim Team	Marclim
1690	Osmington Mills	373000	81000	14/07/2003	0	0	Marclim Team	Marclim
1691	Johnshaven	379000	766000	20/07/2003	0	0	Marclim Team	Marclim
1692	Lulworth Cove	382000	79000	26/04/2002	1	2	Marclim Team	Marclim
1693	Pennan	384000	865000	00/00/1980	0	0	N.C.C., I.S.U.	Cunningham et al., 1984
1694	Stonehaven	388000	786000	20/07/2003	0	0	Marclim Team	Marclim
1695	Kimmeridge	390000	79000	00/00/1977	1	10	Hawthorn	Cunningham et al., 1984
1696	Kimmeridge	390000	79000	27/04/2002	0	0	Marclim Team	Marclim
1697	Kimmeridge	390000	79000	10/05/2013	0	0	PMWR Wardens	MarLIN (*)
1698	Cove Bay	395000	800000	20/07/2003	0	0	Marclim Team	Marclim

1699	Aberdeen area	395000	808000	00/00/1981	0	0	Rafaelli	Cunningham et al., 1984
1700	Aberdeen area	395000	808000	00/00/1982	0	0	Rafaelli	Cunningham et al., 1984
1701	Aberdeen area	395000	808000	00/00/1983	0	0	Rafaelli	Cunningham et al., 1984
1702	Aberdeen area	395000	808000	00/00/1984	0	0	Rafaelli	Cunningham et al., 1984
1703	Swanage	403000	77000	00/00/1984	0	0	Hawkins	Cunningham et al., 1984
1704	Colliston	404000	828000	18/07/2003	0	0	Marclim Team	Marclim
1705	Cruden Bay	409000	835000	18/07/2003	0	0	Marclim Team	Marclim
1706	Craster	425000	620000	00/00/1992	1	10	Holt	Marine Recorder
1707	GreymareRock	425000	622000	00/00/1992	1	10	Holt	DASSHcom(*)
1708	Alum Bay	430000	85000	27/04/2002	0	0	Marclim Team	Marclim
1709	Bembridge	465000	87000	28/04/2002	0	0	Marclim Team	Marclim
1710	Seaford	549000	97000	11/04/2003	0	0	Marclim Team	Marclim
1711	Shakespeare Cliff (Kent)	627000	138000	11/02/1986	1	3	George	MNCR-JNCC
1712	Dover, proposed reclamation area (Kent)	629000	133000	13/05/1986	1	10	Unknown	MNCR-JNCC
1713	Central Area, Folkestone Warren SSSI (Kent)	629000	139000	13/05/1986	1	10	Unknown	MNCR-JNCC

Appendix 2.3: Collated *Sabellaria alveolata* presence and abundance data from suitable sites, from the 1970s to the 2010s (n = 1303). Location data includes site name, OSGB coordinates, reported sampling date (dd/mm/yy with unknown values represented by 00). Presence is reported as either present (1) or absent (0). Abundance is reported on the SACFOR scale where Superabundant (7) to Rare (2). Additional categories include just presence with no associated abundance data (10), Remains (1) and Not Seen (0).

ID	**Site name**	**Eastin-gs**	**Northin-gs**	**Date**	**Prese-nce**	**Abun-dance**
2	Tresco	88000	16000	00/00/1973	1	3
34	Trevellas	172000	52000	00/00/1979	1	10
44	Abereiddy	179000	231000	00/00/1984	1	2
45	Abereiddy	179000	231000	22/08/2002	0	0
46	Abereiddy, N	179000	231000	05/07/2012	0	0
54	Gann Flats	181000	206000	27/04/ - 08/10/1998	1	10
79	Newtrain Bay (Trevone)	188000	75000	11/04/2002	0	0
80	Trevone	188000	75000	27/05/2013	0	0
89	Harbour Cove (Padstow)	192000	76000	00/00/1970	1	1
90	Harbour Cove, S (Padstow)	192000	76000	27/05/2013	0	0
91	Sites 5 and 6	192000	203000	13/12/1994	1	10
94	Castle Point to Fishguard Breakwater	194000	237000	25/04/2001	1	10
95	Castle Point to Fishguard Breakwater	194000	237000	16/07/2003	1	10
96	Castle Point to Fishguard Breakwater	195000	237000	25/04/2001	1	10
98	Port Quin Harbour	196000	80000	00/00/1970	1	3
99	Port Quin	196000	80000	27/05/2013	0	0
100	The Wash to Long Matthew Point	196000	192000	22/05/2001	1	10
101	St Govans Chapel	196000	192000	24/08/2002	0	0
106	Dinas Head to Castle Point	199000	238000	29/04/2003	1	10
110	Dinas Head to Castle Point	200000	239000	29/04/2003	1	10
111	Freshwater East	201000	197000	31/07/2000	1	10
112	Cwm yr Eglwys, E (Newport)	201000	240000	15/05/1976	1	3
113	Cwm yr Eglwys	201000	240000	05/07/2012	1	4
116	Tregardock Beach	203000	83000	00/00/1970	1	3
117	Tregardock Beach	203000	83000	26/05/2013	1	3
118	Tregardock Beach	203000	84000	26/05/2013	1	3
125	Trebarwith Strand	204000	86000	00/00/1984	0	0
126	Trebarwith Strand	204000	86000	26/05/2013	1	2
127	Parrog	204000	239000	00/00/1984	1	4
128	Parrog to Cwm yr Eglwys	204000	239000	16/05/2003	1	10
129	Parrog	204000	239000	05/07/2012	0	0
130	Parrog	204000	239000	18/02/2014	0	0
136	Newport Sands (Ceibwr Bay toPan y Bal)	205000	241000	10/05/2001	1	10
137	Ceibwr Bay to Peny Bal	205000	241000	06/07/2004	1	10
142	Boscastle	208000	91000	26/05/2013	1	2
144	Priests Nose to Lydstep Point	208000	197000	06/08/1997	1	10
147	Polkerris	209000	52000	29/03/2002	1	5
150	Ceibwr Bay (Cardigan)	210000	245000	23/06/1997	1	5
151	Sandhead	210000	549000	00/00/2000	1	5
152	Sandhead	210000	549000	24/07/2014	1	3
154	Cardigan Bay SAC	211000	245000	26/07/2002	1	5
155	Logan Mills (Solway, N)	211000	543000	15/09/1989	1	3
156	Logan Mills (Solway, N)	211000	543000	00/00/2000	1	5
157	Logan Mills (Solway, N)	211000	543000	25/07/2014	1	4
159	Tripods (2m trawl)	212000	328000	27/07/2001	1	10
160	Terally Point	212000	540000	00/00/2000	1	5
161	Terally Point	212000	540000	25/07/2014	1	4
163	Crackington Haven	213000	96000	01/05/2003	0	0
164	Crackington Haven, SW	213000	96000	26/05/2013	1	4
165	Crackington Haven, N	213000	97000	00/00/1984	1	3
166	Crackington Haven, N	213000	97000	26/05/2013	1	4
167	Tenby	213000	200000	00/00/1984	0	0
168	Overhangs (Saint Catherines)	213000	200000	17/09/2008	1	10
169	Tenby	213000	200000	28/04/2013	0	0
170	Overhangs (Waterwynch)	213000	201000	16/09/2008	1	10
171	Cardigan Bay SAC	213000	249000	25/07/2002	1	6
172	Crackington Haven	214000	96000	26/05/2013	1	4
173	Monkstone Point (Saundersfoot)	214000	203000	00/00/1984	0	0
174	Monkstone Point (Saundersfoot)	214000	203000	28/04/2013	1	2
175	Teifi Estuary to Ceibwr Bay	214000	249000	18/07/1996	1	10

176	East Tarbert	214000	530000	00/00/2000	1	4
177	East Tarbert	214000	530000	24/07/2014	1	2
178	Portankill	214000	532000	00/00/2000	1	4
179	Maryport Bay	214000	534000	00/00/2000	1	10
183	Monkstone Point (Saundersfoot)	215000	203000	24/08/2002	0	0
184	Overhangs (Monkstone Point)	215000	203000	18/09/2008	1	10
185	Monkstone Point (Saundersfoot)	215000	203000	28/04/2013	1	2
187	Gwbert	215000	250000	00/00/2002	1	5
188	Cardigan Bay SAC	215000	251000	25/07/2002	1	4
189	Mull of Galloway	215000	530000	00/00/2000	1	4
190	Mull of Galloway	215000	530000	24/07/2014	1	2
192	Cardigan Island Sound (cave, Cardigan)	216000	251000	24/09/1996	1	7
193	Aberdaron	216000	326000	13/08/2003	1	2
199	N Target Base (Luce Sands)	216000	554000	00/00/2000	1	4
209	Millook	218000	100000	00/00/1975	1	10
210	Millook	218000	100000	00/00/1984	1	7
211	Millook	218000	100000	00/00/2012	1	6
214	Black Rock (Widemouth Bay)	219000	101000	00/00/1986	1	6
215	Black Rock (Widemouth Bay)	219000	101000	01/05/2003	0	0
216	Black Rock (Widemouth Bay)	219000	101000	25/05/2013	1	5
217	Widemouth Bay	219000	102000	00/00/1970	1	3
218	Widemouth Bay	219000	102000	01/05/2003	0	0
219	Widemouth Bay	219000	102000	25/05/2013	1	6
220	BudeW	219000	106000	25/05/2013	1	6
221	Bude	219000	107000	18/04/2003	1	6
222	Flexbury (Bude)	219000	107000	25/05/2013	1	6
223	Duckpool (Coombe)	219000	111000	30/05/1961-23/11/1961	1	10
224	Duckpool (Coombe)	219000	111000	07/02-12/12/1962	1	7
225	Duckpool (Coombe)	219000	111000	25/02-01/12/1963	1	10
229	Duckpool (Coombe)	219000	111000	28/01-03/12/1967	1	10
232	Duckpool (Coombe)	219000	111000	11/03-13/11/1970	1	10
233	Duckpool (Coombe)	219000	111000	29/01-02/12/1971	1	10
234	Duckpool (Coombe)	219000	111000	02/01-22/12/1972	1	10
235	Duckpool (Coombe)	219000	111000	04/05/1973	1	10
236	Duckpool (Coombe)	219000	111000	00/00/1975	1	7
237	Duckpool (Coombe)	219000	111000	00/00/1977	1	10
238	Duckpool (Coombe)	219000	111000	00/00/1978	1	10
239	Duckpool (Coombe)	219000	111000	00/00/1984	1	7
240	Duckpool (Coombe)	219000	111000	16/04/1992	1	6
241	Duckpool (Coombe)	219000	111000	11/08/1996	1	5
242	Duckpool (Coombe)	219000	111000	10/08/1998	1	6
243	Duckpool (Coombe)	219000	111000	31/07/1999	1	6
244	Duckpool (Coombe)	219000	111000	28/08/2000	1	6
245	Duckpool (Coombe)	219000	111000	22/09/2001	1	6
246	Duckpool (Coombe)	219000	111000	15/05/2002	1	6
247	Duckpool (Coombe)	219000	111000	12/09/2003	1	10
248	Duckpool (Coombe)	219000	111000	25/05/2013	1	7
257	Bude	220000	106000	00/00/1977	1	10
258	Bude	220000	106000	00/00/1980	1	6
259	Bude	220000	106000	20/04/1997	1	4
260	Bude	220000	106000	20/05/2000	1	6
261	Bude	220000	106000	16/04/2001	1	6
262	Bude	220000	106000	24/03/2012	1	7
263	Bude	220000	106000	25/05/2013	1	6
264	Welcombe Mouth to Longpeak	220000	117000	00/00/1992	1	10
265	Crows Nest	220000	553000	17/06/1991	1	4
266	N of Crows Nest and Burn	220000	553000	16/06/2007	1	6
267	Luce Bay, E	220000	553000	20/07/2012	1	1
268	Luce Sands	220000	554000	20/07/2012	1	1
270	Welcombe Mouth	221000	117000	30/04/2002	1	6
271	Welcombe Mouth	221000	117000	30/04/2003	1	5
272	Welcombe Mouth (Longpeak - Marsland Mouth)	221000	118000	04/04/1992	1	10
279	Speke Mill Mouth (Stoke)	222000	123000	20/04/1992	1	7
280	Hartland Quay	222000	124000	00/00/1977	1	10
281	Hartland Quay	222000	124000	00/00/1984	1	7
282	Hartland Quay	222000	124000	03/04/1993	1	10
283	Hartland Quay	222000	124000	18/04/1999	1	6

284	Hartland Quay	222000	124000	13/02/2002	1	6
285	Hartland Quay	222000	124000	19/04/2003	1	2
286	Hartland Quay	222000	124000	24/03/2012	1	3
287	Hartland Quay	222000	124000	25/05/2013	1	6
288	Hartland Quay	222000	125000	24/03/2012	1	6
289	Hartland Quay, N	222000	125000	26/05/2013	1	6
290	Mull of Sinniness	222000	551000	00/00/2000	1	4
293	Auchenmalg Bay	223000	551000	00/00/1984	1	6
294	Cock Inn	223000	551000	15/09/1989	1	2
295	Auchenmalg Bay	223000	551000	00/00/2000	1	6
296	Cock Inn	223000	551000	18/06/2007	1	7
297	Auchenmalg Bay, SE	223000	551000	20/07/2012	1	6
298	Cock Inn	223000	551000	10/07/2012	1	10
299	Shipload Bay (Titchberry)	224000	127000	15/09/1992	1	3
303	Glenalmar House	224000	551000	17/06/2007	1	7
304	Glenalmar House	224000	551000	07/08/2012	1	10
310	Aberporth	225000	251000	00/00/1984	1	7
311	Traeth Penbryn to Craigy Gwbert	225000	251000	04/06/1996	1	10
312	Aberporth, E	225000	251000	22/06/1997	1	6
313	Aberporth	225000	251000	21/08/2002	1	6
314	Aberporth	225000	251000	03/09/2004	1	5
315	Aberporth	225000	251000	00/00/2005	1	6
316	Aberporth	225000	251000	00/00/2006	1	5
317	Aberporth	225000	251000	16/05/2007	1	10
318	Aberporth	225000	251000	07/05/2008	1	10
319	Aberporth	225000	251000	05/07/2012	1	5
320	Aberporth	225000	251000	18/02/2014	1	5
328	Craignarget, E (Solway, N)	225000	550000	13/07/2012	1	10
329	Craignarget, E (Solway, N)	225000	551000	10/07/2012	1	10
333	Aberporth	226000	251000	21/08/2002	1	6
334	Garheugh Port (Solway, N)	226000	549000	11/07/2012	1	10
335	Garheugh Port, NW	226000	550000	20/06/2007	1	6
336	Garheugh Port, NW	226000	550000	11/07/2012	1	10
337	Tresaith, Treath Penbryn (Aberporth)	227000	251000	16/05/1996	1	10
338	Tresaith, Treath Penbryn (Aberporth)	227000	251000	21/06/1997	1	3
339	Tresaith	227000	251000	03/09/2004	1	5
341	Porth Dinllaen	227000	341000	11/06/2002	0	0
342	Porth Dinllaen	227000	341000	13/04/2013	1	2
346	Penrhyn Bodeilas to Penrhyn Nefyn	229000	341000	18/05/2004	1	10
347	Llangrannog	230000	254000	05/07/2012	1	4
349	House South of road to Changue	230000	546000	19/06/2007	1	6
351	Clovelly	231000	124000	22/09/2002	1	10
352	Clovelly Pier	231000	124000	26/05/2013	1	4
353	Llangranog, Clarach to Aberystwyth Harbou	231000	254000	00/00/1984	1	10
354	Llangrannog	231000	254000	05/07/2012	1	4
355	Llangrannog	231000	254000	18/02/2014	1	5
356	NE Ynys Lochtyn	231000	255000	12/06/1995	1	2
357	Abersoch	231000	328000	00/00/2003	0	0
358	Abersoch	231000	328000	00/00/2004	0	0
359	Abersoch Lifeboat Station	231000	328000	00/00/2009	1	3
360	Abersoch	231000	328000	00/00/2010	0	0
361	Abersoch Lifeboat Station	231000	328000	00/00/2011	0	0
362	Abersoch Lifeboat Station	231000	328000	00/00/2012	0	0
363	Abersoch Lifeboat Station	231000	328000	00/00/2013	0	0
364	Abersoch	231000	328000	00/00/2013	0	0
365	Rhosneigr	231000	372000	00/00/1983	0	0
366	Rhosneigr	231000	372000	14/06/2002	0	0
367	Rhosneigr	231000	372000	00/00/2005	0	0
368	Rhosneigr	231000	372000	00/00/2006	1	2
369	Rhosneigr	231000	372000	00/00/2007	0	0
370	Rhosneigr	231000	372000	00/00/2008	1	5
371	Rhosneigr	231000	372000	00/00/2009	1	2
372	Rhosneigr	231000	372000	00/00/2010	0	0
373	Rhosneigr	231000	372000	00/00/2011	0	0
374	Rhosneigr	231000	372000	02/08/2012	0	0
375	Rhosneigr	231000	372000	00/00/2012	0	0
376	Rhosneigr	231000	372000	13/04/2013	0	0
379	Clovelly	232000	124000	00/00/1983	1	5
380	Clovelly	232000	124000	26/05/2013	1	4

381	Cei Newydd to Traeth Penbryn	232000	255000	17/07/1996	1	10
382	Philip and Mary	232000	545000	18/06/2007	1	6
383	Philip and Mary	232000	545000	11/07/2012	1	10
385	Llanbedrog (Pwllheli)	233000	331000	01/07/1995	1	3
386	Llanbedrog (Pwllheli)	233000	331000	06/06/1996	1	10
387	Llanbedrog	233000	331000	14/08/2003	0	0
388	Porth Cwyfan (Rhosneigr)	233000	368000	31/07/1996	1	3
389	Aberffraw	233000	368000	13/04/2013	0	0
394	Bucks Mills	235000	123000	00/00/1984	1	5
395	Bucks Mills	235000	123000	24/04/1993	1	6
396	Bucks Mills	235000	123000	25/05/2013	1	6
397	Cwmtudu Headland	235000	257000	00/00/1982	1	6
398	Cwmtudu Headland	235000	257000	21/06/1997	1	2
399	Cwmtudu Headland	235000	257000	05/07/2012	1	5
400	Cwmtudu Headland	235000	257000	18/02/2014	1	5
401	Traeth Aberffraw to Dinas Lwyd	236000	365000	11/06/1999	1	10
402	Back Bay	236000	539000	00/00/2000	1	4
403	Monreith Bay	236000	540000	00/00/2000	1	5
408	Peppercombe	238000	124000	08/05/1993	1	6
409	Target Rocks, Carreg Wall to g…	238000	260000	12/06/1995	1	4
410	NewQuay	238000	260000	28/06/2002	1	6
411	Target Rocks, Carreg Wall to g…	238000	260000	01/05/2013	1	5
414	Worms Head	239000	186000	18/09/2001	1	10
415	Worms Head	239000	186000	02/06/2004	1	10
416	Worms Head	239000	186000	15/03/2013	1	5
417	Worms Head	239000	187000	00/00/1973	1	10
418	Worms Head	239000	187000	00/10/1978	1	10
419	Worms Head	239000	187000	18/09/2001	1	10
420	Worms Head	239000	187000	15/03/2013	1	5
421	Greencliff (Abbotsham)	240000	127000	15/11/1993	1	6
422	Greencliff (Abbotsham)	240000	127000	27/09/2007	1	10
423	Greencliff (Abbotsham)	240000	127000	17/09/2008	1	10
424	Greencliff (Abbotsham)	240000	127000	14/07-14/09/2010	1	10
425	Greencliff (Abbotsham)	240000	127000	14/06/2011	1	10
427	Cei Bach	240000	259000	01/09/2004	1	10
428	Cei Bach	240000	259000	18/05/2007	1	10
429	Cei Bach	240000	259000	07/05/2009	1	10
430	Cei Bach	240000	259000	26/04/2010	1	10
431	Cei Bach	240000	260000	01/09/2004	1	5
432	Cei Bach	240000	260000	17-18/05/2007	1	10
433	Cei Bach	240000	260000	05/05/2008	1	10
434	Cei Bach	240000	260000	07/05/2009	1	10
435	Cei Bach	240000	260000	26/04/2010	1	10
437	Abbotsham	241000	127000	06/07/2008	1	10
438	Abbotsham	241000	127000	25/06-18/09/2009	1	10
439	Abbotsham	241000	127000	14/06/2011	1	10
440	Abbotsham	241000	127000	18/09/2013	1	10
441	Aberdesach, SW (Trefor)	241000	350000	29/06/1995	1	2
442	Aberdesach	241000	350000	14/04/2013	0	0
445	Whitsand Bay (Millbrook)	242000	49000	00/00/1970	0	0
446	Westward Ho	242000	129000	00/00/1977	1	10
447	Westward Ho	242000	129000	00/00/1984	1	5
448	Westward Ho	242000	129000	19/05/1988	1	5
449	Westward Ho, W	242000	129000	25/05/2013	1	3
450	Downend (Croyde, Taw Torridge Estuary)	242000	138000	19/05/1988	1	10
451	Tears Point to Port Eynon Point	242000	186000	06/09/2001	1	10
452	Tears Point to Port Eynon Point	242000	186000	06/07/2004	1	10
453	Craig Ddu (Aberaeron)	242000	260000	02/09/2004	1	5
454	Craig Ddu (Aberaeron)	242000	261000	02/09/2004	1	5
457	Cawsands S (Devil's Point to Penlee Point)	243000	50000	15/09/1993	1	2
458	Westward Ho	243000	129000	25/05/2013	1	2
459	Downend (Croyde, S)	243000	138000	00/00/1977	1	10
460	Downend (Croyde, S)	243000	138000	00/00/1978	1	5
461	Downend (Croyde, S)	243000	138000	00/00/1983	1	4
462	Downend (Croyde, S)	243000	138000	24/05/2013	1	6
463	Croyde	243000	139000	16/06/1977	1	10
464	Croyde	243000	139000	18/06/2004	1	10
465	Croyde	243000	139000	24/05/2013	1	6
466	Paviland Cliff	243000	185000	00/00/1973	1	10

467	Paviland Cliff	243000	185000	00/10/1978	1	10
468	Paviland Cliff	243000	185000	13/03/2013	1	3
469	Tears Point to Port Eynon Point	243000	186000	06/08/2001	1	10
470	Tears Point to Port Eynon Point	243000	186000	06/07/2004	1	10
471	Tears Point to Port Eynon Point	243000	261000	13/05/1996	1	10
472	SW of Gilfach yr Halen (Aberaeron)	243000	261000	09/04/1997	1	6
473	SW of Gilfach yr Halen (Aberaeron)	243000	261000	02/09/2004	1	10
474	Penychain (Pwllheli)	243000	335000	01/07/1995	1	2
475	Porth Fechan and Rhosneigr (W of Afon Wen)	243000	335000	31/07/1996	1	3
476	Porth Fechan and Rhosneigr (W of Afon Wen)	243000	335000	05/07/2004	1	10
477	Porth Fechan and Rhosneigr (W of Afon Wen)	243000	335000	06/08/2005	1	10
478	Traeth Afon Wen	243000	336000	02/07/1996	1	10
480	Cawsand Bay	244000	51000	00/00/1984	0	0
481	Barricane Beach, S (Morte Point to Woolacombe)	244000	145000	00/00/1992	1	10
482	Barricane Beach, S (Morte Point to Woolacombe)	244000	145000	00/00/1995	1	10
483	Tears Point to Port Eynon Point	244000	185000	06/08/2001	1	10
484	Tears Point to Port Eynon Point	244000	185000	06/07/2004	1	10
485	Craig Ddu (Aberaeron)	244000	261000	02/09/2004	1	5
486	Aberaeron, S	244000	262000	09/04/1997	1	4
487	Craig Ddu (Aberaeron)	244000	262000	02/09/2004	1	5
488	Afon Wen	244000	336000	03/07/2012	1	5
490	Afon Wen	244000	337000	00/00/1984	1	6
491	Afon Wen	244000	337000	03/07/2012	0	0
493	West Crow Ridge (Braunton)	245000	132000	15/05/1988	1	4
494	Woolacombe	245000	143000	00/00/1983	1	3
495	Woolacombe	245000	143000	18/11/2001	1	2
496	Barricane Beach (Woolacombe, N)	245000	144000	08/10/1994	1	3
497	Rockham Bay (Bull Point to Morte Point)	245000	146000	19/03/1992	1	10
498	Overton	245000	184000	00/00/1973	1	10
499	Overton	245000	184000	13/03/2013	1	3
501	Aberaeron	245000	263000	09/04/1997	1	4
502	Aberaeron	245000	263000	07/08/2002	0	0
503	Aberaeron	245000	263000	02/09/2004	1	10
504	Aberaeron	245000	263000	15/05/2007	1	10
505	Aberaeron	245000	263000	06/05/2008	1	10
506	Aberaeron	245000	263000	06/05/2009	1	10
507	Aberaeron	245000	263000	29/04/2010	1	10
508	Aberaeron	245000	263000	00/00/2010	1	5
509	Aberaeron	245000	263000	00/00/2011	1	5
510	Aberaeron	245000	263000	05/07/2012	1	5
511	Aberaeron	245000	263000	17/02/2014	1	5
512	E of Discharge (Amlwch)	245000	393000	14/02/2003	1	2
513	E of Discharge (Amlwch)	245000	393000	13/04/2013	1	2
516	Overton	246000	184000	00/00/1973	1	10
517	Overton	246000	184000	00/10/1978	1	10
518	Tears Point to Port Eynon Point	246000	184000	06/08/2001	1	10
519	Overton	246000	184000	06/07/2004	1	10
520	Overton	246000	184000	13/03/2013	1	4
521	Aberarth	246000	263000	02/09/2004	1	5
522	Aberarth	246000	263000	17/02/2014	1	6
523	Afon Wen to Criccieth	246000	337000	05/07/1996	1	10
524	Criccieth	246000	337000	05/07/2004	1	4
525	Lee Bay, W (Woolacombe)	247000	146000	25/09/2007	1	10
526	Lee Bay, W (Woolacombe)	247000	146000	07/07/2008	1	10
527	Lee Bay, W (Woolacombe)	247000	146000	13/07-08/10/2010	1	10
528	Lee Bay, W (Woolacombe)	247000	146000	01/07/2011	1	5
529	Lee Bay, W (Woolacombe)	247000	146000	24/05/2013	1	4
530	Port Eynon	247000	184000	00/10/1978	1	10
531	Port Eynon	247000	184000	28/09/2000	1	10
532	Tears Point to Port Eynon Point	247000	184000	06/08/2001	1	10
533	Port Eynon	247000	184000	06/07/2004	1	10
534	Port Eynon	247000	184000	02/07/2011	1	10
535	Port Eynon	247000	184000	13/03/2013	1	6
536	Port Eynon	247000	185000	00/00/1984	1	6
537	Aberarth (Aberaeron)	247000	263000	02/09/2004	1	5
538	Aberarth	247000	263000	17/02/2014	1	6
539	Aberarth (Aberaeron)	247000	264000	02/09/2004	1	5

540	Aberarth	247000	264000	17/02/2014	1	6
541	Criccieth	247000	336000	05/07/2004	1	5
542	Criccieth	247000	337000	13/09/2002	1	10
543	Criccieth	247000	337000	05/07/2004	1	4
544	Afon Dwyfor , W of Transect 9	247000	337000	09/07/2009	1	3
545	Afon Dwyfor	247000	337000	09/07/2009	1	10
546	Afon Dwyfor , W of Transect 9	247000	337000	09/07/2009	1	2
547	Criccieth	247000	337000	03/07/2012	1	5
549	PortyerrockBay	247000	539000	00/00/2000	1	4
550	Lee Bay (Woolacombe)	248000	146000	00/00/1983	1	5
551	Lee Bay, E (Woolacombe)	248000	146000	24/05/2013	1	4
552	Oxwich Point	248000	185000	00/10/1978	1	10
553	Port Eynon Bay to Oxwich Point	248000	185000	28/09/2000	1	10
554	Aberarth (Aberaeron)	248000	264000	09/04/1997	1	7
555	Aberarth (Aberaeron)	248000	264000	30/06/2013	1	5
556	Llangrannog (Aberarth)	248000	264000	30/06/2013	1	5
557	Aberarth (Aberaeron)	248000	264000	17/02/2014	1	6
558	Criccieth, W (Tremadog)	248000	337000	01/07/1995	1	4
559	W of Criccieth (Tremadog)	248000	337000	05/07/2004	1	10
560	Criccieth	248000	337000	05/07/2004	1	6
565	Lynas Point, E (Dulas Bay)	248000	393000	25/07/1997	1	2
566	Lynas Point (Dulas Bay)	248000	393000	13/04/2013	1	2
572	Criccieth	249000	337000	00/00/1984	1	6
573	Afon Wen to Criccieth	249000	337000	05/07/1996	1	10
574	Criccieth Castle (Criccieth)	249000	337000	11/06/2002	0	0
575	Criccieth Castle (Criccieth)	249000	337000	15/08/2003	0	0
576	Criccieth Castle (Criccieth)	249000	337000	05/07/2004	1	10
577	Criccieth Castle (Criccieth)	249000	337000	00/00/2005	0	0
578	Criccieth Castle (Criccieth)	249000	337000	00/00/2006	0	0
579	Criccieth Castle (Criccieth)	249000	337000	00/00/2007	0	0
580	Criccieth Castle (Criccieth)	249000	337000	00/00/2008	0	0
581	Criccieth Castle (Criccieth)	249000	337000	00/00/2009	1	5
582	Criccieth Castle (Criccieth)	249000	337000	00/00/2010	1	6
583	Criccieth Castle (Criccieth)	249000	337000	00/00/2011	0	0
584	Criccieth Castle (Criccieth)	249000	337000	00/00/2012	0	0
585	Criccieth Castle (Criccieth)	249000	337000	08/08/2013	1	6
586	Porth yr Aber (Penysarn)	249000	390000	16/06/2014	1	3
587	Combe Martin	250000	147000	00/00/1977	1	3
588	Wild Pear Beach (CombeMartin)	250000	147000	00/00/1984	1	10
589	Oxwich Point	250000	184000	00/00/1973	1	10
590	Oxwich Point	250000	184000	00/10/1978	1	10
591	Oxwich	250000	184000	13/03/2013	1	3
592	Oxwich	250000	185000	00/00/1973	1	10
593	Oxwich	250000	185000	00/00/1984	1	4
594	Oxwich	250000	185000	13/03/2013	1	6
595	Oxwich	250000	186000	13/03/2013	1	6
596	S of Llanon (Aberaeron)	250000	266000	09/04/1997	1	7
597	S of Llanon (Aberaeron)	250000	266000	28/04/2003	1	6
598	Criccieth Castle, E (Criccieth)	250000	337000	01/07/1995	1	4
599	Criccieth Castle, E (Criccieth)	250000	337000	05/07/1996	1	10
600	Criccieth Castle, E (Criccieth)	250000	337000	18/09/1997	1	10
601	Criccieth Castle, E (Criccieth)	250000	337000	08/08/2013	1	6
602	Criccieth, E (Criccieth)	250000	338000	00/00/2003	1	6
603	Criccieth, E (Criccieth)	250000	338000	00/00/2004	1	6
604	Criccieth, E (Criccieth)	250000	338000	00/00/2006	1	6
605	Criccieth, E (Criccieth)	250000	338000	00/00/2007	1	6
606	Criccieth, E (Criccieth)	250000	338000	00/00/2008	1	6
607	Criccieth, E (Criccieth)	250000	338000	00/00/2009	1	6
608	Criccieth, E (Criccieth)	250000	338000	00/00/2010	1	6
609	Criccieth, E (Criccieth)	250000	338000	00/00/2011	0	0
610	Criccieth, E (Criccieth)	250000	338000	00/00/2012	1	6
611	Criccieth, E (Criccieth)	250000	338000	00/00/2013	1	6
612	Ilfracombe	251000	147000	00/00/1984	1	5
613	Ilfracombe	251000	147000	24/05/2013	0	0
614	Oxwich Bay, W	251000	185000	00/00/1973	1	10
615	Oxwich Bay, W	251000	185000	00/10/1978	1	10
616	Oxwich Bay, W	251000	185000	29/08/2011	1	10
622	Llanrhystud (Aberystwyth)	252000	269000	00/00/1984	1	6
623	Llanrhystud (Aberystwyth)	252000	269000	08/04/1997	1	4

624	Carreg Tipw to Aberarth	252000	269000	28/04/2003	1	10
625	Llanrhystud (Aberystwyth)	252000	269000	04/07/2012	1	6
626	Criccieth to North Bank of Afon Glaslyn	252000	337000	18/09/1997	1	10
627	Plas Newydd	252000	369000	14/03/2014	1	3
628	Cellar (Wembury)	253000	47000	10/04/2001	1	2
629	Cellar (Wembury)	253000	47000	11/09/2002	0	0
630	Cellar (Wembury)	253000	47000	18/09/2003	0	0
631	Hele Bay	253000	147000	24/05/2013	1	5
632	Hele Bay	253000	148000	00/00/1984	1	5
633	Hele Bay	253000	148000	24/05/2013	1	5
634	Carreg Tipw (Aberystwyth)	253000	270000	08/04/1997	1	6
635	Shirecombe	254000	187000	00/00/1973	1	10
636	Shirecombe	254000	187000	00/10/1978	1	10
637	Shirecombe	254000	187000	03/06/2004	1	10
638	Southgate	254000	187000	13/03/2013	1	6
639	Southgate	254000	187000	19/02/2014	1	5
640	Shell Island (Mochras)	254000	326000	04/04/1997	1	7
643	LimesladeBay	255000	186000	22/04/2004	1	10
644	LimesladeBay	255000	186000	14/03/2013	1	6
645	Deep Slade	255000	186000	19/02/2014	1	5
646	Shirecombe to Graves End	255000	187000	22/04/2004	1	10
647	Caswell	255000	187000	13/03/2013	1	4
648	Caswell	255000	187000	19/02/2014	1	5
649	NW of Llanddeiniol (Aberystwyth)	255000	274000	08/04/1997	1	7
650	Blaenplwyf, W (Aberystwyth)	255000	275000	08/04/1997	1	6
651	Tonfanau	255000	303000	00/00/1984	1	5
652	Shell Island (Mochras)	255000	326000	06/07/2004	1	5
653	Shell Island (Mochras)	255000	326000	10/08/2005	1	10
654	Shell Island (Mochras)	255000	326000	04/07/2012	1	6
655	Shell Island (Mochras)	255000	327000	06/07/2004	1	6
656	Shell Island (Mochras)	255000	327000	04/07/2012	1	6
657	Mossyard Bay	255000	551000	00/00/1984	1	6
658	Garvellan Rocks (Mossyard Bay)	255000	551000	00/00/2000	1	4
659	Garvellan Rocks (Mossyard Bay, Newton)	255000	551000	01/11/2011	1	10
660	Mossyard Bay	255000	551000	20/07/2012	1	5
661	Mossyard Bay	255000	551000	10/06/2013	1	10
662	Sandy Bay (Combe Martin)	256000	147000	00/00/1984	1	3
663	Deep Slade (Pwll Du)	256000	186000	1970 to 1980	1	3
664	Deep Slade	256000	186000	00/00/1973	1	10
665	Deep Slade	256000	186000	19/08/1978	1	3
666	Deep Slade	256000	186000	1970 to 1980	1	3
667	Shirecombe to Graves End	256000	186000	22/04/2004	1	10
668	Deep Slade	256000	186000	14/03/2013	1	5
669	Deep Slade	256000	186000	19/02/2014	1	5
670	Allt Wen to Morfa Bychan	256000	277000	14/05/2003	1	10
671	Friog	256000	304000	06/07/2004	1	5
672	Tonfanau	256000	304000	06/07/2004	1	10
673	Tonfanau	256000	304000	09/08/2005	1	10
674	Cae Du (Tywyn)	256000	305000	05/04/1997	1	10
675	Friog	256000	305000	06/07/2004	1	5
676	Tonfanau	256000	305000	09/08/2005	1	10
677	Llangelynin beach (Barmouth Bay)	256000	306000	06/04/1997	1	4
678	Friog	256000	306000	06/07/2004	1	6
679	Cae Du (LlangelyninBeach, BarmouthBay)	256000	306000	09/08/2005	1	10
680	Cae-Du	256000	307000	06/07/2004	1	10
681	Shell Island (Mochras)	256000	327000	00/00/1978	1	10
682	Shell Island (Mochras)	256000	327000	00/00/1984	1	7
683	Shell Island (Mochras)	256000	327000	06/07/2004	1	5
684	Shell Island (Mochras)	256000	327000	04/07/2012	1	6
685	Shell Island (Mochras)	256000	328000	06/07/2004	1	4
686	Llandanwg	256000	328000	10/08/2005	1	10
687	Llandanwg	256000	328000	06/07/2009	1	3
688	Llandanwg	256000	328000	06/07/2009	1	3
689	Llandanwg	256000	328000	06/07/2009	1	10
690	Llandanwg	256000	328000	04/07/2012	1	6
691	Llandanwg (Pen Llŷn ar Sarnau)	256000	329000	06/07/2004	1	5
692	Murray Isles (Islands of Fleet, Solway, N)	256000	549000	00/00/1978	1	10
693	Murray Isles (Islands of Fleet, Solway, N)	256000	549000	00/00/2000	1	4
695	Deep Slade	257000	147000	24/05/2013	1	4

696	PwllDu	257000	186000	00/00/1973	1	10
697	PwllDu	257000	186000	00/10/1978	1	10
698	Shirecombe to Graves End	257000	186000	22/04/2004	1	10
699	Allt Wen to Morfa Bychan	257000	278000	14/05/2003	1	10
700	Tanybwlch, S (Aberystwyth)	257000	279000	10/04/1997	1	4
701	Clarach to Aberystwyth harbourmouth	257000	281000	14/05/2003	1	10
702	Castle Rocks (Aberystwyth)	257000	281000	04/09/2005	1	6
703	Castle Rocks (Aberystwyth)	257000	281000	08/06/2006	1	5
704	Castle Rocks, Aberystwyth, Ceredigion	257000	281000	11/05/2008	1	10
705	Aberystwyth	257000	281000	04/07/2012	1	5
706	Aber Dysynni to Aberdyfi	257000	301000	07/04/1997	1	10
707	Cae Du (Tywyn, N)	257000	307000	06/07/2004	1	6
708	Friog (Barmouth Bay)	257000	308000	07/07/2004	1	10
709	Friog	257000	309000	00/07/2004	1	5
710	Llandanwg (Pen Llŷn ar Sarnau)	257000	329000	00/00/1978	1	5
711	Llandanwg	257000	329000	00/00/1984	1	5
712	Llandanwg (Pen Llŷn ar Sarnau)	257000	329000	04/04/1997	1	10
713	Llandanwg (Pen Llŷn ar Sarnau)	257000	329000	06/07/2004	1	5
714	Islands of Fleet (Solway, N)	257000	549000	00/00/1978	1	5
715	Ardwall Isle (Islands of Fleet, Solway, N)	257000	549000	00/00/2000	1	4
716	Carrick	257000	550000	30/05/2013	1	10
717	Caswell	258000	187000	19/04/2004	1	10
718	Caswell	258000	187000	13/03/2013	1	5
719	Aberystwyth	258000	282000	00/00/1984	1	6
720	Castle Rocks, N (Aberystwyth)	258000	282000	10/04/1997	1	6
721	Aberystwyth	258000	282000	07/08/2002	1	6
722	Clarach to Aberystwyth harbourmouth	258000	282000	14/05/2003	1	10
723	Castle Rocks, N (Aberystwyth)	258000	282000	00/00/2005	1	5
724	Castle Rocks, N (Aberystwyth)	258000	282000	00/00/2006	1	3
725	Castle Rocks, N (Aberystwyth)	258000	282000	00/00/2010	1	6
726	Castle Rocks, N (Aberystwyth)	258000	282000	00/00/2011	1	4
727	Castle Rocks, N (Aberystwyth)	258000	282000	04/07/2012	1	5
728	Castle Rocks, N (Aberystwyth)	258000	282000	00/00/2013	1	6
729	Clarach Bay (Aberystwyth)	258000	284000	11/04/1997	1	6
730	Clarach Bay (Aberystwyth)	258000	284000	31/08/2004	1	5
731	Sarn Cynfelyn (Aberystwyth)	258000	285000	07/04/1997	1	6
732	Clarach Bay/Sarn Cynfelyn (Aberystwyth)	258000	285000	31/08/2004	1	6
733	Friog	258000	309000	07/07/2004	1	10
734	Llwyngwril (Barmouth Bay)	258000	310000	05/04/1997	1	6
735	Friog	258000	310000	07/07/2004	1	6
736	Llwyngwril (Barmouth Bay)	258000	310000	04/07/2012	1	6
738	Ardwall Isle (Islands of Fleet, Solway, N)	258000	548000	00/00/1978	1	10
739	Barlocco Isle (Islands of Fleet, Solway, N)	258000	548000	00/00/2000	1	4
740	Caswell	259000	187000	00/00/1973	1	10
741	Borth	259000	286000	08/04/1997	1	10
742	Borth	259000	286000	31/08/2004	1	6
743	Borth	259000	287000	31/08/2004	1	6
744	Borth	259000	288000	08/04/1997	1	10
745	Borth	259000	288000	31/08/2004	1	4
746	Llwyngwril Beach, N (Barmouth Bay)	259000	310000	05/04/1997	1	7
747	Friog	259000	310000	00/07/2004	1	6
748	Llwyngwril (Barmouth Bay)	259000	310000	04/07/2012	1	7
749	Llwyngwril	259000	311000	00/00/1982	1	7
750	Llwyngwril	259000	311000	00/00/1984	1	7
751	Friog	259000	311000	00/07/2004	1	6
752	Llwyngwril (Barmouth Bay)	259000	311000	04/07/2012	1	6
753	NW of Meggerland Point (Kirkandrews Bay)	259000	547000	18/09/1989	1	4
754	Kirkandrews Bay	259000	547000	00/00/2000	1	4
755	Mothecome	260000	47000	23/10/2002	1	6
756	Graves End to Langland Bay	260000	186000	19/04/2004	1	10
757	Graves End to Langland Bay	260000	187000	19/04/2004	1	10
759	Borth	260000	288000	00/00/1984	1	6
760	Upper Borth (Aberdyfi)	260000	288000	07/04/1997	1	6
761	Borth	260000	288000	08/08/2002	1	6
762	Borth	260000	288000	00/00/2004	0	0
763	Borth	260000	288000	13/04/2006	1	10
764	Borth	260000	288000	04/07/2012	1	6
765	Dyfi estuary (Cardigan)	260000	294000	00/00/1982	1	5
766	Friog	260000	311000	00/07/2004	1	6

767	Friog (Barmouth Bay)	260000	311000	08/08/2005	1	10
769	Barmouth	260000	315000	00/00/1984	1	4
770	Barmouth	260000	315000	04/07/2012	0	0
771	Mothecombe Beach	261000	46000	02/08/2003	1	10
772	Mothecombe Beach	261000	46000	24/05/2005	1	10
775	Erme Mouth (Mothecombe)	261000	47000	00/00/1970	0	0
776	Erme Mouth (Mothecombe)	261000	47000	23/10/2002	1	6
777	Graves End to Langland Bay	261000	187000	19/04/2004	1	10
778	Fryars Bay (Beaumaris)	261000	377000	12/06/2014	1	3
779	Limeslade	262000	186000	14/03/2013	1	6
780	LimesladeBay	262000	186000	19/02/2014	1	6
781	Limeslade Bay/Mumbles/Bracelet Bay	262000	187000	00/00/1973	1	10
782	Limeslade Bay/Mumbles/Bracelet Bay	262000	187000	00/00/1984	1	4
783	Langland Bay to Mumbles Head	262000	187000	23/07/2001	1	10
784	Limeslade Bay/Mumbles/Bracelet Bay	262000	187000	03/06/2004	1	10
785	Bracelet Bay/The Mumbles (Swansea)	262000	187000	23/10/2006	1	10
786	Limeslade Bay/Mumbles/Bracelet Bay	262000	187000	28/05/2013	1	6
787	Limeslade Bay/Mumbles/Bracelet Bay	262000	187000	19/02/2014	1	6
788	Norton to Afon Tawe (Swansea Bay)	262000	189000	24/07/2001	1	10
789	Norton to Afon Tawe (Swansea Bay)	262000	189000	11/09/2003	1	10
790	Norton to Afon Tawe (Swansea Bay)	262000	190000	24/07/2001	1	10
791	Norton to Afon Tawe (Swansea Bay)	262000	190000	11/09/2003	1	10
792	Penmon Priory to Black Rock (Menai Strait)	262000	379000	02/08/1992	1	10
794	Bracelet Bay (Swansea)	263000	187000	17/08/1978	1	3
795	Bracelet Bay (Swansea)	263000	187000	00/00/1984	1	7
796	Langland Bay to Mumbles Head	263000	187000	23/07/2001	1	10
797	Survey 122	263000	187000	23/10/2006	1	10
798	Bracelet Bay (Swansea)	263000	187000	17/06-16/08/2011	1	10
799	Bracelet Bay (Swansea)	263000	187000	14/03/2013	1	5
800	Bracelet Bay (Swansea)	263000	187000	19/02/2014	1	5
804	Penmon Point, W (Menai Strait, N)	263000	381000	21/07/1997	1	2
805	Penmon, N	263000	381000	04/07/2012	0	0
806	Penmon, W	263000	381000	14/04/2013	0	0
807	Brighouse Bay (Solway, N)	263000	545000	15/06/1991	1	2
808	Norton to Afon Tawe (Swansea Bay)	264000	191000	24/07/2001	1	10
809	Norton to Afon Tawe (Swansea Bay)	264000	191000	11/09/2003	1	10
810	Puffin Island, S (Menai Strait, N)	264000	381000	22/07/1997	1	3
811	Penmon, N	264000	381000	13/06/2002	0	0
812	Penmon, N	264000	381000	12/08/2003	0	0
813	Fauldbog Bay	264000	544000	00/00/2000	1	4
814	Bantham (Thurlestone)	265000	43000	28/06/2002	1	5
815	Langland Bay to Mumbles Head	265000	191000	24/07/2001	1	10
816	Norton to Afon Tawe (Swansea Bay)	265000	191000	11/09/2003	1	10
817	Swansea Bay	265000	191000	19/02/2014	1	6
818	Meikle Ross (Kirkcudbright Bay)	265000	543000	17/09/1989	1	3
819	Meikle Ross (Kirkcudbright Bay)	265000	543000	00/00/2000	1	4
826	Norton to Afon Tawe (Swansea Bay)	266000	191000	24/07/2001	1	10
827	Norton to Afon Tawe (Swansea Bay)	266000	191000	11/09/2003	1	10
840	Afon Tawe to Baglan Bay	267000	191000	29/10/2003	1	10
841	Balmae Haen	267000	544000	00/00/2000	1	4
842	Torrs Point, N (Kirkcudbright Bay)	267000	545000	19/09/1989	1	3
843	Torrs Point, N (Kirkcudbright Bay)	267000	545000	00/00/2000	1	4
846	Lee Bay (Lynton)	269000	149000	24/05/2013	1	2
847	Afon Tawe to Baglan Bay	269000	191000	29/10/2003	1	10
848	Swansea Bay	269000	191000	19/02/2014	1	6
850	Howell Bay	269000	543000	00/00/2000	1	4
853	Witford Point and Aberavon Sands	271000	191000	12/09/2003	1	10
854	Mullock Bay	271000	543000	00/00/2000	1	5
858	White Port	272000	543000	00/00/2000	1	4
867	Sheep Bught Rock	273000	543000	00/00/2000	1	4
869	Lower Blackhead (Lynmouth)	274000	150000	11/07/1976	1	10
870	Witford Point and Aberavon Sands	274000	186000	12/09/2003	1	10
871	Port Talbot Harbour	274000	187000	30/09/2003	1	10
872	Port Talbot Harbour	274000	187000	04/08/2013	1	10
873	Afon Afan (Witford Point and Aberavon Sands)	274000	188000	12/09/2003	1	10
874	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2003	0	0
875	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2004	0	0
876	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2005	0	0
877	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2006	1	2

878	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2007	0	0
879	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2008	0	0
880	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2009	0	0
881	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2010	0	0
882	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2011	0	0
883	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2012	0	0
884	Trwynygogarth (Great Orme, W)	274000	383000	00/00/2013	0	0
885	Abbey Head	274000	543000	00/00/2000	1	4
886	Abbey Burn Foot	274000	544000	00/00/1984	1	6
887	Abbey Burn Foot	274000	544000	17/09/1989	1	2
888	Abbey Burn Foot	274000	544000	00/00/2000	1	4
889	Margam Sands	275000	187000	10/09/2003	1	10
890	Port Talbot Harbour	275000	188000	30/09/2003	1	10
891	Port Talbot Harbour	275000	188000	01/08/2013	1	10
892	Llandudno (Great Ormes Head, W)	275000	383000	00/00/1984	0	0
893	Llandudno (Great Ormes Head, W)	275000	383000	22/07/1997	1	2
894	Llandudno (Great Ormes Head, W)	275000	383000	2003-4	0	0
895	Llandudno (Great Ormes Head, W)	275000	383000	23/07/2012	0	0
896	Port Mary	275000	545000	29/10/1978	1	5
897	Port Mary	275000	545000	00/00/2000	1	4
898	Margam Sands	276000	185000	10/09/2003	1	10
900	Orroland Heugh	277000	545000	00/00/2000	1	4
903	Sker Point (Kenfig)	278000	179000	00/00/1973	1	3
904	Sker Point (Kenfig)	278000	179000	29/09/2003	1	10
905	Sker Point (Kenfig)	278000	179000	03/06/2004	1	10
906	No site name available	278000	179000	15/06-25/10/2007	1	10
907	Sker Point (Kenfig)	278000	179000	06/06/2008	1	10
908	Kenfig Sands	278000	180000	10/09/2003	1	10
909	Kenfig Sands	278000	181000	10/09/2003	1	10
910	Great Ormes Head, E	278000	383000	02/07/2012	1	2
911	Gorah Rocks (Devon)	279000	36000	04/07/2008	1	10
912	Rest Bay	279000	178000	29/09/2003	1	10
913	Sker Point (Kenfig)	279000	179000	27/09/2003	1	10
914	Barlocco Bay	279000	546000	00/00/2000	1	4
915	Castle Muir Point	279000	547000	00/00/2000	1	4
916	Lannacombe Beach, E (Harris Beach, Little Slead)	280000	37000	06/01/1992	1	10
917	Site 481 (Porthcawl)	280000	171000	27/04/1988	1	10
918	Hutchwns Point (Porthcawl)	280000	176000	00/00/1984	1	7
919	Porthcawl	280000	176000	27/04/1988	1	10
920	Hutchwns Point (Porthcawl)	280000	176000	27/09/2003	1	10
921	Hutchwns Point (Porthcawl)	280000	176000	14/03/2013	1	6
922	Little Ormes Head, W	280000	382000	00/00/2012	1	2
923	Rascarrel Bay (Auchencairn, Solway, N)	280000	548000	19/09/1989	1	4
924	Rascarrel Bay (Auchencairn, Solway, N)	280000	548000	00/00/2000	1	4
925	Porthcawl	281000	176000	14/03/2013	1	6
926	Little Ormes Head	281000	382000	23/07/1997	1	3
927	Little Ormes Head	281000	382000	00/00/2004	0	0
928	Little Ormes Head	281000	382000	00/00/2005	0	0
929	Little Ormes Head	281000	382000	00/00/2006	0	0
930	Little Ormes Head	281000	382000	00/00/2007	1	5
931	Little Ormes Head	281000	382000	00/00/2008	0	0
932	Little Ormes Head	281000	382000	00/00/2009	0	0
933	Little Ormes Head	281000	382000	00/00/2010	0	0
934	Little Ormes Head	281000	382000	00/00/2011	0	0
935	Little Ormes Head	281000	382000	00/00/2012	1	2
936	Little Ormes Head	281000	382000	00/00/2013	1	5
938	Fairy Rock (Bristol Channel, N)	282000	175000	02/07/1979	1	10
939	Hutchwns Point (Porthcawl)	282000	176000	08/09/1971	1	6
940	Hutchwns Point (Porthcawl)	282000	176000	27/09/2003	1	10
941	Hutchwns Point (Porthcawl)	282000	176000	14/03/2013	1	6
942	Groyne (Penrhyn Bay)	282000	381000	23/07/2012	1	4
945	Adams Chair	282000	548000	00/00/2000	1	4
946	Balcary Point (Inner Solway)	282000	549000	00/00/1973	1	4
947	Balcary Point (Inner Solway)	282000	549000	15/08/1991	1	5
948	Balcary Point (Inner Solway)	282000	549000	00/00/1994	0	0
951	Hutchwns Point (Porthcawl)	283000	176000	27/09/2003	1	10
952	Hutchwns Point (Porthcawl)	283000	176000	16/07/2007	1	10
953	No site name available	283000	176000	16/07/2007	1	10

954	Newton Point (Porthcawl)	283000	176000	19/06/2008	1	10
955	HestanIsland	283000	549000	00/00/2000	1	10
956	Dunraven Bay	284000	173000	28/09/2003	1	10
957	Tusker Rock	284000	173000	05/07/2004	1	10
958	Dunraven Bay	284000	173000	01/08/2010	1	6
959	Dunraven Bay	284000	173000	31/01/2011	1	10
960	Tusker Rock	284000	174000	05/07/2004	1	10
961	Hutchwns Point to Traeth yr Afon	284000	176000	27/09/2003	1	10
962	Rhos on Sea	284000	380000	23/07/2012	1	5
964	Rhos Point (Rhos on Sea, Penrhyn Bay)	284000	381000	00/00/1984	0	0
965	Rhos Point (Rhos on Sea, Penrhyn Bay)	284000	381000	2003-4	0	0
966	Rhos Point (Rhos on Sea, Penrhyn Bay)	284000	381000	31/12/2004	0	0
967	Almorness Point	284000	551000	00/00/2000	1	10
968	Porlock	285000	148000	00/00/1976	1	5
969	Gore Point (Porlock)	285000	148000	00/00/1984	1	3
970	Tusker Rock, SE	285000	172000	16/09/2002	1	7
971	Afon Ogwr to Black Rocks	285000	175000	28/09/2003	1	10
972	Hutchwns Point to Traeth yr Afon	285000	176000	27/09/2003	1	10
973	Solway, N (Dumfries and Galloway)	285000	552000	19/06/2013	1	10
974	Porlock	286000	147000	23/05/2013	1	5
975	Porlock Weir	286000	148000	00/00/1984	1	6
976	Porlock	286000	148000	23/05/2013	0	0
977	Black Rocks (Dunraven Bay)	286000	174000	28/09/2003	1	10
978	Black Rocks (Dunraven Bay)	286000	174000	26/03/2005	1	6
979	Black Rocks (Dunraven Bay)	286000	174000	16/08/2008	1	6
980	Black Rocks (Dunraven Bay)	286000	174000	01/10/2012	1	6
981	Afon Ogwr to Black Rocks	286000	175000	28/09/2003	1	10
982	Colwyn Bay	286000	378000	23/07/2012	1	1
983	Colwyn Bay	286000	379000	23/07/2012	1	1
985	Porlock Bay	287000	147000	00/00/1984	1	1
986	Dunraven Bay	287000	173000	28/09/2003	1	10
987	Dunraven Bay	287000	173000	18/02/2014	1	6
988	Dunraven Bay	287000	174000	28/09/2003	1	10
989	Dunraven Bay	287000	174000	31/10/2012	1	7
990	Colwyn Bay	287000	378000	00/00/1984	0	0
991	Colwyn Bay	287000	378000	2003-4	1	2
992	Port O Warren Bay	287000	553000	00/00/1973	1	6
993	Port O Warren Bay	287000	553000	00/00/1992	0	0
994	Port O Warren Bay	287000	553000	20/07/2012	1	6
996	Dancing Beggars (Stoke, Fleming)	288000	48000	26/02/1994	1	2
997	Porlock Bay	288000	148000	23/05/2013	1	4
998	Temples Bay	288000	172000	00/00/1997	1	7
999	Dunraven Bay	288000	172000	28/09/2003	1	6
1000	Dunraven Bay	288000	172000	31/10/2012	1	6
1001	Dunraven Bay	288000	172000	25/05/2013	1	6
1002	Temples Bay	288000	172000	18/02/2014	1	6
1003	Dunraven Bay	288000	173000	00/00/1976	1	6
1004	Dunraven Bay	288000	173000	00/00/1984	1	7
1005	Southerndown	288000	173000	00/00/1997	1	7
1006	Dunraven Bay	288000	173000	28/09/2003	1	10
1007	Dunraven Bay	288000	173000	31/01/2011	1	10
1008	Dunraven Bay	288000	173000	18/02/2014	1	6
1009	Port O Warren Bay	288000	553000	00/00/1984	1	5
1010	Port O Warren Bay	288000	553000	20/07/2012	1	6
1011	Saltern Cove (Goodrington)	289000	58000	14/09/1992	1	7
1012	Goodrington, S	289000	58000	08/03/1993	1	3
1013	Shell Cove (Middle Stone to Elberry Cove)	289000	58000	07/03/1993	1	2
1014	Goodrington Beach	289000	58000	21/08/2004	1	5
1015	Goodrington Sands	289000	59000	00/00/1984	0	0
1016	Goodrington Sands, Reef	289000	59000	26/10/1992	1	5
1017	Goodrington Sands	289000	59000	11/09/2006	1	10
1018	Goodrington Sands	289000	59000	04/07/2007	1	10
1019	No site name available	289000	59000	14/09/2007	1	10
1020	Goodrington Sands, Reef	289000	59000	2003-2004	1	5
1021	Roundham Head, S (Paignton)	289000	60000	13/10/1992	1	5
1022	Fairy Cove, Roundham Head	289000	60000	26/11/1992	1	4
1023	Paignton Harbour	289000	60000	25/03/1993	1	3
1024	Hollicombe Rocks (Torbay)	289000	61000	27/09/1992	1	6
1025	Hollicombe Rocks (Torbay)	289000	61000	27/09/1992	1	3

1026	Hurlstone Point (Bristol Channel S)	289000	149000	14/06/1978	1	10
1027	Traeth Bach to Nash Point	289000	171000	04/06/2004	1	10
1028	Trwyn y Witch to Traeth Bach	289000	172000	00/00/2002	1	10
1029	Trwyn y Witch to Traeth Bach	289000	172000	05/07/2004	1	10
1030	Oil Cove (Paignton)	290000	62000	21/02/1993	1	7
1031	Oil Cove (Paignton)	290000	62000	21/02/1993	1	5
1032	Livermead Head Caves	290000	62000	21/02/1993	1	3
1033	Corbyns Head (Torbay)	290000	63000	26/09/1992	1	5
1034	Torbay	290000	63000	10/04/2002	1	5
1035	Traeth Bach to Nash Point	290000	169000	04/06/2004	1	10
1036	Scabbacombe Sands (Brixham)	291000	52000	15/03/1994	1	3
1038	Nash Point (Bristol Channel, N)	291000	167000	03/07/1979	1	7
1039	Nash Point (Bristol Channel, N)	291000	167000	00/00/1997	1	5
1040	Marcross	291000	167000	14/03/2013	1	5
1041	Marcross	291000	168000	00/00/1976	1	6
1042	Marcross	291000	168000	04/06/2004	1	10
1043	Llanddulas	291000	378000	12/02-30/07/2008	1	6
1044	Llanddulas	291000	378000	12/02-30/07/2008	1	6
1045	Llanddulas	291000	378000	12/02-30/07/2008	1	1
1046	Llanddulas	291000	378000	00/00/2010	0	0
1047	Llanddulas	291000	378000	29/07/2012	1	6
1048	Llanddulas	291000	378000	23/07/2012	1	6
1049	Llanddulas	291000	378000	07/04/2012	1	6
1050	Llanddulas	291000	378000	05/04/2013	1	6
1051	Llanddulas	291000	378000	06/04/2014	1	6
1052	Llanddulas	291000	378000	29/07/2014	1	7
1054	Scabbacombe Sands (Brixham)	292000	51000	15/03/1994	1	3
1055	Cod Rocks, Scabbacombe (Brixham)	292000	52000	27/04/1994	1	4
1056	Man Sands (Brixham)	292000	53000	14/03/1994	1	3
1057	Oddicombe Beach (Torquay)	292000	65000	11/04/1994	1	3
1058	Watcombe Cove (North Bay)	292000	67000	14/08/1992	1	10
1059	Watcombe Cove	292000	67000	11/04/1994	1	5
1060	Maidencombe	292000	68000	28/07/1992	1	6
1061	Nash Point to Tresilian Bay	292000	167000	04/06/2004	1	10
1062	St Marys Bay (Brixham)	293000	54000	05/05/1993	1	3
1063	Brixham	293000	55000	00/00/1984	0	0
1064	St Marys Bay, N (Brixham)	293000	55000	06/05/1993	1	3
1066	St Donats Point and West (Bristol Channel, N)	293000	167000	03/07/1979	1	7
1067	St Donats Point and West	293000	167000	04/06/2004	1	10
1068	Teignmouth Beach, Rocks	294000	73000	12/03/1994	1	4
1069	Reynards Cave, Tresilian (Bristol Channel, N)	294000	167000	03/07/1979	1	3
1070	Reynards Cave	294000	167000	04/06/2004	1	10
1072	Saint Bees Head	294000	512000	00/00/1989	1	4
1073	Fleswick Bay, S	294000	512000	08/04/1989	1	4
1074	Saint Bees Head	294000	512000	00/00/1991	1	4
1075	Saint Bees Head(Tomlin)	294000	512000	05/07/2000	1	3
1076	Saint Bees Head	294000	515000	04/07/2000	1	3
1077	Hopes Nose (Torquay)	295000	63000	24/04/2010	1	2
1078	Sprey Point (Teignmouth)	295000	73000	12/03/1994	1	5
1079	Man Sands (Sharkham Point to Scabbacombe Head)	295000	73000	14/03/1994	1	2
1080	Greenaleigh Point, W (Minehead)	295000	148000	05/07/1979	1	5
1082	Llantwit Major	295000	167000	15/05/1976	1	10
1083	Llantwit Major	295000	167000	00/00/1984	1	3
1084	Llantwit Major	295000	167000	01/07/2004	1	10
1085	Llantwit Major	295000	167000	14/03/2013	1	5
1086	Saint Bees	295000	511000	00/00/1984	1	3
1087	South Head, SE	295000	511000	08/04/1989	1	3
1088	Saint Bees	295000	511000	00/00/1991	0	0
1089	Saint Bees	295000	511000	07/12/2003	1	6
1090	Saint Bees, NE	295000	511000	21/07/2012	1	6
1094	Corytons Cove (Dawlish)	296000	76000	00/00/1984	1	6
1095	Corytons Cove (Dawlish)	296000	76000	16/06/1992	1	4
1096	Tresilian Bay to Limpert Bay	296000	167000	01/07/2004	1	10
1097	Saint Bees, S	296000	509000	01/03/2002	1	6
1098	Saint Bees, SW	296000	510000	01/03/2002	1	7
1099	Saint Bees, SW	296000	510000	21/07/2012	1	7
1100	Grab samples F	296000	549000	01/07/2004	1	5
1101	Grab samples F	296000	549000	01-31/07/2006	1	5

1102	Transect 1 (Solway Firth)	296000	554000	23/09/1999	1	3
1103	Transect 2 (Solway Firth)	296000	554000	23/09/1999	1	3
1104	Langstone Reef (Dawlish)	297000	78000	16/06/1992	1	7
1105	Minehead	297000	147000	00/00/1976	1	5
1106	Minehead	297000	147000	00/00/1984	1	5
1107	Minehead, W	297000	147000	00/00/1984	1	5
1108	Minehead	297000	147000	07/10/2002	1	5
1109	Minehead	297000	147000	23/05/2013	0	0
1110	Tresilian Bay to Limpert Bay	297000	166000	01/07/2004	1	10
1111	Coulderton (Saint Bees)	297000	508000	01/03/2002	1	6
1112	Saint Bees, S	297000	510000	01/03/2002	1	6
1113	CunningPoint	297000	522000	07/07/2000	1	3
1115	Southerness (Solway, N)	297000	554000	00/00/1973	1	10
1116	Southerness (Solway, N)	297000	554000	00/00/1984	1	4
1117	Southerness Point (Solway, N)	297000	554000	13/08/1991	1	3
1118	Southerness (Solway, N)	297000	554000	00/00/1994	1	4
1119	Southerness Lighthouse (Solway, N)	297000	554000	22/09/1999	1	4
1120	Transect 3 (Solway Firth)	297000	554000	23/09/1999	1	3
1121	Southernness Point (Solway, N)	297000	554000	00/00/2000	1	4
1122	Southernness Point (Solway, N)	297000	554000	20/07/2012	1	5
1123	Exe estuary	298000	82000	00/00/1978	1	10
1124	Site 223 (Upper Bristol Channel)	298000	147000	14/04/1988	1	10
1125	Nethertown (Saint Bees)	298000	506000	01/03/2002	1	7
1126	Nethertown	298000	507000	00/00/1984	1	6
1127	Nethertown	298000	507000	30/11/1994	1	6
1128	Nethertown	298000	507000	00/00/1995	1	7
1129	Nethertown	298000	507000	07/07/2000	1	6
1130	Nethertown (Saint Bees)	298000	507000	01/03/2002	1	7
1131	Nethertown	298000	507000	20/03/2004	1	6
1132	Nethertown	298000	507000	21/07/2012	1	6
1133	Coulderton (Saint Bees)	298000	508000	01/03/2002	1	6
1134	Harrington	298000	525000	00/00/1984	0	0
1135	Moss Bay (Harrington)	298000	525000	21/07/2012	1	5
1137	MossBay	298000	526000	06/07/2000	1	5
1138	MossBay	298000	526000	21/07/2012	1	6
1139	Grab samples G	298000	553000	01/07/2004	1	5
1140	Grab samples G	298000	553000	01-31/07/2007	1	5
1141	Black Craigs and Gillfoot Bay (Solway)	298000	554000	22/09/1999	1	3
1142	Gillfoot Bay (Southerness, Solway, N)	298000	554000	20/07/2012	1	3
1143	Tresilian Bay to Limpert Bay	299000	166000	01/07/2004	1	10
1145	Nethertown (Saint Bees)	299000	506000	01/03/2002	1	7
1146	Nethertown (Saint Bees)	299000	507000	01/03/2002	1	7
1147	Northside	299000	530000	16/09/1984	1	5
1148	Siddick Point, S (Parton Bay)	299000	530000	13/06/1991	1	4
1149	Siddick Scar	299000	531000	00/00/1999	1	5
1150	Siddick Scar	299000	531000	05/07/2000	1	5
1151	Siddick (Seaton)	299000	531000	01/03/2002	1	6
1152	Siddick (Lam)	299000	532000	01/04/1971	1	2
1153	N of North Side (Parton Bay)	299000	533000	15/07/1991	1	3
1156	Tresilian Bay to Limpert Bay	300000	166000	02/07-05/08/2004	1	10
1157	Sellafield	300000	504000	01/03/2002	1	6
1158	Sellafield	300000	504000	21/07/2012	1	6
1159	Siddick Scar	300000	531000	21/07/2012	1	6
1160	Saint Helens (Seaton)	300000	532000	01/03/2002	1	7
1161	Flimby	300000	533000	01/03/2002	1	7
1164	Mear Rocks (Exmouth)	301000	79000	00/00/1970	1	6
1165	Mear Rocks (Exmouth)	301000	79000	00/00/1984	0	0
1166	Mear Rocks (Exmouth)	301000	79000	09/11/1991	1	2
1167	Bristol Channel	301000	163000	01/08/1972	1	10
1169	Limpert Bay (Aberthaw)	301000	165000	00/00/1976	1	7
1170	Limpert Bay (Aberthaw)	301000	165000	14/03/2013	1	6
1171	Limpert Bay (Aberthaw)	301000	166000	02/08/2004	1	10
1172	Limpert Bay (Aberthaw)	301000	166000	14/03/2013	1	5
1173	Sellafield	301000	503000	00/00/1984	1	4
1174	Sellafield	301000	503000	05/08/2000	1	4
1175	Sellafield	301000	503000	01/03/2002	1	6
1176	Sellafield	301000	503000	20/03/2004	1	7
1177	Sellafield	301000	503000	21/07/2012	1	6
1178	Sellafield	301000	504000	01/03/2002	1	10

1179	Saint Helens	301000	533000	16/09/1984	1	5
1180	Flimby	301000	533000	01/03/2002	1	7
1182	Flimby Scar	301000	534000	00/00/2000	1	5
1183	Exemouth (Orcombe Point)	302000	79000	00/00/1980	1	10
1184	Orcombe Point (Exmouth)	302000	79000	00/00/1984	0	0
1185	Limpert Bay (Aberthaw)	302000	165000	02/08/2004	1	10
1186	Flimby central (Parton Bay)	302000	533000	30/05/1991	1	3
1187	Risehow Scar	302000	535000	00/00/1991	1	6
1188	Risehow Scar	302000	535000	00/00/2000	0	0
1189	Maryport, South Pier (Parton Bay)	302000	536000	00/00/2000	1	5
1192	Blue Anchor	303000	143000	06/10/2002	1	5
1193	Blue Anchor	303000	143000	24/05/2013	1	5
1195	Blue Anchor	303000	144000	00/00/1976	1	6
1196	Blue Anchor	303000	144000	00/00/1978	1	6
1197	Blue Anchor	303000	144000	00/00/1984	1	6
1198	Blue Anchor	303000	144000	24/05/2013	1	5
1199	Site 226 (Upper Bristol Channel)	303000	145000	14/04/1988	1	10
1200	Site 525 (Upper Bristol Channel)	303000	163000	28/04/1988	1	10
1201	Barns Scar (Drigg)	303000	498000	01/08/2000	1	5
1202	Barns Scar (Drigg)	303000	498000	01/03/2002	1	6
1203	Whitriggs Scar (Seascale)	303000	500000	07/04/1989	1	7
1204	Seascale	303000	500000	20/03/2004	1	6
1205	Seascale	303000	500000	21/07/2012	1	7
1207	Seascale	303000	501000	00/00/1984	1	3
1208	Seascale	303000	501000	21/07/2012	1	7
1209	Maryport, S (Parton Bay)	303000	536000	29/05/1991	1	6
1210	Maryport, North Pier (Parton Bay)	303000	536000	00/00/2000	1	5
1211	Maryport, N (Parton Bay)	303000	537000	28/05/1991	1	6
1212	Museum Scar (Maryport, Parton Bay)	303000	537000	00/00/2000	1	5
1213	Maryport (Parton Bay)	303000	537000	01/03/2002	1	6
1214	Maryport, N (Parton Bay)	303000	537000	21/07/2012	1	6
1215	Seabrows Scar (Maryport, Parton Bay)	303000	538000	00/00/2000	1	5
1216	Bank End Scar, S (Maryport, Parton Bay)	303000	538000	01/03/2002	1	6
1217	Seabrows Scar (Maryport, Parton Bay)	303000	538000	21/07/2012	1	6
1218	Otter Cove and Ledges (Littleham Cove to Straight Point)	304000	79000	05/05/1993	1	10
1219	Otter Cove and Ledges (Littleham Cove to Straight Point)	304000	79000	00/00/1994	1	10
1220	Breaksea Point to Watch House Point	304000	165000	03/08/2004	1	10
1221	Drigg	304000	498000	00/00/1984	1	6
1222	Barns Scar (Drigg)	304000	498000	02/08/2000	1	5
1223	Barns Scar (Drigg)	304000	498000	01/03/2002	1	7
1224	Drigg	304000	498000	20/03/2004	1	6
1225	Drigg, Mid Shore	304000	498000	21/07/2012	1	6
1228	Bank End Scar (Maryport, Parton Bay)	304000	538000	04/07/2000	1	6
1229	Bank End Scar (Maryport, Parton Bay)	304000	538000	01/03/2002	1	7
1230	Bank End Scar (Maryport, Parton Bay)	304000	538000	21/07/2012	1	6
1231	Bank End Scar (Maryport, Parton Bay)	304000	539000	01/03/2002	1	7
1232	Crosscanonby (Allonby Bay)	304000	539000	21/07/2012	1	6
1233	Site 252 (Upper Bristol Channel)	305000	147000	15/04/1988	1	10
1234	Watch House Point to Rhoose Point	305000	165000	16/09/2004	1	10
1235	Prestatyn groyne	305000	383000	23/07/2012	1	4
1236	Brown Rigg, NW (Allonby Bay)	305000	539000	09/08/1991	1	5
1237	Maryport Golf Course (Allonby Bay)	305000	539000	00/00/2000	1	6
1238	Brownrigg, Crosscanonby (Allonby Bay)	305000	539000	01/03/2002	1	7
1239	Crosscanonby (Allonby Bay)	305000	539000	21/07/2012	1	6
1240	Crosscanonby (Allonby Bay)	305000	540000	00/00/1984	1	7
1241	Crosscanonby (Allonby Bay)	305000	540000	00/00/2000	1	6
1242	Crosscanonby (Allonby Bay)	305000	540000	21/07/2012	1	7
1243	Dubmill Point, N (Mawbray)	305000	546000	01/03/2002	1	6
1244	Ellisons Scar (Mawbray Bank, Mawbray)	305000	547000	00/00/2000	1	6
1245	Ellisons Scar (Mawbray Bank, Mawbray)	305000	547000	01/03/2002	1	6
1246	Ellisons Scar (Mawbray Bank, Mawbray)	305000	547000	21/07/2012	1	6
1248	Prestatyn groyne	306000	384000	23/07/2012	1	4
1249	Crosscanonby Scar (Allonby Bay)	306000	539000	00/00/2000	1	6
1250	Crosscanonby (Allonby Bay)	306000	539000	21/07/2012	1	6
1251	Saltpans, Crosscanonby (Allonby Bay)	306000	540000	01/03/2002	1	7
1252	Saltpans, N, Crosscanonby (Allonby Bay)	306000	541000	01/03/2002	1	6
1253	Dubmill Scar (Mawbray)	306000	544000	01/03/2002	1	5

1254	Dubmill Point (Mawbray)	306000	545000	01/03/2002	1	5
1255	Dubmill Point (Mawbray)	306000	545000	21/07/2012	1	6
1256	Dubmill Point, N (Mawbray)	306000	546000	01/03/2002	1	6
1257	Dubmill Point, N (Mawbray)	306000	546000	21/07/2012	1	5
1258	Mawbray Scar (Mawbray)	306000	547000	00/00/1998	1	6
1259	Mawbray Scar (Mawbray)	306000	547000	00/00/1999	1	4
1260	Mawbray Scar (Mawbray)	306000	547000	02/08/2000	1	4
1261	Mawbray Scar (Mawbray)	306000	547000	01/03/2002	1	6
1262	Ellisons Scar (Mawbray Bank, Mawbray)	306000	547000	21/07/2012	1	6
1263	Grab samples C	306000	549000	01/07/2004	1	5
1264	Grab samples C	306000	549000	01-31/07/2005	1	5
1265	Budleigh Salterton	307000	81000	05/09/2002	0	0
1266	Otterton Ledge (Black Head to Otterton Ledge)	307000	81800	14/09/1992	1	10
1267	Otterton Ledge (Black Head to Otterton Ledge)	307000	81800	05/09/2002	1	10
1268	Watchet	307000	143000	00/00/1976	1	3
1269	Watchet	307000	143000	24/05/2013	0	0
1270	Site 179 (Upper Bristol Channel)	307000	149000	12/04/1988	1	10
1271	Rhoose Point to Bullcliff Rocks	307000	165000	15/09/2004	1	10
1272	Annaside Bank	307000	487000	01/03/2002	1	7
1273	Coastguard Lookout (Selker Bay, Annaside Bank)	307000	488000	06/04/1989	1	5
1274	Selker Bay (Annaside Bank)	307000	488000	01/03/2002	1	7
1275	Tarn Point	307000	489000	03/08/2000	1	6
1276	Tarn Bay	307000	489000	01/03/2002	1	7
1277	Tarn Bay	307000	489000	22/07/2012	1	6
1278	Tarn Bay	307000	490000	00/00/1984	1	7
1279	Ravenglass (Tarn Bay)	307000	490000	13/07/1991	1	5
1280	Tarn Bay, N	307000	490000	01/03/2002	1	7
1281	Tarn Bay	307000	490000	20/03/2004	1	6
1282	Tarn Bay	307000	490000	22/07/2012	1	6
1283	River Esk (Saltcoats, SW)	307000	495000	29/07/1999	1	6
1284	Allonby Bay	307000	541000	00/00/1970	1	6
1285	Allonby Bay	307000	541000	00/00/1970	1	10
1286	Allonby Bay	307000	541000	00/00/1974	1	6
1287	Allonby Bay	307000	541000	00/00/1974	1	10
1288	Allonby Bay	307000	541000	00/00/1978	1	5
1289	Allonby Bay	307000	541000	00/00/1978	1	10
1290	Blue Dial (Allonby Bay)	307000	541000	01/03/2002	1	6
1291	Allonby Bay	307000	541000	21/07/2012	1	6
1292	Allonby Bay	307000	542000	00/00/1970	1	6
1293	Allonby Bay	307000	542000	00/00/1974	1	6
1294	Allonby Bay	307000	542000	00/00/2000	1	6
1295	Allonby (Allonby Bay)	307000	542000	01/03/2002	1	6
1296	Allonby Bay	307000	542000	21/07/2012	1	6
1298	North Lodge Scar (Allonby Bay)	307000	543000	00/00/2000	1	5
1299	Allonby, N (Allonby Bay)	307000	543000	01/03/2002	1	6
1300	North Lodge Scar (Allonby Bay)	307000	543000	21/07/2012	1	6
1301	Dubmill Scar (Mawbray)	307000	544000	01/03/2002	1	5
1302	Dubmill Scar	307000	545000	00/00/1984	1	4
1303	Dubmill Scar	307000	545000	10/08/1991	1	5
1304	Dubmill Scar	307000	545000	00/00/1999	1	3
1305	Dubmill Point (Mawbray)	307000	545000	03/07/2000	1	6
1306	Dubmill Point (Mawbray)	307000	545000	01/03/2002	1	5
1307	Dubmill Scar	307000	545000	21/07/2012	1	6
1309	Mawbray Bank (Mawbray)	307000	547000	01/03/2002	0	0
1310	Mawbray Scar (Mawbray)	307000	547000	21/07/2012	1	6
1311	Stinking Crag (Mawbray)	307000	548000	01/03/2002	1	4
1312	Lowhagstock Crag, S (Beckfoot)	307000	549000	01/03/2002	0	0
1313	Beckfoot	307000	549000	21/07/2012	1	4
1314	Beckfoot	307000	550000	00/00/1984	0	0
1315	Lowhagstock Crag, N (Beckfoot)	307000	550000	01/03/2002	1	5
1316	Beckfoot	307000	550000	21/07/2012	1	4
1317	Grab samples C	307000	551000	01/07/2004	1	6
1318	Poolness Beach (Budleigh)	308000	83000	05/10/1994	1	7
1319	Brandy Head/Poolness Beach (Crab Ledge to Black Head, Otterton)	308000	83000	05/10/1994	1	3
1320	Site 333 (Upper Bristol Channel)	308000	155000	17/04/1988	1	10
1321	Site 444 (Upper Bristol Channel)	308000	161000	26/04/1988	1	10
1322	Annaside Bank	308000	485000	01/03/2002	1	7

1323	Annaside Bank	308000	486000	01/03/2002	1	7
1324	Annaside Bank	308000	486000	20/03/2004	1	6
1325	Annaside Bank	308000	486000	22/07/2012	1	6
1326	Annaside Bank	308000	487000	01/03/2002	1	7
1328	Crab Ledge (Otterton)	309000	84000	07/09/1994	1	6
1329	Smallstones Point (Otterton)	309000	84000	26/06/1994	1	6
1330	Smallstones Point to Crab Ledge (Otterton)	309000	84000	07/09/1994	1	6
1331	Smallstones Point to Crab Ledge (Otterton)	309000	84000	20/06/2007	1	3
1332	Ladram Bay (Otterton)	309000	85000	07/03/1992	1	3
1333	Hern Rock Bay (Otterton)	309000	85000	27/04/1994	1	7
1334	Doniford	309000	143000	00/00/1984	1	6
1335	Hurlestone Point (Doniford)	309000	143000	07/10/2002	0	0
1336	Site 255 (Upper Bristol Channel)	309000	145000	15/04/1988	1	10
1337	Annaside Bank	309000	484000	00/00/1984	1	6
1338	Gutterby Spa	309000	484000	06/04/1989	1	6
1339	Gutterby Spa	309000	484000	01/03/2002	1	6
1340	Annaside Bank	309000	484000	22/07/2012	1	6
1341	St Audries Bay (Doniford)	310000	143000	00/00/1984	1	6
1342	St Audries Bay (Doniford)	310000	143000	24/05/2013	1	5
1343	Site 276 (Upper Bristol Channel)	310000	146000	16/04/1988	1	10
1344	Site 181 (Upper Bristol Channel)	310000	149000	12/04/1988	1	10
1345	Site 329 (Upper Bristol Channel)	310000	152000	17/04/1988	1	10
1346	Cold Knap Point to Barry Dock	310000	165000	14/09/2004	1	10
1347	Gutterby, S	310000	482000	01/03/2002	1	4
1348	Gutterby	310000	483000	01/03/2002	1	4
1349	Gutterby Spa (Annaside Bank)	310000	484000	01/03/2002	1	6
1352	Rough Scar	310000	563000	00/00/2000	1	10
1353	Site 530 (Upper Bristol Channel)	311000	163000	28/04/1988	1	10
1354	Site 29 (Upper Bristol Channel)	311000	164000	07/04/1988	1	10
1355	Barry Island	311000	165000	14/03/2013	1	6
1356	Gutterby, S	311000	481000	01/03/2002	1	4
1357	Gutterby, S	311000	482000	01/03/2002	1	4
1358	Sidmouth (Jacobs Ladder)	312000	86000	00/00/1980	1	10
1359	Sidmouth	312000	86000	14/01/1998	1	4
1360	Sidmouth	312000	86000	05/09/2002	1	6
1361	Chit Rocks (Sidmouth)	312000	87000	02/09/1992	1	3
1362	Site 257 (Upper Bristol Channel)	312000	145000	15/04/1988	1	10
1363	Brewing Scar	312000	563000	00/00/1987	1	10
1364	Priestdale Bank (Solway, N)	312000	564000	26/09/1994	1	6
1366	Barry	313000	166000	14/03/2013	1	5
1367	Barry Dock to Sully Island	313000	167000	10/09/2002	1	10
1369	Kilve	314000	144000	00/00/1976	1	6
1370	Kilve	314000	144000	24/05/2013	0	0
1371	Barry Dock to Sully Island	314000	167000	27/08/2002	1	10
1372	Brow Scar	314000	559000	00/00/2000	1	4
1373	Hook Ebb (Sidmouth)	315000	87000	23/08/1994	1	3
1374	Hook Ebb (Beer Head to Chit Rocks, Sidmouth)	315000	87000	23/08/1994	1	3
1375	Site 326 (Upper Bristol Channel)	315000	152000	17/04/1988	1	10
1376	Site 338 (Upper Bristol Channel)	315000	155000	17/04/1988	1	10
1377	Site 69 (Upper Bristol Channel)	315000	160000	08/04/1988	1	10
1378	Barry Dock to Sully Island	315000	167000	10/09/2002	1	10
1379	Site 325 (Upper Bristol Channel)	316000	152000	17/04/1988	1	10
1382	Sully Island	316000	166000	00/00/1973	1	3
1383	Barry Dock to Sully Island	316000	166000	10/09/2002	1	10
1384	Barry Dock to Sully Island	316000	166000	10/09/2002	1	10
1385	Sully Island	316000	166000	14/03/2013	1	5
1386	Sully Island	316000	166000	2002-2004	1	10
1387	Sully Island	316000	167000	24/10/1976	1	6
1388	Sully Island	316000	167000	24/10/1976	1	10
1389	Earnse Bay (Walney Island)	316000	469000	00/00/2002	1	4
1390	Weston Ebb (Weston)	317000	87000	24/08/1994	1	5
1391	Weston Ebb (Beer Head to Chit Rocks, Weston)	317000	87000	24/08/1994	1	5
1392	Bent Haw Scar (Walney Island)	317000	466000	01/03/2002	1	6
1393	Tummer Hill Scar (Walney Island)	317000	467000	01/03/2002	1	7
1394	Earnse Bay (Walney Island)	317000	469000	16/02/2012	1	10
1395	Earnse Bay (Walney Island)	317000	469000	16/02/2012	1	10
1397	Site 438 (Upper Bristol Channel)	318000	161000	26/04/1988	1	10

1398	Lavernock Point	318000	167000	00/00/1976	1	5
1399	Lavernock Point	318000	167000	00/00/1984	1	6
1400	Sully Island to Lavernock Point	318000	167000	10/09/2002	1	10
1401	Lavernock Point	318000	167000	14/03/2013	1	6
1402	Lavernock Point to Cardiff Bay	318000	168000	27/08/2002	1	10
1403	Lavernock Point to Cardiff Bay	318000	170000	27/08/2002	1	10
1406	Hilbre Island	318000	387000	00/00/1979	1	2
1407	Hilbre Island	318000	387000	00/00/1984	0	0
1408	Hilbre Island	318000	387000	07/03/2004	1	6
1409	Hilbre Island	318000	387000	17/07/2005	1	6
1410	Hilbre Island	318000	387000	08/03/2006	1	10
1411	HilbreIsland, SW	318000	387000	23/07/2012	1	6
1412	North Bay (Hilbre Island)	318000	388000	07/03/2004	1	6
1413	North Bay (Hilbre Island)	318000	388000	24/07/2012	1	6
1414	Cross Dyke Scar (Walney Island)	318000	464000	01/03/2002	1	6
1415	Bent Haw Scar (Walney Island)	318000	466000	01/03/2002	1	6
1417	Branscombe Ebb	319000	87000	00/00/1980	1	5
1418	Branscombe Ebb	319000	87000	25/08/1994	1	6
1419	Hinckley Point	319000	146000	26-30/07/1993	1	5
1420	Hinckley Point	319000	146000	26-30/07/1993	1	5
1421	Hinckley Point	319000	146000	26-30/07/1993	1	5
1422	Lavernock Point to Cardiff Bay	319000	171000	27/08/2002	1	10
1423	Lavernock Point to Cardiff Bay	319000	171000	27/04/2002	1	10
1424	South End Scar (Walney Island)	319000	462000	30/08/2007	1	6
1425	South End Scar (Walney Island)	319000	462000	18/09/2007	1	6
1426	Cross Dyke Scar (Walney Island)	319000	463000	01/03/2002	1	6
1427	South End Scar (Walney Island)	319000	463000	18/09/2007	1	6
1428	Cross Dyke Scar (Walney Island)	319000	464000	01/03/2002	1	6
1429	Cross Dyke Scar (Walney Island)	319000	464000	22/07/2012	1	6
1431	Hinckley Point	320000	146000	00/00/1984	1	5
1432	Hinckley Point	320000	146000	00/00/1985	1	5
1433	Hinckley Point	320000	146000	00/02/1986	1	5
1434	Hinckley Point	320000	146000	00/04/1986	1	5
1435	Hinckley Point	320000	146000	00/06/1986	1	5
1436	Hinckley Point	320000	146000	00/07/1986	1	5
1437	Hinckley Point	320000	146000	00/08/1990	1	5
1438	Hinckley Point	320000	146000	00/09/1990	1	5
1439	Hinckley Point	320000	146000	00/10/1991	1	5
1440	Hinckley Point	320000	146000	00/12/1991	1	5
1441	Hinckley Point	320000	146000	21/01/1992	1	5
1442	Hinckley Point	320000	146000	18-19/02/1992	1	5
1443	Hinckley Point	320000	146000	00/11/1992	1	5
1444	Hinckley Point	320000	146000	00/12/1992	1	5
1445	Hinckley Point	320000	146000	00/03/1993	1	5
1446	Hinckley Point	320000	146000	26-30/07/1993	1	6
1447	Hinckley Point	320000	146000	26-30/07/1993	1	6
1448	Hinckley Point	320000	146000	26-30/07/1993	1	6
1449	Site 64 (Upper Bristol Channel)	320000	163000	08/04/1988	1	10
1450	Site 63 (Severn Estuary)	320000	164000	08/04/1988	1	10
1451	Site 61 (Severn Estuary)	320000	167000	08/04/1988	1	10
1454	South End (Walney Island)	320000	463000	22/07/2012	1	6
1455	Hinckley Point	321000	146000	00/00/1976	1	5
1456	Hinckley Point	321000	146000	00/00/1982	1	4
1457	Hinckley Point	321000	146000	00/00/1984	1	6
1458	Hinckley Point	321000	146000	00/00/1985	1	6
1459	Hinckley Point	321000	146000	00/02/1986	1	6
1460	Hinckley Point	321000	146000	00/04/1986	1	6
1461	Hinckley Point	321000	146000	00/06/1986	1	6
1462	Hinckley Point	321000	146000	00/07/1986	1	6
1463	Hinckley Point	321000	146000	00/08/1990	1	6
1464	Hinckley Point	321000	146000	00/09/1990	1	6
1465	Hinckley Point	321000	146000	00/10/1991	1	10
1466	Hinckley Point	321000	146000	00/12/1991	1	10
1467	Hinckley Point	321000	146000	21/01/1992	1	10
1468	Hinckley Point	321000	146000	18-19/02/1992	1	10
1469	Hinckley Point	321000	146000	00/11/1992	1	10
1470	Hinckley Point	321000	146000	00/12/1992	1	10
1471	Hinckley Point	321000	146000	00/03/1993	1	10
1472	Hinckley Point	321000	146000	26-30/07/1993	1	6

1473	Hinckley Point	321000	146000	00/00/1994	1	6
1474	Hinckley Point	321000	146000	00/08/1996	1	6
1475	Site 289 (Upper Bristol Channel)	321000	147000	16/04/1988	1	10
1476	Site 162 (Severn Estuary)	321000	161000	12/04/1988	1	10
1482	Beer Head	322000	87000	00/00/1984	1	6
1484	Beer	322000	88000	00/00/1970	1	6
1485	Beer	322000	88000	00/00/1977	1	6
1486	Big Ledge(Beer)	322000	88000	24/06/1994	1	3
1487	Site name protected	322000	160000	12/08/1995	1	10
1488	Ynys Echni (The Wolves & Monkstone Rock)	322000	164000	27/08/2002	1	10
1489	Ynys Echni (The Wolves & Monkstone Rock)	322000	165000	27/08/2002	1	10
1490	Pickle Scar, N (Piel Channel, Morecombe Bay)	322000	464000	15/09/1998	1	5
1491	NW of No. 2 buoy, Piel Channel (Morecombe)	322000	464000	17/09/1998	1	2
1492	E of Pickle Scar Beacon(Morecombe)	322000	464000	15/09/1998	1	4
1493	Head Scar Beacon (Morecombe)	322000	464000	15/09/1998	1	4
1494	Head Scar (Piel Channel, Morecombe Bay)	322000	465000	26/09/1999	1	2
1495	Head Scar (Barrow, Morecombe Bay)	322000	465000	01/03/2002	0	0
1499	Beer	323000	88000	00/00/1970	1	6
1500	Beer	323000	88000	03/09/1992	1	4
1501	Seaton Hole	323000	89000	22/06/1994	1	2
1504	Unknown	323000	160000	12/08/1995	1	10
1505	SE Point (Walney Island)	323000	461000	01/03/2002	1	4
1507	Site 313 (Severn Estuary)	324000	165000	17/04/1988	1	10
1508	Site 311 (Severn Estuary)	324000	168000	17/04/1988	1	10
1509	Site 310 (Severn Estuary)	324000	170000	17/04/1988	1	10
1510	Site 309 (Severn Estuary)	324000	171000	17/04/1988	1	10
1511	Site 129 (Severn Estuary)	324000	173000	11/04/1988	1	10
1512	Leasowe BW, W of Lighthouse (Wirral)	324000	391000	00/00/2003	1	2
1513	Leasowe BW, W of Lighthouse (Wirral)	324000	391000	24/07/2012	1	3
1514	East Scar Buoy, N (Piel Channel, Morecombe)	324000	462000	16/09/1999	1	2
1515	Piel East Buoy (Piel Channel, Morecambe)	324000	463000	16/09/1999	1	3
1516	SE of Castle Buoy (Morecombe Bay)	324000	463000	17/09/1999	1	2
1517	Piel West Buoy, Pile Channel (Morecombe)	324000	463000	17/09/1999	1	2
1518	E of Ridge Buoy, Piel Channel (Morecombe)	324000	463000	16/09/1999	1	3
1525	Sparrowbush Ledge (Seaton)	326000	89000	22/09/1994	1	3
1526	Sparrowbush Ledge (Seaton)	326000	89000	28/06/2002	1	10
1527	Site 378 (Severn Estuary)	326000	161000	19/04/1988	1	10
1528	Site 376 (Severn Estuary)	326000	164000	19/04/1988	1	10
1529	Site 373 (Severn Estuary)	326000	168000	19/04/1988	1	10
1530	Site 130 (Severn Estuary)	326000	173000	11/04/1988	1	10
1531	Site 308 (Severn Estuary)	326000	176000	17/04/1988	1	10
1532	Leasowe BW, Mid (Wirral Foreshore)	326000	392000	00/00/2003	1	5
1533	Leasowe BW, Mid (Wirral Foreshore)	326000	392000	24/07/2012	1	5
1536	Culverhole Point (Lyme Regis)	327000	89000	25/06/1994	1	6
1537	Site 269 (Upper Bristol Channel)	327000	155000	16/04/1988	1	10
1538	Site 385 (Severn Estuary)	327000	168000	19/04/1988	1	10
1539	Site 131 (Severn Estuary)	327000	173000	11/04/1988	1	10
1540	Leasowe BW, East (Wirral Foreshore)	327000	392000	24/07/2012	1	1
1541	Site 380 (Severn Estuary)	328000	162000	19/04/1988	1	10
1542	Kings Parade, W (Wirral Foreshore)	328000	393000	24/07/2012	1	5
1545	Site 400 (Severn Estuary)	329000	170000	20/04/1988	1	10
1546	Kings Parade, E (Wirral Foreshore)	329000	394000	00/00/2003	1	5
1547	Kings Parade, E (Wirral Foreshore)	329000	394000	24/07/2012	1	5
1549	Birnbeck (Weston Super Mare)	330000	162000	00/00/1984	1	4
1550	Birnbeck (Weston Super Mare)	330000	162000	28/05/2013	1	4
1551	Site 456 (Severn Estuary)	330000	165000	26/04/1988	1	10
1552	Site 399 (Severn Estuary)	330000	170000	20/04/1988	1	10
1553	N Brighton Lighthouse, W (Wirral Foreshore)	330000	394000	00/00/2003	0	0
1554	N Brighton Lighthouse, W (Wirral Foreshore)	330000	394000	24/07/2012	1	5
1555	Blackpool Sea Wall	330000	432000	04/02/2012	1	2
1556	Rossal Point (Fleetwood)	330000	447000	22/07/2012	1	4
1557	Humble Point, E (Lyme Regis)	331000	90000	20/09/1994	1	5
1558	Pinhay East (Beer Head to Burton Bradstock)	331000	90000	23/06/1994	1	3
1559	Sand Point (Kewstoke)	331000	165000	00/00/1984	1	4
1560	Sand Point (Kewstoke)	331000	165000	28/05/2013	0	0
1562	Seaward Groyne (Mersey)	331000	393000	24/07/2012	1	4
1563	N Brighton Lighthouse, E (Wirral Foreshore)	331000	394000	00/00/2003	1	5
1564	N Brighton Lighthouse, E (Wirral Foreshore)	331000	394000	24/07/2012	1	5
1568	Rossal Point (Fleetwood)	331000	447000	00/00/1984	0	0

1569	Rossal Point (Fleetwood)	331000	447000	18/03/2004	1	4
1570	Rossal Point (Fleetwood)	331000	447000	22/07/2012	0	0
1573	Pinhay, W (Lyme Regis)	332000	90000	23/06/1994	1	7
1574	Seven Rock Point	332000	90000	23/06/1994	1	2
1575	Lyme Regis	332000	90000	30/01/2002	0	0
1576	Lyme Regis	332000	90000	15/07/2003	1	4
1577	Site 538 (Severn Estuary)	332000	168000	28/04/1988	1	10
1578	Site 398 (Severn Estuary)	332000	170000	20/04/1988	1	10
1581	Monmouth Beach (Lyme Regis)	333000	91000	00/00/1981	1	5
1582	Lyme Regis	333000	91000	00/00/1984	0	0
1583	Devonshire Head (Lyme Regis)	333000	91000	27/05/1994	1	7
1584	Devonshire Head (Lyme Regis)	333000	91000	30/04 & 14/10/2011	1	10
1585	Middle Hope Cove (Kewstoke)	333000	166000	00/00/1984	1	4
1586	Middle Hope Cove (Kewstoke)	333000	166000	28/05/2013	1	5
1588	Broad Ledges (Lyme Regis)	334000	92000	28/03/1994	1	3
1589	Broad Ledges (Lyme Regis)	334000	92000	27/05/1994	1	3
1590	Lyme Regis	334000	92000	09/06/1997	1	6
1591	Lyme Regis	334000	92000	15/04/1999	1	6
1592	Lyme Regis	334000	92000	15/06/2000	1	6
1593	Lyme Regis	334000	92000	26/04/2001	1	6
1594	Lyme Regis	334000	92000	25/04/2002	1	5
1595	Lyme Regis	334000	92000	01/06/2003	1	6
1596	Lyme Regis	334000	92000	08/05/2012	1	6
1597	Severn Estuary	334000	176000	00/00/1988	1	10
1598	Bar Ledges (Lyme Regis)	335000	92000	26/05/1994	1	2
1599	Charmouth	335000	92000	15/10/2008	1	10
1600	Site 461 (Severn Estuary)	335000	167000	26/04/1988	1	10
1602	Charmouth, N	336000	92000	09/08/1994	1	3
1603	Site 376 and Site 412 (Severn Estuary)	336000	180000	19/04/1988	1	10
1604	Site 26 (Severn Estuary)N	336000	181000	01/07/1980	1	10
1608	Black Rocks (Clevedon)	338000	170000	23/05/2013	1	6
1610	Foot Skear (Heysham Sands)	339000	462000	25/09/1999	1	6
1611	Knot End (Heysham Sands)	339000	462000	01/03/2002	1	7
1612	Foot Skear (Heysham Sands)	339000	462000	00/00/2003	1	10
1613	Heysham Flats	339000	462000	30/08/2011	1	10
1614	Foot Skear (Heysham Sands)	339000	462000	14/08/2012	1	7
1615	Foot Skear (Heysham Sands)	339000	462000	28/08/2013	1	7
1619	Clevedon	340000	172000	00/00/1976	1	5
1620	Clevedon	340000	172000	00/00/1984	1	3
1621	Clevedon	340000	172000	23/05/2013	0	0
1625	Heysham Village	340000	460000	00/00/1984	0	0
1626	Heysham Village	340000	460000	21/03/2004	0	0
1627	Heysham Power Station	340000	460000	00/00/2012	1	5
1628	Foot Skear (Heysham Sands)	340000	461000	00/00/2012	1	6
1629	Foot Skear (Heysham Sands)	340000	461000	07/02/2012	1	4
1630	Foot Skear (Heysham Sands)	340000	462000	00/00/1997	1	6
1631	Foot Skear (Heysham Sands)	340000	462000	25/09/1999	1	6
1632	Foot Skear (Heysham Sands)	340000	462000	01/03/2002	1	7
1633	Heysham Flats	340000	462000	27/09/2011	1	10
1634	Heysham Flats	340000	462000	27/09/2011	1	10
1635	Heysham Flats	340000	462000	27/09/2011	1	10
1636	Heysham Flats	340000	462000	27/09/2011	1	10
1637	Heysham Flats	340000	462000	27/09/2011	1	10
1638	Heysham Flats	340000	462000	27/09/2011	1	10
1639	Heysham Flats	340000	462000	30/08/2011	1	10
1640	Heysham Flats	340000	462000	30/08/2011	1	10
1641	Heysham Flats	340000	462000	30/08/2011	1	10
1642	Heysham Flats	340000	462000	30/08/2011	1	10
1643	Heysham Flats	340000	462000	30/08/2011	1	10
1644	Heysham Flats	340000	462000	30/08/2011	1	10
1645	Heysham Flats	340000	462000	27/09/2011	1	10
1646	Heysham Flats	340000	462000	27/09/2011	1	10
1647	Heysham Flats	340000	462000	27/09/2011	1	10
1648	Heysham Flats	340000	462000	27/09/2011	1	10
1649	Heysham Flats	340000	462000	30/08/2011	1	10
1650	Foot Skear (Heysham Sands)	340000	462000	14/08/2012	1	6
1651	Foot Skear (Heysham Sands)	340000	462000	28/08/2013	1	6
1656	Foot Skear Inshore (Heysham Sands)	341000	463000	28/11/1997	1	5
1657	Foot Skear Inshore (Heysham Sands)	341000	463000	01/03/2002	0	0

1658	Foot Skear Inshore (Heysham Sands)	341000	463000	14/08/2012	1	5
1659	Foot Skear Inshore (Heysham Sands)	341000	463000	28/08/2013	0	0
1663	Portishead	343000	175000	23/05/2013	1	6
1671	Portishead	346000	177000	00/00/1974	1	6
1672	Portishead	346000	177000	00/00/1984	1	3
1673	Portishead	346000	177000	23/05/2013	0	0
1676	English Stones (Severn Estuary)	351000	186000	23/07/1997	1	7
1678	Chapel Rock (Severn Estuary, ST)	354000	189000	22/07/1997	1	2
1679	Aust Rocks (Severn Estuary, ST)	356000	190000	21/07/1997	1	6
1692	Lulworth Cove	382000	79000	26/04/2002	1	2
1695	Kimmeridge	390000	79000	00/00/1977	1	10
1696	Kimmeridge	390000	79000	27/04/2002	0	0
1697	Kimmeridge	390000	79000	10/05/2013	0	0

Appendix 2.4: Suitable *Sabellaria alveolata* sites with collated data paired between decades from the 1980s to the 2010s. This dataset is referred to throughout the document as paired area data. Location data includes site name, OSGB coordinates, and sampled years. Original record identifying codes are included for paired area data (see Appendix 2.2), in addition to identifying codes for each paired area (see Appendix 2.3).

Original record ID (Appendix 2.2)	**Site name**	**Eastin-gs**	**Northin-gs**	**Sampled years**	**Paired Area ID**
1063/1064	St Marys Bay, N (Brixham)	293000	55000	1984/1993	P2
1011/1012/1013/1014	Saltern Cove (Goodrington)	289000	58000	1992/1993/1993/2004	P3
1015/1016/1017/1018/1019/1020	Goodrington, Sands Reef	289000	59000	1984/1992/2006/2007/2007/2003-2004	P4
1033/1034	Torbay	290000	63000	1992/2002	P5
78/79/80	Trevone	188000	75000	1968/2002/2013	P6
1094/1095	Corytons Cove (Dawlish)	296000	76000	1984/1992	P8
1265/1266/1267	Black Head to Otterton Ledge (Otterton)	307000	81000	2002/1992/2002	P12
1328/1329/1330/1331	Smallstones Point to CrabLedge (Otterton)	309000	84000	1994/1994/1994/2007	P14
125/126	Trebarwith Strand	204000	86000	1984/2013	P15
1358/1359/1360	Sidmouth	312000	86000	1980/1998/2002	P16
1416/1417/1418	Branscombe Ebb	319000	87000	1964/1980/1994	P17
1525/1526	Sparrowbush Ledge (Seaton)	326000	89000	1994/2002	P20
1573/1574/1575/1576	Pinhay, W (Lyme Regis)	332000	90000	1994/1994/2002/2003	P21
1580/1581/1582/1583/1584	Devonshire Head (Lyme Regis)	333000	91000	1964/1981/1984/1994/2011	P22
1588/1589/1590/1591/1592/1593/1594/1595/1596	Lyme Regis	334000	92000	1994/1994/1997/1999/2000/2001/2002/2003/2012	P23
1598/1599	Bar Ledges (Lyme Regis)	335000	92000	1994/2008	P24
163/164	Crackington Haven, SW	213000	96000	2003/2013	P25
165/166	Crackington Haven, N	213000	97000	1984/2013	P26
208/209/210/211	Millook	218000	100000	1957/1975/1984/2012	P27
214/215/216	Black Rock (WidemouthBay)	219000	101000	1986/2003/2013	P28
217/218/219	Widemouth Bay	219000	102000	1970/2003/2013	P29
257/258/259/260/261/262/263	Bude	220000	106000	1977/1980/1997/2000/2001/2012/2013	P30
221/222	Flexbury (Bude)	219000	107000	2003/2013	P31
223/224/225/226/227/228/229/230/231/232/233/234/235/236/237/238/239/240/241/242/243/244/245/246/247/248	Duckpool (Coombe)	219000	111000	1961/1962/1963/1964/1965/1966/1967/1968/1969/1970/1971/1972/1973/1975/1977/1978/1984/1992/1996/1998/1999/2000/2001/2002/2003/2013	P32
394/395/396	Bucks Mills	235000	123000	1984/1993/2013	P33
280/281/282/283/284/285/286/287	Hartland Quay	222000	124000	1977/1984/1993/1999/2002/2003/2012/2013	P34
351/352	Clovelly Pier	231000	124000	2002/2013	P35
379/380	Clovelly	232000	124000	1983/2013	P36
421/422/423/424/425	Greencliff (Abbotsham)	240000	127000	1993/2007/2008/2010/2011	P37
437/438/439/440	Abbotsham	241000	127000	2008/2009/2011/2013	P38
446/447/448/449	Westward Ho	242000	129000	1977/1984/1988/2013	P39
459/460/461/462	Downend (Croyde, S)	243000	138000	1977/1978/1983/2013	P40
463/464/465	Croyde	243000	139000	1977/2004/2013	P41
494/495	Woolacombe	245000	143000	1983/2001	P42
1192/1193	Blue Anchor	303000	143000	2002/2013	P43
1334/1335	Doniford	309000	143000	1984/2002	P45
1341/1342	St Audries Bay (Doniford)	310000	143000	1984/2013	P46
1194/1195/1196/1197/1198	Blue Anchor	303000	144000	1941/1976/1978/1984/2013	P47
525/526/527/528/529	Lee Bay, W (Woolacombe)	247000	146000	2007/2008/2010/2011/2013	P49
550/551	Lee Bay (Woolacombe)	248000	146000	1983/2013	P50
1431/1432/1433/1434/1435/1436/1437/1438/1439/1440/1441/1442/1443/1444/1445/1446/1447/1448	Hinckley Point	320000	146000	1984/1985/1986/1986/1986/1986/1990/1990/1991/1991/1991/1991/1992/1992/1993/1993/1994/1996	P51
1455/1456/1457/1458/1459/1460/1461/1462/1463/1464/1465/1466/1467/1468/1469/1470/1471/1472/14	Hinckley Point	321000	146000	1976/1982/1984/1985/1986/1986/1986/1986/1990/1990/1991/1991/1991/1991/1992/1992/1993/1993/1994/1996	P52

73/1474					
612/613	Ilfracombe	251000	147000	1984/2013	P54
1105/1106/1107/1108/1109	Minehead	297000	147000	1976/1984/1984/2002/2013	P55
632/633	HeleBay	253000	148000	1984/2013	P56
975/976	Porlock Weir	286000	148000	1984/2013	P58
1548/1549/1550	Birnbeck (Weston Super Mare)	330000	162000	1941/1984/2013	P59
1559/1560	Sand Point (Kewstoke)	331000	165000	1984/2013	P61
1171/1172	Limpert Bay (Aberthaw)	301000	166000	2004/2013	P62
1380/1381/1382/1383/1384/1385/1386	Sully Island	316000	166000	1957/1964/1973/2002/2002/2013/2002-2004	P63
1585/1586	Middle Hope Cove (Kewstoke)	333000	166000	1984/2013	P64
1038/1039/1040	Nash Point (Bristol Channel, N)	291000	167000	1979/1997/2013	P65
1081/1082/1083/1084/1085	Llantwit Major	295000	167000	1957/1976/1984/2004/2013	P68
1398/1399/1400/1401	Lavernock Point (Penarth)	318000	167000	1976/1984/2002/2013	P69
998/999/1000/ 1001/1002	Temples Bay	288000	172000	1997/2003/2012/2013/2014	P71
1619/1620/1621	Clevedon	340000	172000	1976/1984/2013	P72
956/957/958/959	Dunraven Bay	284000	173000	2003/2004/2010/2011	P73
986/987	Dunraven Bay	287000	173000	2003/2014	P74
1003/1004/1005/1006/1007/1008	Dunraven Bay	288000	173000	1976/1984/1997/2003/2011/2014	P75
977/978/979/980	Black Rocks (Dunraven Bay)	286000	174000	2003/2005/2008/2012	P76
988/989	Dunraven Bay	287000	174000	2003/2012	P77
918/919/920/921	Hutchwns Point (Porthcawl)	280000	176000	1984/1988/2003/2013	P78
939/940/941	Hutchwns Point (Porthcawl)	282000	176000	1971/2003/2013	P79
1668/1669/1670/1671/1672/1673	Portishead	346000	177000	1924/1939/1941/1974/1984/2013	P80
516/517/518/519/520	Overton	246000	184000	1973/1978/2001/2004/2013	P83
530/531/532/533/534/535	Port Eynon	247000	184000	1978/2000/2001/2004/2011/2013	P84
592/593/594	Oxwich	250000	185000	1973/1984/2013	P88
414/415/416	Worms Head	239000	186000	2001/2004/2013	P90
643/644/645	Limeslade Bay	255000	186000	2004/2013/2014	P91
663/664/665/666/667/668/669	Deep Slade	256000	186000	1970/1973/1978/1980/2004/2013/2014	P92
696/697/698	Shirecombe to Graves End	257000	186000	1973/1978/2004	P93
417/418/419/420	Worms Head	239000	187000	1973/1978/2001/2013	P94
635/636/637/638/639	Southgate	254000	187000	1973/1978/2004/2013/2014	P95
646/647/648	Caswell	255000	187000	2004/2013/2014	P96
717/718	Caswell	258000	187000	2004/2013	P97
781/782/783/784/785/786/787	LimesladeBay (The Mumbles, Swansea)	262000	187000	1973/1984/2001/2004/2006/2013/2014	P98
794/795/796/797/798/799/800	Bracelet Bay (Swansea)	263000	187000	1978/1984/2001/2006/2011/2013/2014	P99
871/872	Port Talbot Harbour	274000	187000	2003/2013	P100
890/891	Port Talbot Harbour	275000	188000	2003/2013	P101
815/816/817	Swansea Bay	265000	191000	2001/2003/2014	P102
847/848	Swansea Bay	269000	191000	2003/2014	P103
167/168/169	Overhangs (Saint Catherines)	213000	200000	1984/2008/2013	P104
173/174	Monkstone Point (Saundersfoot)	214000	203000	1984/2013	P105
183/184/185	Monkstone Point (Saundersfoot)	215000	203000	2002/2008/2013	P106
44/45/46	Abereiddy	179000	231000	1984/2002/2012	P107
127/128/129/130	Parrog	204000	239000	1984/2003/2012/2014	P108
310/311/312/313/314/315/316/317/318/319/320	Aberporth	225000	251000	1984/1996/1997/2002/2004/2005/2006/2007/2008/2012/2014	P110
337/338/339	Tresaith	227000	251000	1996/1997/2004	P111
353/354/355	Llangrannog	231000	254000	1984/2012/2014	P112
397/398/399/400	Cwmtudu Headland	235000	257000	1982/1997/2012/2014	P113
427/428/429/430	Cei Bach	240000	259000	2004/2007/2009/2010	P114
409/410/411	New Quay	238000	260000	1995/2002/2013	P115
431/432/433/434/435	Cei Bach	240000	260000	2004/2007/2008/2009/2010	P116
471/472/473	Gilfach yr Halen, SW (Aberaeron)	243000	261000	1996/1997/2004	P117

486/487	Craig Ddu (Aberaeron)	244000	262000	1997/2004	P118
500/501/502/503/504/505/506/507/508/509/510/511	Aberaeron	245000	263000	1964/1997/2002/2004/2007/2008/2009/2010/2010/2011/2012/2014	P119
521/522	Aberarth	246000	263000	2004/2014	P120
537/538	Aberarth	247000	263000	2004/2014	P121
539/540	Aberarth	247000	264000	2004/2014	P122
554/555/556/557	Aberarth (Aberaeron)	248000	264000	1997/2013/2013/2014	P123
596/597	Llanon, S (Aberaeron)	250000	266000	1997/2003	P124
622/623/624/625	Llanrhystud (Aberystwyth)	252000	269000	1984/1997/2003/2012	P125
701/702/703/704/705	Castle Rocks (Aberystwyth)	257000	281000	2003/2005/2006/2008/2012	P126
719/720/721/722/723/724/725/726/727/728	Castle Rocks, N (Aberystwyth)	258000	282000	1984/1997/2002/2003/2005/2006/2010/2011/2012/2013	P127
729/730	Clarach Bay (Aberystwyth)	258000	284000	1997/2004	P128
731/732	Sarn Cynfelyn (Aberystwyth)	258000	285000	1997/2004	P129
741/742	Borth	259000	286000	1997/2004	P130
744/745	Borth	259000	288000	1997/2004	P131
758/759/760/761/762/763/764	Borth	260000	288000	1935/1984/1997/2002/2004/2006/2012	P132
674/675/676	Friog	256000	305000	1997/2004/2005	P133
677/678/679	Friog	256000	306000	1997/2004/2005	P134
734/735/736	Llwyngwril (Barmouth Bay)	258000	310000	1997/2004/2012	P135
746/747/748	Llwyngwril (Barmouth Bay)	259000	310000	1997/2004/2012	P136
749/750/751/752	Llwyngwril	259000	311000	1982/1984/2004/2012	P137
769/770	Barmouth	260000	315000	1984/2012	P138
652/653/654	Shell Island (Mochras)	255000	326000	2004/2005/2012	P139
655/656	Shell Island (Mochras)	255000	327000	2004/2012	P140
681/682/683/684	Shell Island (Mochras)	256000	327000	1978/1984/2004/2012	P141
357/358/359/360/361/362/363/364	Abersoch (Lifeboat Station)	231000	328000	2003/2004/2009/2010/2011/2012/2013/2013	P142
685/686/687/688/689/690	Llandanwg	256000	328000	2004/2005/2009/2009/2009/2012	P143
710/711/712/713	Llandanwg (Pen Llŷn ar Sarnau)	257000	329000	1978/1984/1997/2004	P144
385/386/387	Llanbedrog (Pwllheli)	233000	331000	1995/1996/2003	P145
474/475/476/477	Porth Fechan and Rhosneigr (W of Afon Wen)	243000	335000	1995/1996/2004/2005	P146
489/490/491	Afon Wen	244000	337000	1964/1984/2012	P147
523/524	Criccieth	246000	337000	1996/2004	P148
542/543/544/545/546/547	Criccieth	247000	337000	2002/2004/2009/2009/2009/2012	P149
558/559/560	Criccieth	248000	337000	1995/2004/2004	P150
570/571/572/573/574/575/576/577/578/579/580/581/582/583/584/585	Criccieth Castle	249000	337000	1950/1964/1984/1996/2002/2003/2004/2005/2006/2007/2008/2009/2010/2011/2012/2013	P151
598/599/600/601	Criccieth Castle, E (Criccieth)	250000	337000	1995/1996/1997/2013	P152
602/603/604/605/606/607/608/609/610/611	Criccieth, E (Criccieth)	250000	338000	2003/2004/2006/2007/2008/2009/2010/2011/2012/2013	P153
341/342	Porth Dinllaen	227000	341000	2002/2013	P154
441/442	Aberdesach, SW (Trefor)	241000	350000	1995/2013	P155
388/389	Porth Cwyfan (Rhosneigr)	233000	368000	1996/2013	P156
365/366/367/368/369/370/371/372/373/374/375/376	Rhosneigr	231000	372000	1983/2002/2005/2006/2007/2008/2009/2010/2011/2012/2012/2013	P157
990/991	Colwyn Bay	287000	378000	1984/2003	P158
1043/1044/1045/1046/1047/1048/1049/1050/1051/1052	Llanddulas	291000	378000	2008/2008/2008/2010/2011/2012/2012/2013/2014/2014	P159
804/805/806	Penmon Point, W (Menai Strait, N)	263000	381000	1997/2012/2013	P160
810/811/812	Puffin Island, S (Menai Strait, N)	264000	381000	1997/2002/2003	P161
963/964/965/966	Penrhyn Bay (Rhos Point)	284000	381000	1923/1984/2003/2004	P162
926/927/928/928/930/931/932/933/934/935/936	Little Ormes Head	281000	382000	1997/2004/2005/2005/2007/2008/2009/2010/2011/2012/2013	P163
874/875/876/877/878/879/880/881/882/883/884	Trwynygogarth (Great Orme, W)	274000	383000	2003/2004/2005/2006/2007/2008/2009/2010/2011/2012/2013	P164
892/893/894/895	Great Ormes Head, W (Llandudno)	275000	383000	1984/1997/2003/2012	P165

1404/1405/1406/1407/1408/1409/1410/1411	Hilbre Island, SW	318000	387000	1919/1940/1979/1984/2004/2005/2006/2012	P166
1412/1413	North Bay (Hilbre Island)	318000	388000	2004/2012	P167
1512/1513	Leasowe BW, W of Lighthouse (Wirral Foreshore)	324000	391000	2003/2012	P168
1532/1533	Leasowe BW, Mid (Wirral Foreshore)	326000	392000	2003/2012	P169
512/513	E of Discharge (Amlwch)	245000	393000	2003/2013	P170
565/566	Lynas Point (Dulas Bay)	248000	393000	1997/2013	P171
1546/1547	Kings Parade, E (Wirral Foreshore)	329000	394000	2003/2012	P172
1553/1554	N Brighton Lighthouse, W (Wirral Foreshore)	330000	394000	2003/2012	P173
1563/1564	N Brighton Lighthouse, E (Wirral Foreshore)	331000	394000	2003/2012	P174
1568/1569/1570	Rossal Point (Fleetwood)	331000	447000	1984/2004/2012	P175
1622/1623/1624/1625/1626/1627	Heysham Power Station (Heysham)	340000	460000	1959/1960/1961/1984/2003/2012	P176
1610/1611/1612/1613/1614/1615	Foot Skear (Heysham Sands)	339000	462000	1999/2002/2003/2011/2012/2013	P177
1630/1631/1632/1633/1634/1635/1636/1637/1638/1639/1640/1641/1642/1643/1644/1645/1646/1647/1648/1649/1650/1651	Foot Skear (Heysham Sands)	340000	462000	1997/1999/2002/2011/2011/2011/2011/2011/2011/2011/2011/2011/2011/2011/2011/2011/2011/2011/2011/2011/2012/2013	P178
1656/1657/1658/1659	Foot Skear Inshore (Heysham Sands)	341000	463000	1997/2002/2012/2013	P179
1428/1429	Cross Dyke Scar (WalneyIsland)	319000	464000	2002/2012	P180
1494/1495	Head Scar (Piel Channel, Morecombe Bay)	322000	465000	1999/2002	P181
1337/1338/1339/1340	Annaside Bank	309000	484000	1984/1989/2002/2012	P182
1323/1324/1325	Annaside Bank	308000	486000	2002/2004/2012	P183
1273/1274	Selker Bay (Annaside Bank)	307000	488000	1989/2002	P184
1275/1276/1277	Tarn Bay	307000	489000	2000/2002/2012	P185
1278/1279/1280/1281/1282	Tarn Bay	307000	490000	1984/1991/2002/2004/2012	P186
1221/1222/1223/1224/1225	Drigg	304000	498000	1984/2000/2002/2004/2012	P187
1203/1204/1205	Seascale	303000	500000	1989/2004/2012	P188
1206/1207/1208	Seascale	303000	501000	1915/1984/2012	P189
1173/1174/1175/1176/1177	Sellafield	301000	503000	1984/2000/2002/2004/2012	P190
1157/1158	Sellafield	300000	504000	2002/2012	P191
1126/1127/1128/1129/1130/1131/1132	Nethertown	298000	507000	1984/1994/1995/2000/2002/2004/2012	P192
1098/1099	Saint Bees, SW	296000	510000	2002/2012	P193
1086/1087/1088/1089/1090	Saint Bees, NE	295000	511000	1984/1989/1991/2003/2012	P194
1071/1072/1073/1074/1075	Saint Bees Head	294000	512000	1954/1989/1989/1991/2000	P195
1134/1135	Moss Bay (Harrington)	298000	525000	1984/2012	P196
1136/1137/1138	Moss Bay	298000	526000	1952/2000/2012	P197
176/177	East Tarbert	214000	530000	2000/2014	P198
189/190	Mull of Galloway (Solway, N)	215000	530000	2000/2014	P199
1147/1148	Northside	299000	530000	1984/1991	P200
1149/1150/1151	Siddick (Seaton)	299000	531000	1999/2000/2002	P201
1179/1180	Flimby (St. Helens)	301000	533000	1984/2002	P202
1187/1188	Risehow Scar (Maryport)	302000	535000	1991/2000	P203
1209/1210	Maryport, S (Parton Bay)	303000	536000	1991/2000	P204
1211/1212/1213/1214	Maryport, N (Parton Bay)	303000	537000	1991/2000/2002/2012	P205
1215/1216/1217	Seabrows Scar (Maryport)	303000	538000	2000/2002/2012	P206
1226/1227/1228/1229/1230	Bank End Scar (Maryport)	304000	538000	1938/1953/2000/2002/2012	P207
1231/1232	Crosscanonby (Allonby Bay)	304000	539000	2002/2012	P208
1236/1237/1238/1239	Crosscanonby (Allonby Bay)	305000	539000	1991/2000/2002/2012	P209
1249/1250	Crosscanonby (Allonby Bay)	306000	539000	2000/2012	P210
160/161	Teralley Point	212000	540000	2000/2014	P211
1240/1241/1242	Crosscanonby (Allonby Bay)	305000	540000	1984/2000/2012	P212

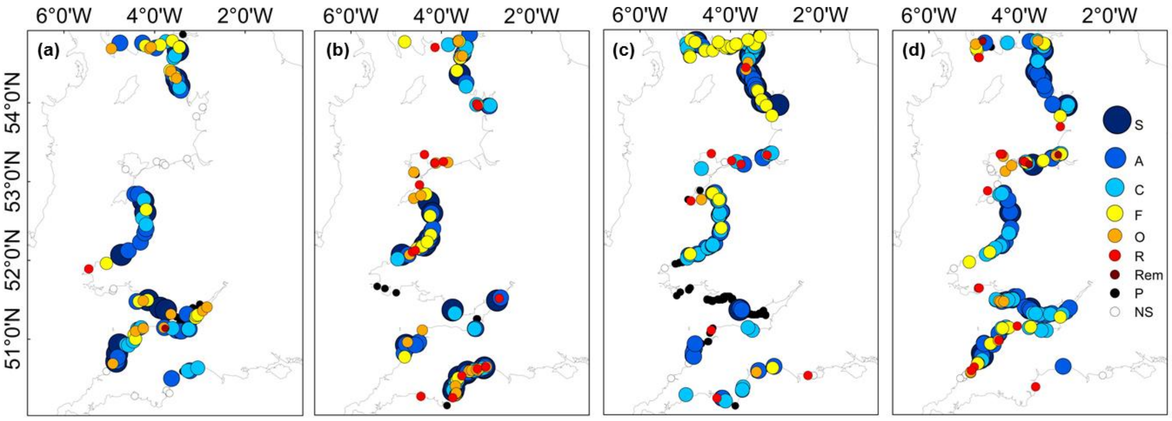
1284/1285/1286/1287/1288/1289/1290/1291	Allonby Bay	307000	541000	1970/1970/1974/1974/1978/1978/2002/2012	P213
1292/1293/1294/1295/1296	Allonby Bay	307000	542000	1970/1974/2000/2002/2012	P214
155/156/157	Logan Mills (Solway, N)	211000	543000	1989/2000/2014	P215
818/819	Meikle Ross (KirkcudbrightBay, Solway, N)	265000	543000	1989/2000	P216
1297/1298/1299/1300	North Lodge Scar (Allonby)	307000	543000	1950/2000/2002/2012	P217
886/887/888	Abbey Burn Foot (Solway, N)	274000	544000	1984/1989/2000	P218
382/383	Philip and Mary	232000	545000	2007/2012	P219
842/843	Torrs Point, N (KirkcudbrightBay, Solway, N)	267000	545000	1989/2000	P220
1254/1255	Dubmill Point (Mawbray)	306000	545000	2002/2012	P222
1302/1303/1304/1305/1306/1307	Dubmill Scar (Mawbray)	307000	545000	1984/1991/1999/2000/2002/2012	P223
1256/1257	Dubmill Point, N (Mawbray)	306000	546000	2002/2012	P224
753/754	Kirkandrews Bay (Solway, N)	259000	547000	1989/2000	P225
1244/1245/1246	Ellisons Scar (Mawbray Bank, Mawbray)	305000	547000	2000/2002/2012	P226
1258/1259/1260/1261/1262	Ellisons Scar (Mawbray Bank, Mawbray)	306000	547000	1998/1999/2000/2002/2012	P227
1309/1310	Mawbray Scar (Mawbray)	307000	547000	2002/2012	P228
923/924	RascarrelBay (Auchencairn, Solway, N)	280000	548000	1989/2000	P230
151/152	Sandhead	210000	549000	2000/2014	P231
946/947/948	Balcary Point (Inner Solway)	282000	549000	1973/1991/1994	P234
1312/1313	Beckfoot (Silloth)	307000	549000	2002/2012	P235
335/336	Garheugh Port, NW	226000	550000	2007/2012	P236
1314/1315/1316	Beckfoot (Silloth)	307000	550000	1984/2002/2012	P237
293/294/295/296/297/298	Auchenmalg, Cock Inn	223000	551000	1984/1989/2000/2007/2012/2012	P238
303/304	Glenalmar House	224000	551000	2007/2012	P239
657/658/659/660/661	Mossyard Bay	255000	551000	1984/2000/2011/2012/2013	P240
265/266/267	N of Crows Nest and Burn	220000	553000	1991/2007/2012	P241
992/993/994	Port O Warren Bay (Solway, N)	287000	553000	1973/1992/2012	P242
1009/1010	Port O Warren Bay (Solway, N)	288000	553000	1984/2012	P243
1114/1115/1116/1117/1118/1119/1120/1121/1122	Southerness Point (Solway, N)	297000	554000	1964/1973/1984/1991/1994/1999/1999/2000/2012	P244

Appendix 2.5: Paired collated *Sabellaria alveolata* records from suitable sites, paired between the baseline survey of Cunningham et al., 1984 (1980-1984) and the contemporary survey (2012-2014). This dataset is referred to throughout the document as baseline to contemporary data. Location data includes site name, OSGB coordinates, and sampled years. Original record identifying codes are included for paired area data (see Appendix 2.2), in addition to identifying codes for each paired area (see Appendix 2.3).

Original record ID (Appendix 2.2.)	**Site name**	**Eastings**	**Northings**	**Years**	**Paired area ID**
125/126	Trebarwith Strand	204000	86000	1984/2013	P15
165/166	Crackington Haven, N	213000	97000	1984/2013	P26
208/209/210/211	Millook	218000	100000	1957/1975/1984/2012	P27
257/258/259/260/261/262/263	Bude	220000	106000	1977/1980/1997/2000/2001/2012/2013	P30
223/224/225/226/227/228/229/230/231/232/233/234/235/236/237/238/239/240/241/242/243/244/245/246/247/248	Duckpool (Coombe)	219000	111000	1961/1962/1963/1964/1965/1966/1967/1968/1969/1970/1971/1972/1973/1975/1977/1978/1984/1992/1996/1998/1999/2000/2001/2002/2003/2013	P32
394/395/396	Bucks Mills	235000	123000	1984/1993/2013	P33
280/281/282/283/284/285/286/287	Hartland Quay	222000	124000	1977/1984/1993/1999/2002/2003/2012/2013	P34
379/380	Clovelly	232000	124000	1983/2013	P36
446/447/448/449	Westward Ho	242000	129000	1977/1984/1988/2013	P39
459/460/461/462	Downend (Croyde, S)	243000	138000	1977/1978/1983/2013	P40
1341/1342	St Audries Bay (Doniford)	310000	143000	1984/2013	P46
1194/1195/1196/1197/1198	Blue Anchor	303000	144000	1941/1976/1978/1984/2013	P47
550/551	Lee Bay (Woolacombe)	248000	146000	1983/2013	P50
612/613	Ilfracombe	251000	147000	1984/2013	P54
1105/1106/1107/1108/1109	Minehead	297000	147000	1976/1984/1984/2002/2013	P55
632/633	HeleBay	253000	148000	1984/2013	P56
975/976	Porlock Weir	286000	148000	1984/2013	P58
1548/1549/1550	Birnbeck (Weston Super Mare)	330000	162000	1941/1984/2013	P59
1559/1560	Sand Point (Kewstoke)	331000	165000	1984/2013	P61
1585/1586	Middle Hope Cove (Kewstoke)	333000	166000	1984/2013	P64
1081/1082/1083/1084/1085	Llantwit Major	295000	167000	1957/1976/1984/2004/2013	P68
1398/1399/1400/1401	Lavernock Point (Penarth)	318000	167000	1976/1984/2002/2013	P69
1619/1620/1621	Clevedon	340000	172000	1976/1984/2013	P72
1003/1004/1005/1006/1007/1008	Dunraven Bay	288000	173000	1976/1984/1997/2003/2011/2014	P75
918/919/920/921	Hutchwns Point (Porthcawl)	280000	176000	1984/1988/2003/2013	P78
1668/1669/1670/1671/1672/1673	Portishead	346000	177000	1924/1939/1941/1974/1984/2013	P80
592/593/594	Oxwich	250000	185000	1973/1984/2013	P88
781/782/783/784/785/786/787	LimesladeBay (The Mumbles, Swansea)	262000	187000	1973/1984/2001/2004/2006/2013/2014	P98
794/795/796/797/798/799/800	Bracelet Bay (Swansea)	263000	187000	1978/1984/2001/2006/2011/2013/2014	P99
167/168/169	Overhangs (Saint Catherines)	213000	200000	1984/2008/2013	P104
173/174	Monkstone Point (Saundersfoot)	214000	203000	1984/2013	P105
44/45/46	Abereiddy	179000	231000	1984/2002/2012	P107
127/128/129/130	Parrog	204000	239000	1984/2003/2012/2014	P108
310/311/312/313/314/315/316/317/318/319/320	Aberporth	225000	251000	1984/1996/1997/2002/2004/2005/2006/2007/2008/2012/2014	P110
353/354/355	Llangrannog	231000	254000	1984/2012/2014	P112
397/398/399/400	Cwmtudu Headland	235000	257000	1982/1997/2012/2014	P113
622/623/624/625	Llanrhystud (Aberystwyth)	252000	269000	1984/1997/2003/2012	P124
719/720/721/722/723/724/725/726/727/728	Castle Rocks, N (Aberystwyth)	258000	282000	1984/1997/2002/2003/2005/2006/2010/2011/2012/2013	P126
758/759/760/761/762/763/764	Borth	260000	288000	1935/1984/1997/2002/2004/2006/2012	P131
749/750/751/752	Llwyngwril	259000	311000	1982/1984/2004/2012	P136

769/770	Barmouth	260000	315000	1984/2012	P137
681/682/683/684	Shell Island (Mochras)	256000	327000	1978/1984/2004/2012	P140
489/490/491	Afon Wen	244000	337000	1964/1984/2012	P146
570/571/572/573/574/575/576/577/578/579/580/581/582/583/584/585	Criccieth Castle	249000	337000	1950/1964/1984/1996/2002/2003/2004/2005/2006/2007/2008/2009/2010/2011/2012/2013	P150
365/366/367/368/369/370/371/372/373/374/375/376	Rhosneigr	231000	372000	1983/2002/2005/2006/2007/2008/2009/2010/2011/2012/2012/2013	P156
892/893/894/895	Great Ormes Head, W (Llandudno)	275000	383000	1984/1997/2003/2012	P164
1404/1405/1406/1407/1408/1409/1410/1411	Hilbre Island, SW	318000	387000	1919/1940/1979/1984/2004/2005/2006/2012	P165
1568/1569/1570	Rossal Point (Fleetwood)	331000	447000	1984/2004/2012	P174
1622/1623/1624/1625/1626/1627	Heysham Power Station (Heysham)	340000	460000	1959/1960/1961/1984/2003/2012	P175
1337/1338/1339/1340	Annaside Bank	309000	484000	1984/1989/2002/2012	P181
1278/1279/1280/1281/1282	Tarn Bay	307000	490000	1984/1991/2002/2004/2012	P185
1221/1222/1223/1224/1225	Drigg	304000	498000	1984/2000/2002/2004/2012	P186
1206/1207/1208	Seascale	303000	501000	1915/1984/2012	P188
1173/1174/1175/1176/1177	Sellafield	301000	503000	1984/2000/2002/2004/2012	P189
1126/1127/1128/1129/1130/1131/1132	Nethertown	298000	507000	1984/1994/1995/2000/2002/2004/2012	P191
1086/1087/1088/1089/1090	Saint Bees, NE	295000	511000	1984/1989/1991/2003/2012	P193
1134/1135	Moss Bay (Harrington)	298000	525000	1984/2012	P195
1240/1241/1242	Crosscanonby (Allonby Bay)	305000	540000	1984/2000/2012	P211
1302/1303/1304/1305/1306/1307	Dubmill Scar (Mawbray)	307000	545000	1984/1991/1999/2000/2002/2012	P222
1314/1315/1316	Beckfoot (Silloth)	307000	550000	1984/2002/2012	P236
293/294/295/296/297/298	Auchenmalg, Cock Inn	223000	551000	1984/1989/2000/2007/2012/2012	P237
657/658/659/660/661	Mossyard Bay	255000	551000	1984/2000/2011/2012/2013	P239
1009/1010	Port O Warren Bay (Solway, N)	288000	553000	1984/2012	P242
1114/1115/1116/1117/1118/1119/1120/1121/1122	Southerness Point (Solway, N)	297000	554000	1964/1973/1984/1991/1994/1999/1999/2000/2012	P243

Appendix 2.6: SACFOR abundance of *Sabellaria alveolata* from suitable sites, within Britain, in all available data, from the 1980s to the 2010s. (a) 1980s (n = 174); (b) 1990s (n = 222); (c) 2000s (n = 489); and (d) 2010s (n = 314).



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3. Regional-scale dynamics of *Sabellaria alveolata* abundance and distribution over 3 decades

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Declaration

I declare that this manuscript is entirely my own work, with the exception of the generation of fetch bearings that was completed using a pre-programmed script courtesy of A.J.D. L.B.F assisted with fieldwork from North Wales to South Scotland. S.J.H. and A.J.D. provided supervision. The abundance and distribution dataset was collated in Bush et al., Chapter 2, but spatially filtered for consideration in this manuscript.

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3.1. Abstract

Natural ecosystems are controlled by a complex combination of interactions. The relative importance of these interactions can vary spatially. Through regional comparisons of historical and contemporary data, this study documented patterns of change in *Sabellaria alveolata* from the 1980s to the 2010s, and related contradictory patterns to extreme weather events and general climate trends. Long-term broad-scale persistence was demonstrated, nested within which short-term, small-scale changes in distribution, SACFOR abundance and morphology (e.g. encrusting to emergent reef forms) were observed: no significant difference in distribution occurred in any decadal comparison in either region (> 70 % of paired areas exhibited persistence), with the exception of a significant increase from the 1980s to the 2000s. Increases in abundance and morphology, however, were documented near the northern range edge (e.g. from the 1980s and 1990s to 2000s, and 1990s to 2010s in all available data, and from the 1980s to 2000s and 2010s in paired data). Further stability was demonstrated well within the range, with the exception of significant increases in morphology in paired area data from the 1980s to 1990s, followed by significant decreases from the 1990s to 2010s. Near the northern range edge, temperature was the dominant driver of change explaining ≥47.2%: expanding distribution, increased abundance and enlarged morphology were associated with increased temperature and decreased magnitude/duration of cold spells, and extirpations and decreases to encrusting morphology with opposing changes in temperature. In contrast, well within the range, change was predominantly driven by wave exposure explaining ≥50%: colonisations were associated with decreased wave exposure; whilst extirpations, and decreases in abundance and morphology were associated with increased wave exposure. Well within the range, decreases in abundance and morphology were also associated with extremely cold winters (e.g. 2009-2010). This study highlights the importance of scale when assessing the impact of climate change. Under predicted scenarios of increased temperature, increased frequency of extreme events and increased wind speeds, colonisations, and increases in abundance and occurrence of reef morphology are predicted near the northern range edge. In contrast opposing decreases are predicted well within the range and near the southern range edge.

3.2. Introduction

The spatial distribution of most species is controlled by environmental factors (Brown et al., 1996). Consequently, climate change is predicted to have a substantial impact on coastal ecology at global, regional, and local scales, with biogeographic changes expected for many species (Parmesan et al., 2005). Whilst some environmental parameters have demonstrated change along a latitudinal gradient (e.g. average temperature), others have featured regionally specific patterns of change (e.g. changes in wind regimes and extremes of temperature; Hader et al., 2014; Fisher et al., 2015). The impacts of latitudinal climate trends may be counteracted or exasperated by regional extreme weather events. For example, positive responses to increasing average temperatures may be mediated by extremely cold winters (Firth et al., 2011; Wethey et al., 2011), whilst negative responses may be multiplied by extreme heat waves (Firth & Williams, 2009; Smale & Wernberg, 2012; Wernberg et al., 2013). The combined effects of changes in multiple environmental parameters may be additive, synergistic, or antagonistic to one another (Griffith et al., 2012; Hader et al., 2014). Understanding how multiple stressors will interact to influence biogeographic change on a local to global scale is a major challenge in intertidal community ecology.

The stress that climate changes exert on an organism, and therefore the response of a population, will likely be dependent on its location within the species biogeographic range. For example, under conditions of long-term warming, southern species expected to experience poleward range extensions at the north of their range, in association with increased abundance near the leading range edge (Hiscock et al., 2004; Hawkins et al., 2008; Firth et al., 2009; Merzouk & Johnson, 2011). Some intertidal species have shown range extensions of as much as 50 km per decade (Helmuth et al., 2006; Hawkins et al., 2013; Mieszkowska et al., 2014). In contrast, populations near the southern range edge are predicted to experience range retractions, and decreases in abundance near their equatorial range edge (e.g. Simkanin et al., 2005; Mieszkowska et al., 2006; 2014; Lima et al., 2007; Jones et al., 2010; Hawkins et al., 2013), whilst populations well within the range may demonstrate no response to warming (e.g. Lima et al., 2007).

Biological responses to changes in latitudinal temperature gradients may be altered by local environment (Hiscock et al., 2004; Southward, 1958; Helmuth et al., 2006; Maggs et al., 2008; Ford et al., 2013), and in some cases biologically mediated (Moore et al., 2007). During historical periods of climate change, some species survived in isolated areas, whilst populations in surrounding areas were extinguished. For example, during the Last Glacial Maximum, some isolated populations of temperate species survived in glacial refugia (Andersen & Borns, 1994; Maggs et al., 2008). In physically heterogeneous areas, such as rocky shores, large differences in climate can occur over small spatial scales, for example, between sheltered or exposed, shaded or unshaded, and sloping or flat habitat (Helmuth & Hofmann, 2001; Denny et al., 2011; Seabra et al., 2011). Additionally, refugia can be created by biotic factors such as seaweed cover (Coombes et al., 2013). Some sheltered populations of a southern species may survive a period of extreme cold, whilst adjacent exposed populations suffer extirpations (Crisp, 1964; Coombes et al., 2013; Ford et al., 2013). Conversely, some shaded populations of northern species may survive at their southern limits despite adjacent populations dying out due to excessive warming (Helmuth et al., 2011; Seabra et al., 2011; Ford et al., 2013).

Changes in the abundance and distribution of ecosystem engineers will alter community structure, patterns of associated biodiversity and ecological processes (Crooks, 2002). The Lusitanian polychaete *Sabellaria alveolata* creates biogenic reefs from sand and shell fragments, stabilising the substrata, and potentially increasing biodiversity (Dubois et al., 2002; Desroy et al., 2011). The biogeographic range of *S. alveolata* extends from Morocco in the south, to Britain in the north, where it has been reported predominantly intertidally from the English Channel to the Solway Firth (Cunningham et al., 1984; Bush et al., Chapter 2). This polychaete is known to be sensitive to temperature with increases in both growth and productivity of the adult reported with increases in temperature (Gruet, 1982; Bamber & Irving, 1997), and decreases in the rate of larval development and success with lower temperatures (Dubois et al., 2007; Slater, 2013).

Despite several decades of warming within the British Isles (Hawkins et al., 2009; Firth et al., 2015), long-term broad-scale persistence, and stability in abundance of *S. alveolata* has been demonstrated from the cooler 1980s to the warmer present (Bush et al., Chapter 2). However, changes have been reported on smaller spatial and temporal scales (Crisp, 1964; Wilson, 1971; Cunningham et al., 1984; Frost et al., 2004; Firth et al., 2015; Bush et al., Chapter 2). A short-term increase in the proportion of low abundance populations was demonstrated nationally during the 1990s (Bush et al., Chapter 2), whilst increases in abundance and distribution have been documented in the far north of the range (Frost et al., 2004; Firth et al., 2015). Across northern Europe, temperature has increased overall since the 1900s with fluctuations of cold and warm periods. With the exception of recent winters (2009-11), a warming trend has occurred from the cooler 1980s to the warmer present day (Hawkins et al., 2009; Wethey et al., 2011; Kröncke et al., 2013). Periods of extreme cold correlate with historical absences and extirpations in the far north of the range (Crisp, 1964; Gubbay, 1988; Frost et al., 2004; Mieszkowska et al., 2006; Firth et al., 2015). Within the central Irish Sea, reliable records of healthy populations of *S. alveolata* were reported during the warm period of the 1930s-1950s, prior to the extremely cold winter of 1962-1963 (Cunningham et al., 1984; Firth et al., 2015). Mass mortality occurred on the North Wales coastline thereafter (Crisp, 1964) with no recolonisations reported until the 2000s (Frost et al., 2004; Firth et al., 2015). It is speculated that extremely cold winters during the 1970s-1980s suppressed populations in the north of the range. Following the subsequent release from extreme cold, under a warming climate, recolonisation occurred (Frost et al., 2004; Firth et al., 2015).

Increased storminess has been detected across northern Europe from the 1970s to the 1990s (Alexandersson et al., 1998), with the early 1990s featured some of the highest winds on record, particularly on southwest coasts (Alexander & Tett, 2005; Allan et al., 2009; Wang et al., 2011; Earl et al., 2013). Continued increases in storminess are often predicted under climate change scenarios (e.g. Giorgi et al., 2004; Beniston et al., 2007). *Sabellaria alveolata* require a degree of wave exposure to suspend available sediment. Frost et al. (2004) suggested that increases in *S. alveolata* in the north of the range during this time were partially due to increases in sediment supply due to increased storminess. In contrast, it is widely reported that elevated wave exposure can negatively impact coastal species, resulting in physical damage and mortality (Denny, 1995), altering behaviour and morphology (Dayton, 1971; Akester & Martel, 2000; Fowler-Walker et al., 2006; Hayne & Palmer, 2013) and affecting distribution (Paine & Levin, 1981). For example, Wilson (1971) reported that wave action was the dominant cause of *S. alveolata* reef destruction at exposed sites. Additionally, increased storminess can result in substrate displacement, with sand removal and smothering both reported to negatively influence the growth and survival of *S. alveolata* (Wilson, 1971; Porras et al., 1996; Strachan, 2013). Predicted increases in storminess may have context dependent localised effects proving beneficial to population establishment and growth in some locations but detrimental at others.

Interactions amongst multiple drivers of change may be responsible for unexpected patterns of change (e.g. Lima et al., 2009; Wethey et al., 2011; Poloczanska et al., 2013; Seabra et al., 2015). In a changing climate, regional populations may show opposing patterns of change in response to different environmental parameters. Populations near the northern range edge are potentially exposed to a greater frequency and magnitude of adverse cold temperatures. Under a warming climate, however, more favourable temperatures will likely occur with a lower occurrence of extreme cold events (Bates et al., 2014). For populations well within the range (e.g. in the southwest of the British Isles), the importance of temperature is expected to be less. Well within the range, *S. alveolata* populations may not be regulated by temperature but by other environmental (e.g. wave exposure or sediment supply) or biotic (e.g. food or larval supply) parameters.

This study investigated changes in *S. alveolata* distribution, abundance, and morphology near its range edge and well within its range on coastlines of the British Isles. Previously collated historical data were separated, by latitude, into distinct geographical areas, allowing spatio-temporal comparisons on a regional scale over a period of approximately thirty years (1980-2013). The aims of this long-term regional-scale study were to: (i) Document changes in the distribution, abundance and morphology of *S. alveolata* populations on a regional scale on the west coast of mainland Britain with comparisons between the northern range edge, and well within the range; and (ii) relate regional scale changes in *S. alveolata* to region specific changes in both temperature and wave exposure. It was hypothesised firstly that, despite reported national stability (Bush et al., Chapter 2), *S. alveolata* will have increased in distribution, abundance, and morphology in the far north of its range, in response to increasing temperature; and secondly that *S. alveolata* will have been limited in distribution, abundance and morphology further south, in response to increasing wave exposure.

3.3. Study Area and Methods

3.3.1. Study area

The northern range limit of *S. alveolata* occurs within the British Isles (Cunningham et al., 1984), where presence records have been consistently reported from southern and western coasts since the 1960s (Bush et al., Chapter 2). Although persistence in distribution and stability in abundance have been demonstrated nationally within Britain (Chapter 2), changes in distribution and abundance have been previously reported from near the northern range edge (e.g. North Wales to southwest Scotland; Frost et al., 2004; Firth et al., 2015). To facilitate comparisons of change between spatially distinct populations near the northern range edge and populations well within the range, data were filtered by regions of persistent absence (i.e. southwest Cornwall, Saint Davids Head, Llŷn Peninsula and the tip of Galloway). Consequently, populations located from northwest Wales to southwest Scotland were considered to be near the northern range edge, whilst populations from southwest Wales to southwest England were considered to be well within the range, separated by populations within mid Wales (Figure 3.1).

3.3.2. Historical *Sabellaria alveolata* abundance data within Britain

A spatially and temporally filtered database of historical distribution and abundance data for *S. alveolata* within Britain at 1 km^2 resolution (georectified to the British National Grid) was generated from available literature, and databases. Abundance data were predominantly reported on the modified semi-quantitative SACFOR scale from superabundant to rare (Crisp & Southward, 1958; Cunningham et al., 1984). Records for which the species were reported as Not Seen were assumed to be absence records. This approach is justified, as *S. alveolata* is an ecosystem engineer generating biogenic structures that are obvious to a scientific observer. Reported remains (i.e. dead reef structure with no living worms) indicate a change in abundance had occurred. Thus they were considered as an additional category of the SACFOR scale for abundance analysis; but were considered as absence records for the purpose of distribution analysis, as despite being evidence of recent

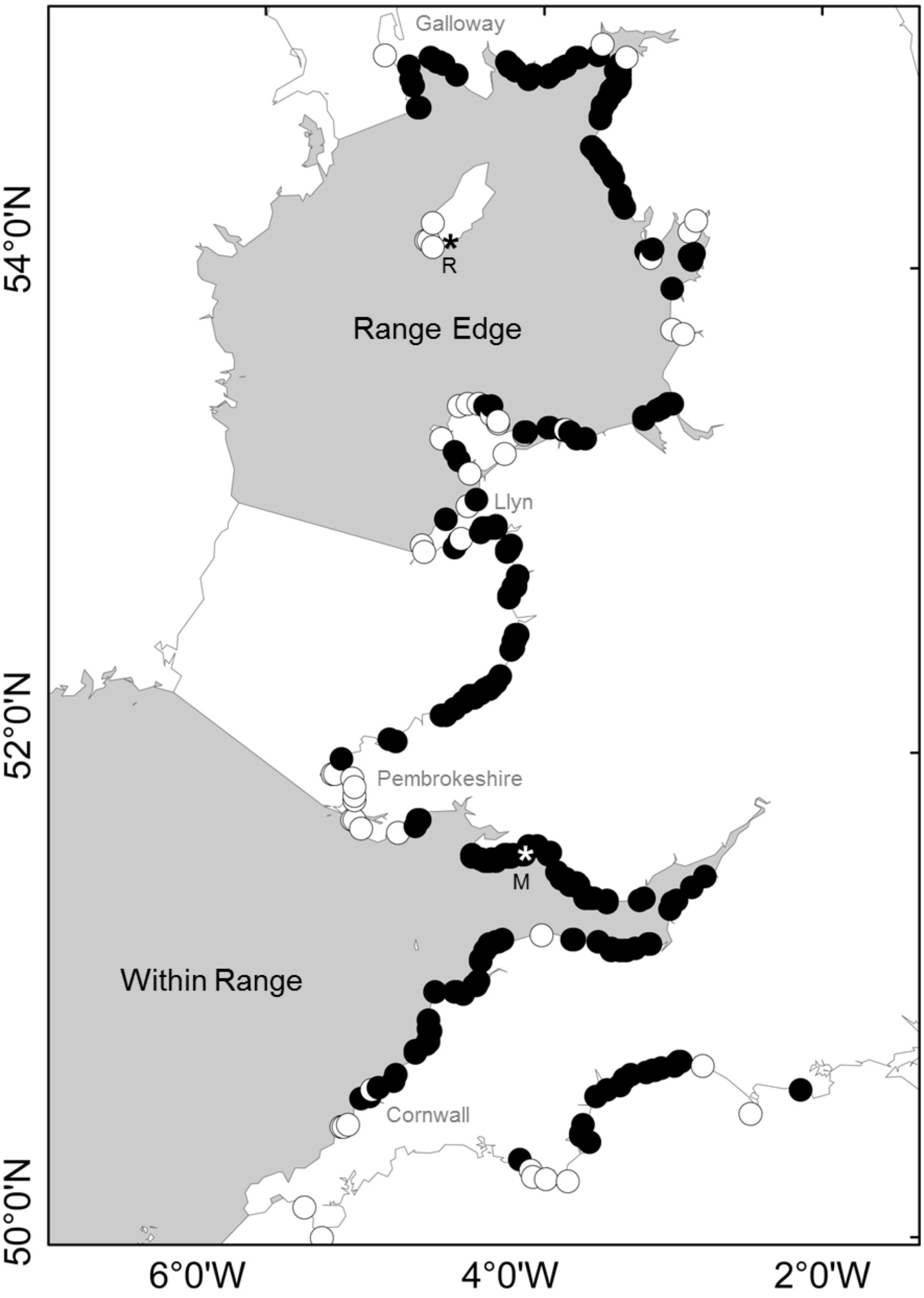

Figure 3.1: Reported locations of *Sabellaria alveolata* presence (black) and absence (white) on southwest coastlines of Britain (paired sites only). Range end and within range regions are highlighted in grey. Weather stations are demarked by asterisks, and M represents the Mumbles, whilst R represents Ronaldsway.

presence, the life-time of the uninhabited biogenic reef structure is unknown. Abundance data were descriptive of morphology (i.e. height, percentage cover, patch size), and were also considered on a two-point scale as ‘reef’ or ‘encrusting’ morphology (see Bush et al., (Chapter 2) for detailed methodology). Collated data were spatially filtered into regions. Data for mid Wales were omitted from further analysis, and for the remainder of this manuscript, populations near the northern range edge will be referred to as ‘range edge’ populations, whilst those well within the range will be referred to as ‘within the range’ populations.

3.3.3. Assessing regional change in distribution, abundance and morphology

Presence data, SACFOR abundance data and morphological data from suitable sites (e.g. those where presence has been reported at least once) were compared by decade in both regions. Regional data were considered in three distinct ways: (a) decadal comparisons of all available data (available in Bush et al., Chapter 2, Appendix 2.3); (b) area-specific decadal comparisons (available in Bush et al., Chapter 2, Appendix 2.4); and (c) a site-specific comparison between three directly comparable datasets, a baseline dataset collected by Cunningham et al. (1984), a contemporary dataset collected by the authors, and near the range edge only, an intermediate dataset collected by Frost et al. (2004) (Appendix 3.1-3.2).

Decadal comparisons of all available data:

Regional data from the 1980s, 2000s, and 2010s were considered for assessment of changes in distribution, abundance, and morphology (see Bush et al. (Chapter 2) for detailed methodology). The 1990s not considered for assessment of changes in distribution as no species focused survey was carried out in this decade. Consequently, it was assumed that absence records were underreported and this data was biased by presence data. The Wilcoxon rank-sum test (WRS) with continuity correction was used to assess if significant differences in the proportion of distribution, abundance, and morphology categories occurred spatially (i.e. between range edge and within range, in each decade) or temporally (i.e. between decades, at both the range edge and within range).

Area-specific decadal comparisons:

Changes in paired area data (i.e. matched sites within 1 km of each other) within regions were assessed using one-tailed sign tests (OTS). Changes in distribution (i.e. colonisation or extirpation), abundance (i.e. increase or decrease of greater than one category of the SACFOR scale), or morphology (i.e. increase or decrease from encrusting morphology and reef) were compared (see Firth et al., 2015 for detailed methodology).

Site-specific comparisons:

Site-specific data collected using identical methodology in different decades were collated in Bush et al. (Chapter 2). In both regions an initial baseline dataset was collected from 1980 to 1984 (Cunningham et al., 1984) and a contemporary dataset from 2012 to 2014 (Bush et al., Chapter 2). Near the range edge, an intermediate dataset was also collected from 2003 to 2004 (Frost et al., 2004). One-tailed sign tests were used to compare the number of locations exhibiting a change in distribution, abundance, and morphology between decades.

3.3.4. Assessing regional change in environmental parameters

Daily temperature and wind datasets from 1980 to 2014 for both the Mumbles and Ronaldsway (Figure 3.1) were downloaded from Met Office Integrated Data Archive System (MIDAS) Land and Marine Surface Stations Data (1853-current), accessed through the British Atmospheric Data Centre (http://www.ceda-wps2.badc.rl.ac.uk, accessed on 01 June 2015). Decadal weather data were allocated to *S. alveolata* sites dependent on region: All stations within the range were assigned to the Mumbles (i.e. south Wales and southwest England), and all stations near the northern range edge, to Ronaldsway (i.e. north Wales to southwest Scotland).

Temperature:

Daily maximum and minimum air temperature data were calculated for each weather data site (i.e. Ronaldsway and the Mumbles). Minimum decadal temperature (MT) was assumed to be the minimum temperature given, although temperature was only monitored once daily and consequently, the absolute minimum air temperature is likely to have not been recorded. Average decadal air temperature (AT) was estimated as the median temperature given a known maximum and minimum. The frequency of negative temperature events (days when minimum temperature was less than 0 °C) per decade (FNT) was also calculated and normalised to the number of days of data per decade. Region-specific changes in temperature parameters were then calculated between decades.

Relative wave exposure:

Site-specific fetch distances were estimated by the methodology of Davies and Johnson (2006). A series of radiating lines were generated from the centre of each site at 10° intervals. All lines generated were cropped by a 1 km resolution British coastline to give the maximum functional fetch on each bearing, which extended to a maximum distance of 200 km offshore. The longer the distance that wind blows over the sea surface, the more developed the wave state and the larger the waves on the shore (Harborne et al., 2006).

Regional daily maximum and average wind speed data were collated along open bearings. Relative wave exposure values were estimated from: (i) decadal averages of wind speed per direction (RWEwa); (ii) decadal wind frequency (RWEwf). Relative wave exposures were estimated as the average of the exposure values of all 36 open bearings around a specific site, where exposure was calculated as: (i) average regional wind speed (knots) squared (to emphasis higher wind speeds), multiplied by site-specific fetch distance for each bearing (Keddy, 1984; Thomas, 1986; Resio et al., 2002; Davies and Johnson, 2006); or (ii) normalised frequency of wind events (number of days per decade with a wind speed of greater than 24 knots) multiplied by site-specific fetch distance for each bearing (Keddy, 1984; Ekebom et al., 2003; Davies & Johnson, 2006). Site-specific changes in relative wave exposure parameters were then calculated between decades.

3.3.5. Changes in *Sabellaria alveolata* distribution, abundance and morphology related to environmental parameters

Within each region, multiple correspondence analysis was carried out to relate site-specific changes in *S. alveolata* populations (distribution, abundance and morphology) to associated changes in environmental variables (i.e. MT, FNT, AT, RWEwa, and RWEwf) between two decades (e.g. 1980s to 1990s). Changes in *S. alveolata* distribution, abundance and morphology were assessed on a three-point scale (increase, stable or decrease), whilst changes in environmental variables were assessed on a two-point scale (increase or decrease). Changes in distribution equated to colonisations or extirpations, changes in abundance were defined as changes of more than one category of the SACFOR scale, whilst changes in morphology were defined as changes between absent, encrusting and reef-forming populations. Analysis was conducted with R (FactoMineR package).

3.4. Results

3.4.1. Regional change in distribution

Decadal comparisons of all available data:

When all available data were considered, no significant differences in the proportion of populated suitable sites were demonstrated in either region, in any comparable decade (1980s, 2000s and 2010s; 1990s not considered for distribution comparisons as assumed to be biased by presence only reporting; WRS, p-value > 0.05; Table 3.1, Row 1a and 4a). The proportion of populated suitable sites was significantly greater within the range than near the range edge in both the 1980s and 2000s (WRS, p-value < 0.01; Table 3.2, Row 1), but not the 2010s (WRS, p-value > 0.05). This is associated with increases in the proportion of populated suitable sites from the 1980s to the 2010s near the range edge (Figure 3.2 a) and decreases within the range (Figure 3.2 d).

Area-specific decadal comparisons:

Similarly at paired areas, no significant differences in the proportion of populated suitable sites occurred within regions (OTS, p-value > 0.05; Table 3.1, Row 1b and 4b), with the exception of from the 1980s to the 2000s near the northern range edge (OTS, p-value = 0.03). In all decadal comparisons, in both regions, the majority of paired areas demonstrated a high proportion of persistence through time (Figure 3.3). Near the range edge, all changes in distribution, from the 1980s to both the 2000s and 2010s, were colonisations (Figure 3.3 a). In contrast, within the range the majority of changes in distribution were extirpations (Figure 3.3 b). From the 2000s to 2010s, similar proportions of extirpations and colonisations occurred in both regions (Figure 3.3).

Site-specific comparisons:

At paired sites, no significant differences in distribution were exhibited in comparisons between the baseline, intermediate and contemporary data (OTS, p-

Table 3.1: Changes in distribution, abundance and morphology of *Sabellaria alveolata* in Britain (in near range edge populations and populations well within the range), from the 1980s to the 2010s. Changes were considered in all available data on decadal timescales, site-specific data decadally and between baseline (Base.), intermediate (Int.), and contemporary (Cont.) datasets. The 1990s were assumed biased by presence only reporting, and changes in distribution to this decade are not considered further (grey). However, the 1990s were included for abundance and morphology comparisons as the majority of presence records were reported with associated abundance. Significance in all available data were assessed with Wilcoxon rank sum tests with continuity correction, whilst significance in paired data (area and site) were assessed using one-tailed sign tests. Significant increases (↑) are depicted in blue, significant decreases (↓) are depicted in red.

Region	Analysis	Dataset	1980s – 1990s	1980s – 2000s	1980s – 2010s	1990s – 2000s	1990s – 2010s	2000s – 2010s	Base. – Int.	Base. – Cont.	Int. – Cont.
Near range edge	(1) Distribution	(a) All	*↑ W = 883.5, P = 0.01*	↔ W = 3456, P = 0.18	↔ W = 2568, P = 0.40	*↔ W = 5814, P = 0.08*	*↓ W = 4300, P = 0.03*	↔ W = 13948, P = 0.50			
		(b) Pair	↔ P = 0.5	↑ P = 0.03	↔ P = 0.06	↔ P = 0.16	↔ P = 0.16	↔ P = 0.21	↔ P = 0.13	↔ P = 0.06	↔ P = 0.25
	(2) Abundance	(a) All	↔ W = 882.5, P = 0.07	↑ W = 1713.5, P = 0.02	↔ W = 1142.5, P = 0.30	↑ W = 2055, P < 0.01	↑ W = 1488, P < 0.01	↔ W = 7868, P = 0.21			
		(b) Pair	↔ P = 0.25	↑ P = 0.02	↑ P < 0.01	↔ P = 0.27	↔ P = 0.31	↔ P = 0.23	↑ P = 0.03	↑ P < 0.01	↔ P = 0.38
	(3) Morphology	(a) All	↔ W = 850.5, P = 0.08	↑ W = 1830.5, P = 0.03	↔ W = 1065, P = 0.08	↑ W = 2320.5, P < 0.01	↑ W = 1365, P < 0.01	↔ W = 88.5, P = 0.66			
		(b) Pair	↔ P = 0.38	↑ P = 0.04	↑ P < 0.01	↔ P = 0.22	↔ P = 0.25	↔ P = 0.17	↑ P = 0.03	↑ P < 0.01	↔ P = 0.38
Well within the range	(4) Distribution	(a) All	*↔ W = 2754, P = 0.15*	↔ W = 7509, P = 0.85	↔ W = 6399, P = 0.05	*↔ W = 3969, P = 0.13*	*↓ W = 3375, P = 0.01*	↔ W = 8473.5, P = 0.05			
		(b) Pair	↔ P = 1	↔ P = 0.38	↔ P = 0.12	↔ P = 1	↔ P = 1	↔ P = 0.31		↔ P = 0.11	
	(5) Abundance	(a) All	↔ W =789, P = 0.09	↔ W = 330.5, P = 0.11	↔ W = 2253, P = 0.79	↔ W = 290, P = 0.52	↔ W = 1989, P = 0.10	↔ W = 947, P = 0.08			
		(b) Pair	↔ P = 0.5	↔ P = 0.25	↔ P = 0.1571	↔ P = 0.5	↔ P = 0.5	↔ P = 0.25		↔ P = 0.12	
	(6) Morphology	(a) All	↑ W = 769, P = 0.01	↔ W = 349.5, P = 0.10	↔ W = 2207.5, P = 0.57	↔ W = 327, P = 0.91	↓ W = 769, P = 0.02	↔ W = 880, P = 0.16			
		(b) Pair	↔ P = 0.5	↔ P = 0.5	↔ P = 0.19	↔ P = 0.5	↔ P = 0.5	↔ P = 0.25		↔ P = 0.17	

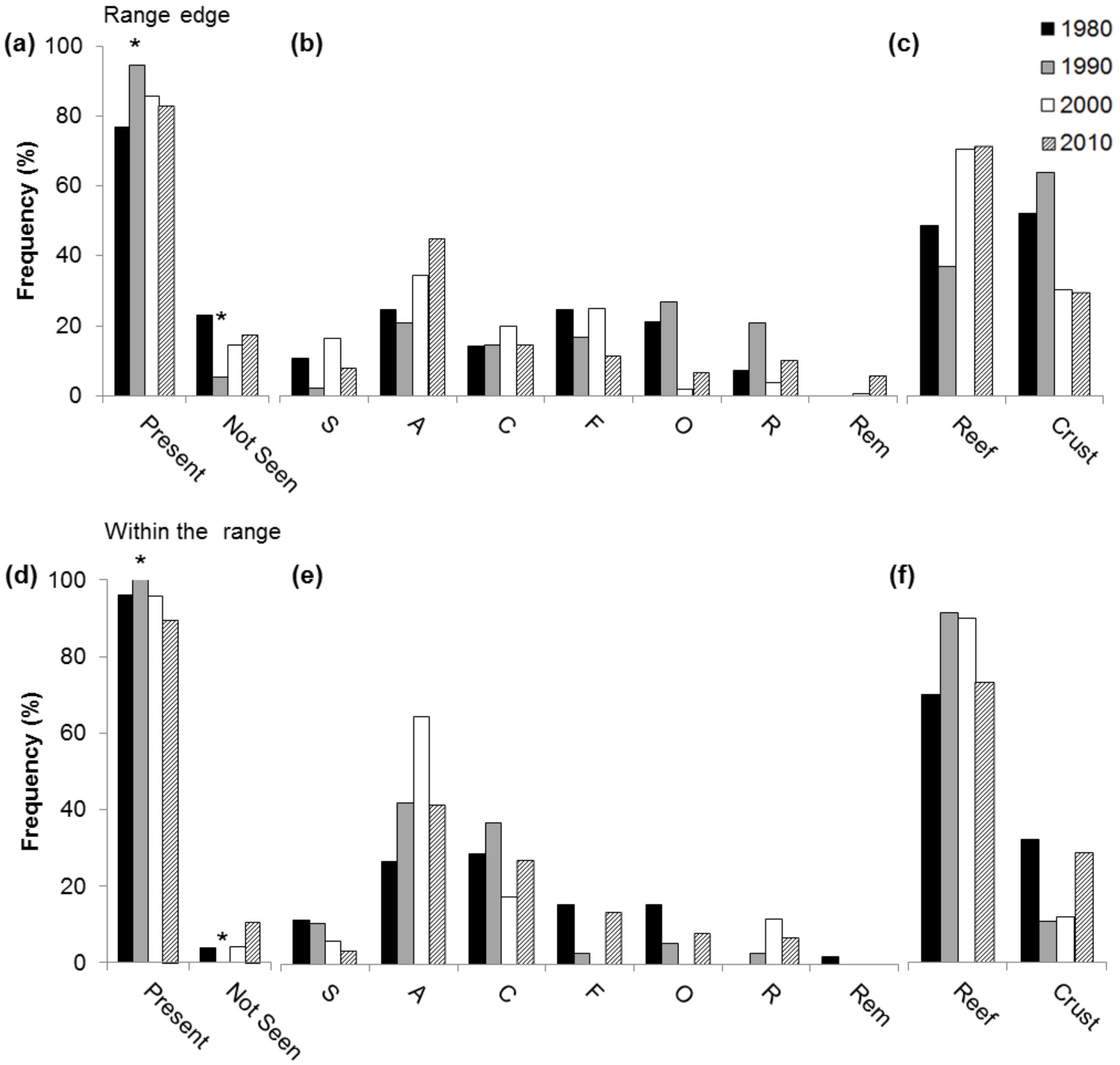

Figure 3.2: Regional decadal changes of *Sabellaria alveolata* distribution and abundance from the 1980s to the 2010s from all available data. (a-c) Near the range edge populations. (d-f) Populations well within the range. Proportions of (a, d) presence to absence data (* highlights 1990s data which is assumed to be presence biased and not considered further); (b, e) SACFOR abundance data; and (c, f) morphological data.

value > 0.05; Table 3.1, Row 1 and 4, right). Despite this, as with spatially-paired areas, the majority of changes in distribution through time near the range edge were colonisations (Figure 3.4 a-c), whilst within the range the majority of changes from the baseline to the contemporary were extirpations (Figure 3.5 a).

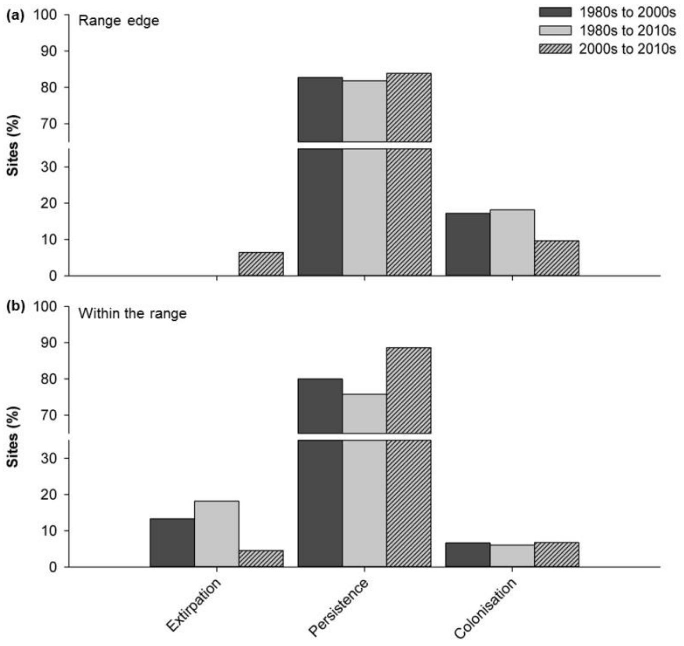

Figure 3.3: Regional changes in the presence to absence ratio of *Sabellaria alveolata*, at suitable areas of western Britain, from the 1980s to the 2010s. (a) Near range edge populations ($n_{1980\text{-}2000}$ = 29, $n_{1980\text{-}2010}$ = 22, $n_{2000\text{-}2010}$ = 62); (b) Populations well within the range ($n_{1980\text{-}2000}$ = 15, $n_{1980\text{-}2010}$ = 33, $n_{2000\text{-}2010}$ = 44). Extirpation = Increase from presence to absence, colonisation = opposing decrease.

3.4.2. Regional change in SACFOR abundance and morphology

Decadal comparisons of all available data:

Near the range edge significant differences in both abundance and morphology were demonstrated from the 1980s and 1990s to the 2000s, and from the 1990s to the 2010s when all available data were considered (WRS, p-value < 0.05; Table 3.1, Rows 2a, 3a). The 1980s and 1990s featured a smaller proportion of Frequent, Common, Abundant and Superabundant categories (Figure 3.2 b), and thus a lower proportion of reef-forming populations (Figure 3.2 c) than the 2000s. The 1990s also featured a lower proportion of Remains, Abundant and Superabundant and a higher proportion of Rare and Occasional categories (Figure 3.2 b), and thus a lower proportion of reef-forming populations than the 2010s (Figure 3.2 c). Within the range, no significant differences in abundance were demonstrated in any decadal comparisons when all available data were considered (WRS, p-value > 0.05; Table 3.1, Row 5a; Figure 3.2 e). Despite this, significant differences in morphology were

Table 3.2: Comparisons of the distribution, abundance and morphology of *Sabellaria alveolata* at known suitable sites near the range edge with populations well within the range, from the 1980s to the 2010s. Comparisons of distribution were represented by comparison of the proportion of presence to absence data, comparisons of abundance by comparison of SACFOR abundance categories, and comparisons of morphology by comparison between reef and encrusting forms. The 1990s were assumed presence biased and distribution differences within this decade are not considered further (grey). Significance in all available data were assessed with Wilcoxon rank sum tests with continuity correction. Significantly greater *S. alveolata* in populations well within the range in comparison to near range edge populations are depicted in blue (↑) (p-value < 0.05), and no significant differences in white (↔).

Dataset	1980s	1990s	2000s	2010s
(1) Distribution	↑ W = 2466, P < 0.01	↔ W = 1566 P = 0.09	↑ W = 15069 P < 0.01	↔ W = 8426 P = 0.14
(**2**) Abundance	↔ W = 867 P = 0.26	↑ W = 1430 P <0.01	↔ W = 1525.5 P = 0.39	↔ W = 3942.5 P = 0.85
(**3**) Morphology	↔ W = 897.5 P = 0.10	↑ W = 1498 P <0.01	↔ W = 1616.5 P = 0.10	↔ W = 4215 P = 0.45

demonstrated from the 1980s to 1990s and 1990s to 2010s (WRS, p-value < 0.05; Table 3.1, Row 6a), associated with an increase in the proportion of reef-forming populations in the 1990s (Figure 3.2 f). Between regions, no significant differences were demonstrated in abundance or morphology in any decade (WRS, p-value > 0.05; Table 3.2, Row 3), with the exception of in the 1990s (WRS, p-value < 0.01; Table 3.2, Row 3) correlating with the previously mentioned peak in reef-forming populations within the range. During the 1990s, populations near the range edge exhibited a lower proportion of Superabundant, Abundant and Common categories, and a greater proportion of Frequent, Occasional and Rare categories (Figure 3.2 b, d), and consequently, a greater proportion of encrusting populations than within the range (Figure 3.2 c, f).

Area-specific decadal comparisons:

In both regions, the majority of paired areas demonstrated stability (no change in either abundance or morphology occurred in more than 50 % of areas; Figure 3.6). Despite this, significant differences in both abundance and morphology were demonstrated from the 1980s to both the 2000s and 2010s near the range edge

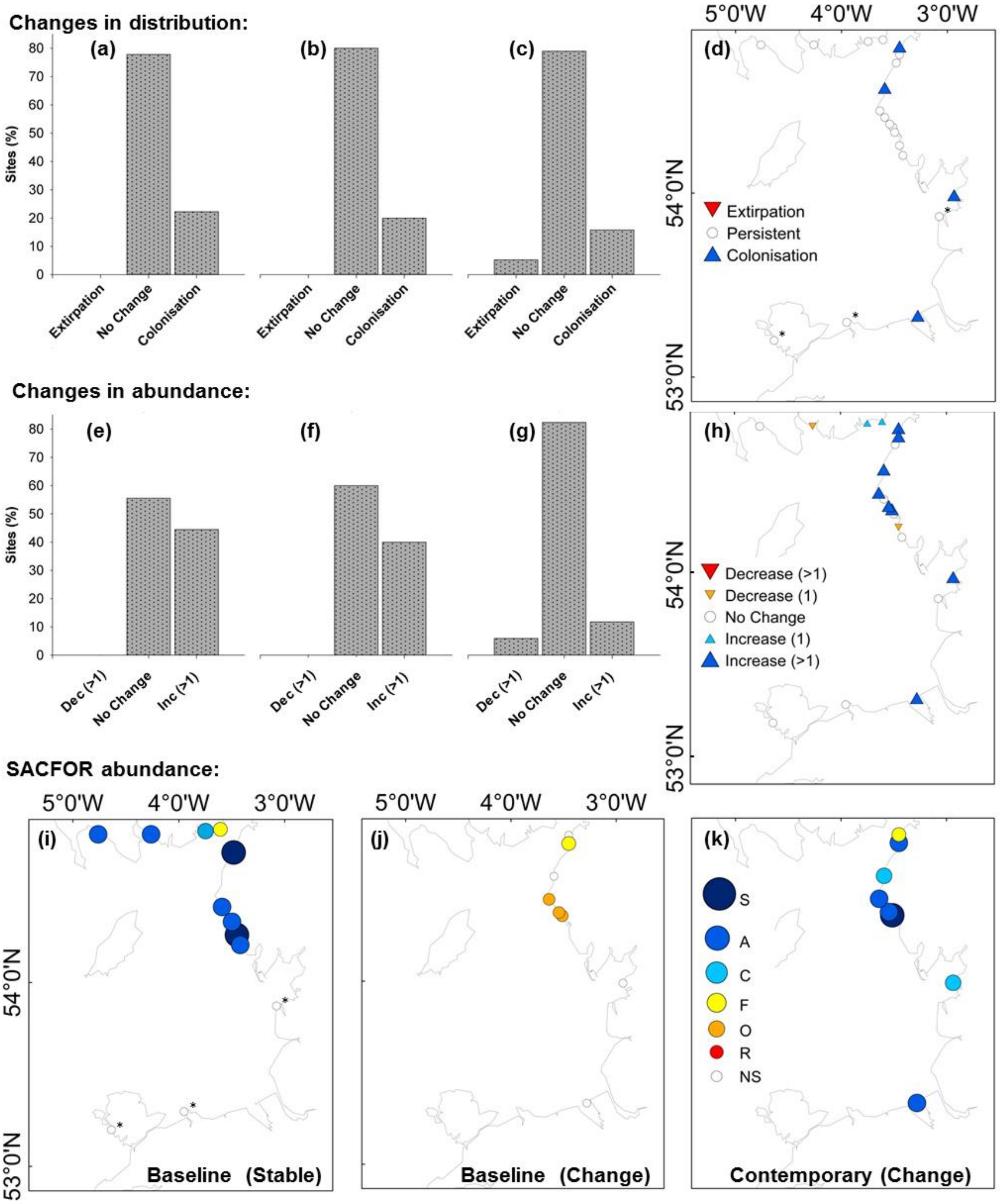

Figure 3.4: Reported changes in *Sabellaria alveolata* distribution and abundance at paired sites in near range edge populations. (a-d) Changes in distribution. Decrease from present to absent = ‘Extirpation’/▽, opposing increase = ‘Colonisation’/△, and persistence = ‘No Change’/○ (* = unpopulated suitable sites in all directly comparable surveys): (a) baseline-intermediate (n = 11); (b) baseline-contemporary (n = 20); (c) intermediate-contemporary (n = 19); (d) Spatial positioning of changes from baseline to contemporary. (e-h) Changes in abundance. Gain of ≥ 2 SACFOR categories = Increase/△, opposing loss = Decrease/▽), and all changes ≤ 1 category = No Change (○ = stable; note △/▽= little change of 1 category and were not considered further). (e) baseline-intermediate (n = 11); (f) baseline-contemporary (n = 20); (g) intermediate-contemporary (n = 17). (h) Spatial positioning of changes from baseline to contemporary. (i-k) Comparisons of abundance colour-coded to SACFOR scale. (i) Baseline abundance at relatively stable sites. (j) Baseline abundance at sites of altered abundance. (k) Contemporary abundance at sites of altered abundance.

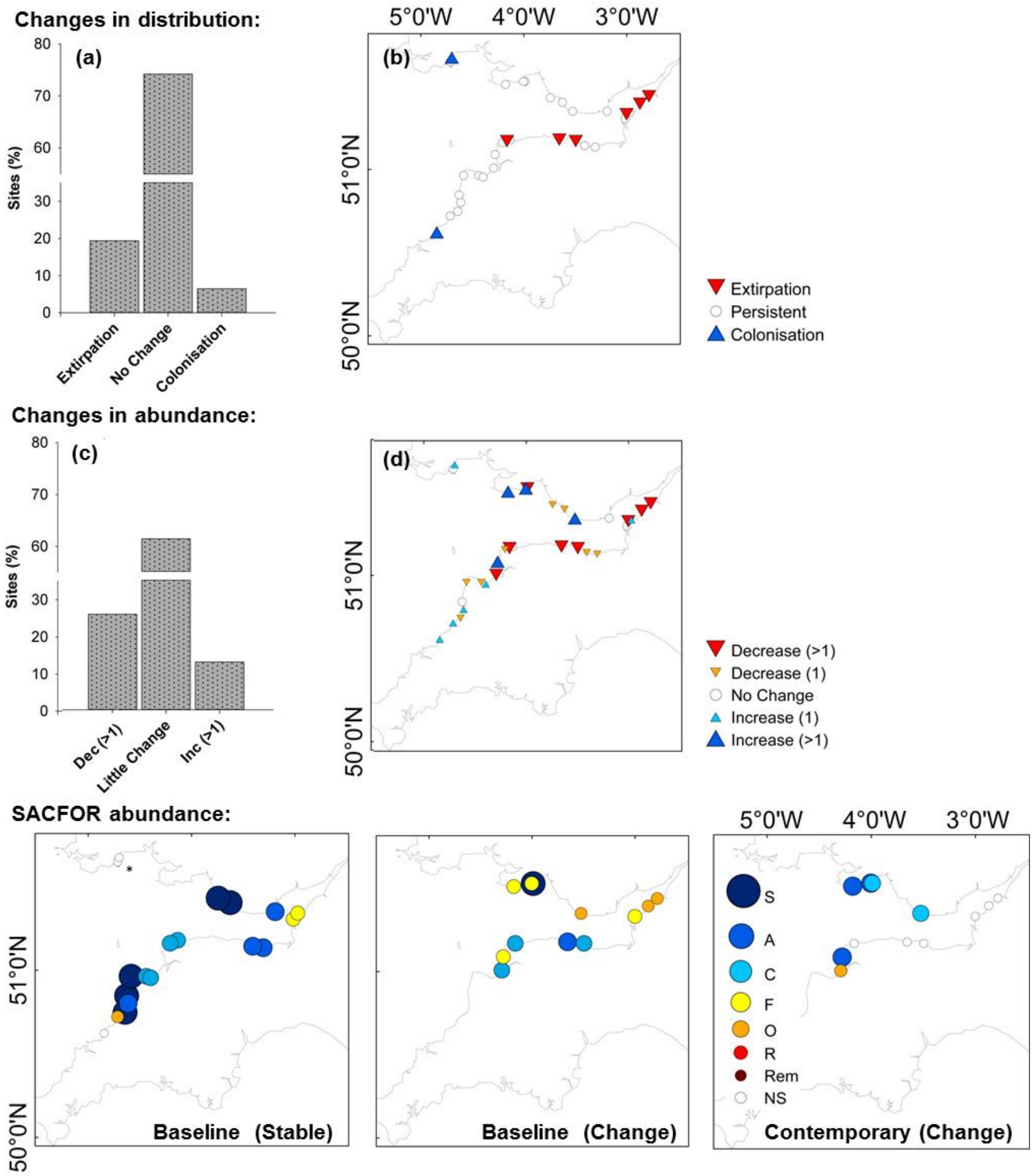

Figure 3.5: Reported changes in *Sabellaria alveolata* distribution and abundance at paired sites well within the range (between baseline and contemporary datasets). (a, b) Distribution (n = 31). Decrease from present to absent = 'Extirpation'/▽, opposing increase = 'Colonisation'/△, and persistence = 'No Change'/○ (* = unpopulated suitable sites in all directly comparable surveys). (c, d) Abundance (n = 31). Gain of ≥ 2 SACFOR categories = Increase/△, opposing loss = Decrease/▽), and all changes ≤ 1 category = No Change (○ = stable; note △/▽= little change of 1 category and were not considered further). (e-g) Comparisons of abundance from baseline-contemporary colour-coded to SACFOR scale. (e) Baseline abundance at relatively stable sites. (f) Baseline abundance at sites of altered abundance. (g) Contemporary abundance at sites of altered abundance.

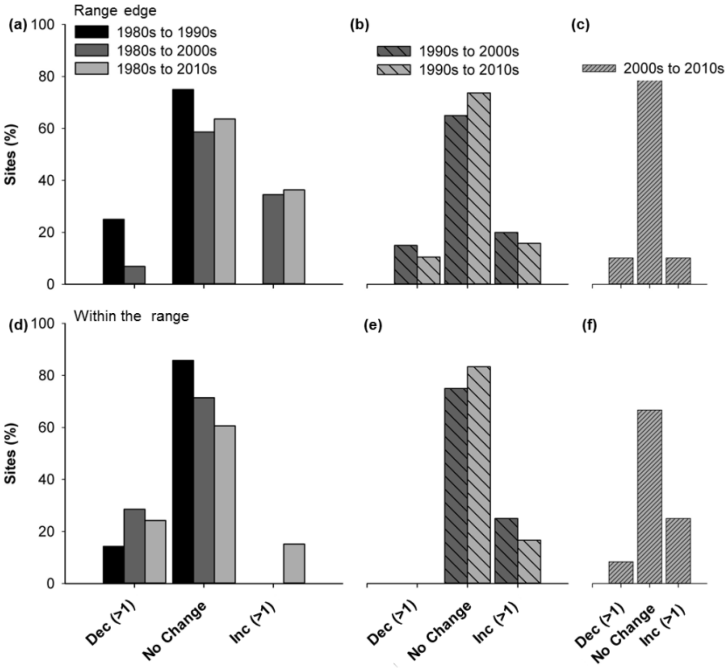

Figure 3.6: Regional changes in the SACFOR abundance of *Sabellaria alveolata*, at suitable areas within western Britain, from the 1980s to the 2010s. (a-c) populations near the range edge: (a) 1980s to subsequent decades ($n_{1980s\text{-}1990s}$ = 8, $n_{1980s\text{-}2000s}$ = 29, and $n_{1980s\text{-}2010s}$ = 22); (b) 1990s to subsequent decades ($n_{1990s\text{-}2000s}$ = 20 and $n_{1990s\text{-}2010s}$ = 19); (c) 2000s to 2010s ($n_{2000s\text{-}2010s}$ = 59). (g-i) populations well within the range: (g) 1980s to subsequent decades ($_{n1980s\text{-}1990s}$ = 7, $n_{1980s\text{-}2000s}$ = 7, and $n_{1980s\text{-}2010s}$ = 33); (h) 1990s to subsequent decades ($n_{1990s\text{-}2000s}$ = 4 and $n_{1990s\text{-}2010s}$ = 6); (i) 2000s to 2010s ($n_{2000s\text{-}2010s}$ = 12).

(OTS, p-value < 0.05; Table 3.1, Rows 2b, 3b). All changes in abundance from the 1980s to the 1990s were decreases; whilst changes from the 1980s to both the 2000s and 2010s exhibited more increases than decreases (Figure 3.6 a). Comparisons between subsequent decades revealed little overall change in abundance (Figure 3.6 b, c). No significant change in SACFOR abundance or morphology was demonstrated within the range (OTS, p-value > 0.05; Table 3.1, Rows 5b, 6b), but similar the near the range edge, the majority of changes from the 1980s were decreases in abundance (Figure 3.6 d), whilst from the 1990s, the majority were increases (Figure 3.6 e, f).

Site-specific comparisons:

Similarly, when site-specific data were considered, no significant differences in the proportion of abundance or morphology were exhibited within the range (OTS, p-value > 0.05; Table 3.1, Rows 5-6, right), but more decreases than increases in abundance occurred from the baseline to the contemporary (Figure 3.5 b). Within the range, the majority of increases in abundance occurred in the north, whilst the majority of decreases occurred in the south (Figure 3.5 d). Near the range edge significant differences in both abundance and morphology were demonstrated from the baseline to both the intermediate and contemporary (OTS, p-value < 0.05; Table 3.1, Rows 2-3, right), with no significant differences from the intermediate to the contemporary (OTS, p-value > 0.05; Table 3.1, Rows 2-3, right). The majority of changes in abundance were increases, particularly from the baseline (Figure 3.4 d-h). In both regions sites that demonstrated stable abundance were predominantly reported as reef-forming morphology (i.e. Common to Superabundant categories) within the baseline survey (Figure 3.4 i, 3.5 e). In contrast, sites at which change in abundance occurred were predominantly reported as Rare to Frequent in the baseline survey (Figure 3.4 j, 3.5 f) and either Absent (Figure 3.5 g) or Common to Superabundant categories (Figure 3.4 k, 3.5 g) in the contemporary survey, representing either an extirpation or an increase in abundance and reef-forming morphology.

3.4.3. Regional changes in environmental parameters

Little change in relative wave exposure occurred near the range edge through time (Figure 3.7 a, b) although maximum relative wave exposure due to the frequency of wind events (RWEwf) was greater in both the 1990s and 2000s than the 1980s and 2010s (i.e. greater maximum RWEwf in the 1990s and 2000s; Figure 3.7 b). Within the range maximum relative wind exposure due to average wind speed (RWEwa) and RWEwf increased through time (i.e. greater maximum RWEwa and RWEwf in the 1990s than 1980s, and 2000s and 2010s than 1990s; Figure 3.7 c, d). Consequently, although the range of RWEwa was lower within the range than near the range edge in the 1980s (Figure 3.7 a, c), in both the 2000s and 2010s the range of RWEwa and RWEwf were greater within the range than near the range edge (Figure 3.7 a-d). In both regions decadally averaged air temperature (AT) demonstrated an increase from the 1980s to the 2010s, with a peak in the 2000s (Figure 3.7 e, h), whilst the frequency of negative temperature events (FNT) demonstrated a reverse pattern with a peak in the 1980s decreasing to the 2000s

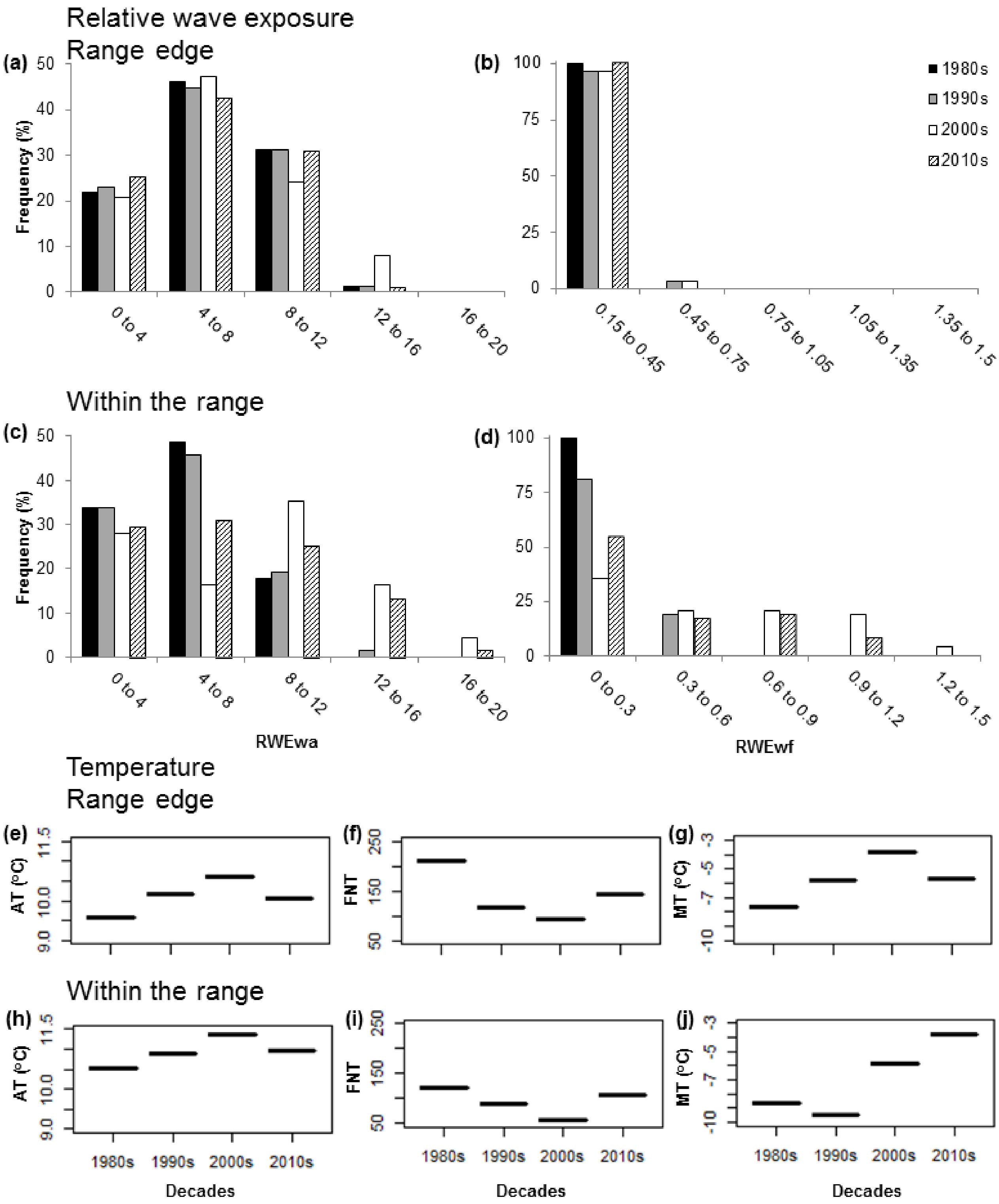

Figure 3.7: Decadal changes in regional environmental parameters from the 1980s to the 2010s, at the range edge (a-b, e-g) and within the range (c-d, h-j). (a, c) Relative wave exposure due to average wind speeds in knots (RWEwa), divided by 1000. (b, d) Relative wave exposure due to the frequency of wind events (RWEwf) divided by 1000. (e, h) Average temperature (°C). (f, i) Frequency of negative temperature events (Number of days per decade). (g, j) Minimum temperature (°C).

(Figure 3.7 f, i). Average air temperature was consistently greater within the range, whilst FNT was consistently greater near the range edge. An increase in minimum temperature (MT) occurred in near the range edge from the 1980s to the 2000s, with a decrease from the 2000s to the 2010s (Figure 3.7 g), whilst within the range a slight decrease occurred from the 1980s to the 1990s, followed by an increase to the 2010s (Figure 3.7 j). In comparisons between regions, the lowest MT was reported from within the range in the 1980s to the 2000s, despite being further south (Figure 3.7 g, j).

3.4.4. Impact of environmental parameters on *Sabellaria alveolata* distribution

Near the range edge, dimension 1 of the multiple correspondence analysis explained 47.2% of the variance, and was predominantly driven by temperature variables, whilst dimension 2 explained just 14.7%, but was driven by wave exposure. Near the range edge, increases in wave exposure (i.e. IncRWEwa and IncRWEwf) were associated with changes in distribution (i.e. expansions in distribution (IncPA) on both dimensions, and reductions in distribution (DecPA) on dimension 2), whilst decreases in wave exposure (i.e. DecRWEwa and DecRWEwf) were associated with persistence (i.e. StaPA on both dimensions; Appendix 3.3 a; Table 3.3, top left). Increases in temperature (i.e. IncAT, IncMT, DecFNT) were associated with increases in distribution (on dimension 1), whilst decreases in temperature were associated with both persistence (on dimension 1) and decreases in distribution (on both dimensions; Appendix 3.3 a; Table 3.3, top left). Decreases in distribution were separated from increases in distribution and persistence on dimension 2 (i.e. occurred with increased wave exposure; Appendix 3.3 a).

Within the range, dimension 1 of the multiple correspondence analysis explained 50% of the variance, and was driven by both temperature and wave exposure variables, whilst dimension 2 explained just 14.9%, and was predominantly driven by minimum temperature. Within the range, increases in wave exposure were associated with reductions in distribution (on dimension 1, or both dimensions); whilst decreases in wave exposure were associated with both persistence and expansions in distribution (on dimension 1, or both dimensions, Appendix 3.3 b; Table 3.3, bottom left). In contrast to near the range edge, increases in temperature,

Table 3.3: Relationships between changes in *Sabellaria alveolata* distribution, abundance and changes in environmental parameters given by the multiple correspondence analysis (RWEwa = relative wave exposure due to average wind speed, RWEwf = relative wave exposure due to frequency of wind events, AT = average temperature, MT = minimum temperature, FNT = Frequency of negative temperature events). Direction of change in environmental parameters is given by arrows. Dimensions of correspondence analysis on which relationship observed is given in brackets (i.e. both dimensions, both; or just dimension 1, D1; or dimension 2, D2).

Environment	Distribution			Abundance			Morphology		
	Increase	Stable	Decrease	Increase	Stable	Decrease	Increase	Stable	Decrease
Near the Range Edge									
RWEwf	↑ (both)	↓ (both)	↑ (D2)	↑ (D1)	↓ (both)	↑ (both)	↑ (both)	↓ (both)	↑ (D2)
RWEwa	↑ (both)	↓ (both)	↑ (D2)	↑ (D1)	↓ (both)	↑ (both)	↑ (both)	↓ (both)	↑ (D2)
AT	↑ (D1)	↓ (D1)	↓ (both)	↑ (both)	↓ (D1)	↓ (D2)	↑ (D1)	↓ (D1)	↓ (both)
MT	↑ (D1)	↓ (D1)	↓ (both)	↑ (both)	↓ (D1)	↓ (D2)	↑ (D1)	↓ (D1)	↓ (both)
FNT	↓ (D1)	↑ (D1)	↑ (both)	↓ (both)	↑ (D1)	↑ (D2)	↓ (D1)	↑ (D1)	↑ (both)
Within the Range									
RWEwf	↓ (D1)	↓ (both)	↑ (D1)	↓ (D1)	↓ (both)	↑ (D1)	↓ (D1)	↓ (both)	↑ (D1)
RWEwa	↓ (both)	↓ (D1)	↑ (both)	↓ (D1)	↓ (both)	↑ (D1)	↓ (D1)	↓ (both)	↑ (D1)
AT	↓ (both)	↓ (D1)	↑ (both)	↓ (D1)	↓ (both)	↑ (D1)	↓ (D1)	↓ (both)	↑ (D1)
MT	↓ (D2)	↑ (both)	↑ (D2)	↑ (both)	↑ (D1)	↓ (both)	↑ (both)	↑ (D1)	↓ (both)
FNT	↑ (D1)	↑ (both)	↓ (D1)	↑ (both)	↑ (D1)	↓ (both)	↑ (both)	↑ (D1)	↓ (both)

particularly minimum temperature, were associated with both persistence and reductions in distribution, whilst decreases were associated with expansions in distribution (on one or both dimensions; Appendix 3.3 b; Table 3.3, bottom left). Expansions in distribution were separated from both persistence and retractions in distribution on dimension 2 (i.e. occurred with decreases in minimum temperature; Appendix 3.3 b).

3.4.5. Impact of environmental parameters on *Sabellaria alveolata* abundance and morphology

As with distribution, near the range edge, dimension 1 of the abundance and morphology multiple correspondence analyses were predominantly driven by temperature (explaining 48.9% of the variance in abundance, and 48.7% in morphology), and dimension 2 by wave exposure (15% of the variance in both; Appendices 3.4 a, 3.5 a). As with distribution, increases in wave exposure were associated with changes in abundance and morphology (i.e. both increases and decreases tended to occur with increases in wave exposure; Appendices 3.4a, 3.5 a;

Table 3.3, top middle and right). Decreases in wave exposure were associated with stability in both abundance and morphology (Appendices 3.4 a, 3.5 a; Table 3.3, top middle), as with distribution (Appendix 3.3 a), in addition to decreases in reef-forming morphology (Appendix 3.5 a; Table 3.3, top right). Increases in temperature were associated with increases in abundance and reef-forming morphology, whilst decreases were associated with stability and decreases in both (Appendices 3.4a, 3.5 a; Table 3.3, top middle and right). Similarly to distribution, decreases in both abundance and reef-forming morphology were separated from stability and increases in abundance on dimension 2, in association with increases in wave exposure (Appendices 3.4 a, 3.5 a).

Within the range, dimension 1 of both the abundance and morphology multiple correspondence analyses were driven by both temperature and wave exposure (explaining 50.4% of the variance in abundance, and 50.7% of the variance in morphology), whilst dimension 2 was predominantly driven by minimum temperature (explaining 15.7% of the variance in abundance, and 15.4% of the variance in morphology). Within the range increases in wave exposure were associated with decreases in abundance and morphology on dimension 1 (Appendices 3.4 b, 3.5 b; Table 3.3, bottom middle and right), whilst decreases were associated with stability (on both dimensions) and decreases (on dimension 1; Appendices 3.4 b, 3.5 b; Table 3.3, bottom middle and right). Decreases in minimum temperature were associated with decreases in both abundance and morphology (on both dimensions; Appendices 3.4 b, 3.5 b; Table 3.3, bottom middle and right), whilst increases were associated with increases (on both dimensions for morphology and dimension 1 for abundance) and stability (on dimension 1; Appendices 3.4 b, 3.5 b; Table 3.3, bottom middle and right). However a mixed relationship was demonstrated with air temperature as associations were reversed for average temperature (Appendices 3.4 b, 3.5 b; Table 3.3, bottom middle and right). Increases in abundance and morphology were directly opposed to decreases, and separated from stability, in association with increases in minimum temperature (Appendices 3.4 b, 3.5 b; Table 3.3, bottom middle and right). Additionally, decreases in both were associated with increases in wave exposure on dimension 1 (Appendices 3.4 b, 3.5 b; Table 3.3, bottom middle and right).

3.5. Discussion

Sabellaria alveolata is a persistent species at established suitable sites on the west coast of Britain. No long-term regional-scale changes (near the northern range edge or well within the range) in distribution were demonstrated from the 1980s to the 2010s. However, near the northern range edge, the majority of changes that did occur were colonisations, with an expansion in distribution filling in gaps within the range demonstrated from the 1980s to the 2000s in paired areas. Well within the range, long-term stability in both abundance and morphology were also demonstrated, despite decadal scale fluctuations in morphology (i.e. an increase from the 1980s to the 1990s, and a subsequent decrease from the 1990s to the 2010s in all available data). However, near the northern range edge increases in both abundance and the incidence of reef-forming morphology were demonstrated from the 1980s and 1990s to the 2010s. Despite national persistence and stability over a period of three decades, patterns of change occurred on reduced spatial and temporal scales that can be related to region-specific changes in temperature and site-specific changes in wave exposure. Regional consideration of observed changes provided evidence of different drivers of change in *S. alveolata* populations within Britain.

3.5.1. Environmental drivers of change

On British coastlines, intertidal communities have been exposed to predominantly warming temperatures from the 1980s to the 2010s (i.e. increases in average temperature and an associated decrease in the magnitude and duration of cold spells). In a warming climate, increases in abundance and poleward range extensions have been predicted and reported for southern species, at the north of their range, both within the British Isles (e.g. Hiscock et al., 2004; Hawkins et al., 2008), and elsewhere (e.g. Merzouk & Johnson, 2011). Over the past three decades, near the range edge changes in *S. alveolata* populations have been principally driven by temperature. Colonisations, and increases in both abundance and reef-forming morphology have predominantly occurred, in association with increases in average temperature and decreases in the magnitude and duration of cold spells (i.e. from the 1980s to the 2000s). Some local extinctions and suppression of reef-forming morphology were also reported, in association with decadal decreases in average temperature and increases in the magnitude and duration of cold spells (i.e. from the 2000s to the 2010s). The Lusitanian-boreal boundary occurs near the northern range edge, within the English Channel near where *S. alveolata* reaches its easternmost extension. The contrasting impacts of extreme winters trimming back distributions and increasing average temperatures leading to increased abundance and expanding species distributions have been well documented in this region (e.g. Crisp, 1964, Southward, 1967; 1991; Southward et al., 1995; Frost et al., 2004; Mieszkowska et al., 2007; Firth et al., 2015). This study provides evidence that the strength of the relationship between air temperature and *S. alveolata* distribution, abundance and morphology is region specific. Well within the range, temperature parameters were not the dominant drivers of change in *S. alveolata* populations, and reported changes in *S. alveolata* were not consistent with reported changes in temperature parameters. For example, well within the range, increases in distribution consistently occurred with decreases in temperature parameters, and increases in abundance and reef-forming morphology occurred with decreases in average temperature, in direct opposition to near the range edge, but increases in abundance and reef-forming morphology tended to occur with increases in minimum temperature as predicted. Well within the range, populations were consistently exposed to greater average temperatures, and it is likely that these was not limiting. In contrast, despite greater average temperatures, reported minimum temperatures well within the range were lower than near the range edge from the 1980s to the 2000s, and were potentially limiting to *S. alveolata* populations. In reality, this variability is likely to be experienced on a smaller scale due to local environmental and biological heterogeneity (Seabra et al., 2011).

Region-specific relationships with changing temperature were potentially buffered, or exasperated, by changes in wind regime, and thus wave exposure. Well within the range, increases in relative wave exposures due to both average wind speed and frequency of wind events were observed from the 1980s to the 2010s, with some increases observed from the 1980s to the 2000s near the range edge. In support of this, it has been well documented that wave height and swell have increased in the

North Atlantic in recent times (Bacon and Carter, 1991; Gulev & Hasse, 1998; 1999; Gulev & Grigorieva, 2004; Hadlet, 2009) in correlation with observed changes in wind speed and the intensity of storms (Gulev & Hasse, 1998; Carretero et al., 2005). In both regions, increases in wave exposure were associated with decreases in distribution, abundance, and morphology in *S. alveolata*, although near the range edge, they were paradoxically also associated with increases in *S. alveolata*. Whilst opposing changes in *S. alveolata* populations in response to increased wave exposure are initially counterintuitive, the impact of increasing wave exposure is probably site/coastal cell specific. A certain degree of wave exposure is essential for population establishment and development (Cunningham et al., 1984), but high wave exposures can be physically damaging, and can lead to increases in sedimentation and thus smothering (Wilson, 1971; 1974). High wave exposure has been reported to be a dominant driver of polychaete reef destruction through physical damage (e.g. Wilson, 1971; McCarthy et al., 2003), through elevated competition (e.g. Branch et al., 2008; 2010), and through smothering by displaced sediment following storms (Wilson, 1971; 1974; McCarthy et al., 2003). It is proposed that small increases in wave exposure have facilitated the establishment of populations at more sheltered sites (e.g. in enclosed seas), whilst at more exposed sites, increases in wave exposure have been detrimental (e.g. on open Atlantic coasts). Elevated populations (e.g. reefs) will be more susceptible to wave damage (Wilson, 1971; 1974), whilst encrusting populations will be potentially facilitated by increases in particulate supply (e.g. food, larvae and suitable coarser sediment; Frost et al., 2004). Further investigation on the role of wave exposure on biogenic reef dynamics is required.

Within the British Isles, increases in wave exposure have occurred in association with increases in average temperature, and it is suggested that wave exposure and temperature act antagonistically to control *S. alveolata* populations. In the north of the range, increases in temperature in the past three decades have positively influenced *S. alveolata* distribution, abundance, and morphology. Nationally, extremely cold winters have negatively influenced *S. alveolata* populations curtailing the impact of a warming climate, and in the south of the range, increases in relative wave exposure have further negatively influenced *S. alveolata* populations. Consequently, although long term stability and persistence has been demonstrated, predicted increases in storminess as often predicted under climate change scenarios (e.g. Giorgi et al., 2004; Beniston et al., 2007) may negatively impact *S. alveolata* populations.

3.5.2. Natural resilience of *Sabellaria alveolata*

Sabellaria alveolata reef structures naturally vary highly in morphology on short-term small-spatial scales. Growth of up to 12 cm annually has been reported (Gruet, 1982), with elevated growth in warmer, highly turbid waters (e.g. at Hinckley Point power station; Bamber & Irving, 1997). Gruet (1982; 1986) suggested reef development followed a natural cyclic pattern of succession from initial settlement, through rapid growth to developed reef, followed by a stagnation phase in which growth is minimal. Secondary settlement and reef replenishment is dependent on settlement stage larvae being present in the water column, and if this process fails repetitively, the reef will ultimately enter the destruction phase. Total destruction is rare as the biogenic structure generated by a successful population is robust (Gruet, 1986, Le Cam et al., 2011), surviving for several years after the reef is effectively dead (Cunningham et al., 1984; Allen et al., 2002; Le Cam et al., 2011), and remaining attractive to settling larvae from host reefs (Wilson, 1968). Within an existent population all developmental stages can occur, as different areas are exposed to different magnitudes of environmental stress (e.g. areas within the reef may be protected from trampling, populations lower on the shore from extreme cold, populations at the back of the reef from extreme wave exposures). Following disturbance events, degraded populations of *S. alveolata* have demonstrated an inherent capability to recover rapidly (e.g. Gubbay, 1988; Strachan, 2013). For example, recovery was reported at Criccieth following almost complete mortality during the extreme winter of 1962/1963 (Firth et al., 2015). Both reef development trajectories and structural robustness facilitate reef persistence through time. This can make interpretation of investigations of long-term change difficult as a lag can occur between episodes of disturbance or a stress event, and the resultant population destruction, during which time secondary settlement may occur and re-establish the reef.

3.5.3. Knowledge gaps and opportunities

Decadal scale changes in temperature and wave exposure variables do not account for all variation in *S. alveolata* populations near the range edge or within the range. Other factors for further consideration include coastal hardening, trampling, biotic interactions, freshwater run off, turbidity, altered hydrodynamics, and food and larval supply, plus natural variability in a highly stochastic fluctuating system on the interface of rocky and sedimentary systems. Frost et al. (2004) and Firth et al. (2015) documented the proliferation of coastal defence structures near the range edge, many populated by *S. alveolata*. Artificial structures may provide suitable habitat in previously unsuitable locations, potentially acting as “stepping stones” to larval dispersal (Frost et al., 2004; Mieszkowska, 2013; Firth et al., 2015). However, they may also alter hydrodynamics, and thus influence both sediment and larval transport to existent populations (Martins et al., 2009), potentially increasing or decreasing particulate supply. Changes in wave regime may also result in the accumulation or loss of sand. Elevated growth rates are known to occur in highly turbid environments (Gruet, 1982). However, in the laboratory, Strachan (2013) demonstrated complete mortality after prolonged smothering by sand, whilst in the field, Wilson (1971) reported reduced growth due to natural smothering, and Porras et al. (1996) reported extirpation due to high siltation and sand accumulation. Cunningham et al. (1984) reported populations north of Weston-Super-Mare, on the south coast of Severn, appeared to be in decline in the early 1980s, and several extirpations had indeed occurred by 2013 within this region, associated with heavy siltation (Bush, pers. obs.). The impact of increased sedimentation and smothering should be investigated further.

This study has highlighted the importance of scale in consideration of climate change investigations. It has considered regional scales changes in environmental drivers, however in reality changes will occur on smaller-spatial scales (Seabra et al., 2011; Fisher et al., 2015). The vertical position of a population on the shore, and the tidal regime, may buffer environmental effects. *Sabellaria alveolata* avoid freezing temperatures by retracting into their tubes during emersion, and have been observed to remain within their tubes when immersed in water temperatures of less than 4 °C

(Bush, unpub.). Moreover, Wilson (1971) reported that whilst reef populations at lower shore levels survived extremely cold winters, those at higher levels were destroyed. Similarly, environmental changes should be considered on reduced temporal scales, as environmental extremes would have less impact on intertidal populations if they occurred on a low neap tide or spring flood tide (e.g. Firth et al., 2011; Ronges et al., 2012). For example, the potential detrimental impact of an extremely cold night may be buffered by submersion in the north of the British Isles, but not in the south as in the English Channel, low tide occurs at approximately midnight and midday (Hawkins, pers. obs.).

Physical disturbance can also influence *Sabellaria alveolata* populations. Reefs are susceptible to long-term trampling (Cunningham et al., 1984; Strachan, 2013), particularly at the reef edge. Aquaculture can also negatively impact *S. alveolata* reefs locally, elevating populations of oysters and mussels on the reefs themselves and directly increasing competition for space and food (e.g. *Mytilus edulis*, *Crassostrea gigas*; Cunningham et al., 1984; Dubois et al., 2006; Desroy et al., 2011). Increased numbers of shellfish attract fishermen at low spring, and thus increasing trampling (Dubois et al., 2002; Desroy et al., 2011). Increased anthropogenic use of the coastline may have a detrimental impact on *S. alveolata* populations, especially if impacts occur during settlement, as juvenile tubes are more fragile (Bush, pers. obs.). Substrate type must also be considered as increased wave exposure can have greater impacts on populations affixed to loose substrata. *Sabellaria alveolata* can stabilise the sediment, growing over pebble scars to create a solid substrata of pebble and accumulated biogenic cement (e.g. Morecambe Bay, many sites in Cardigan Bay; Desroy et al., 2010; Le Cam et al., 2011). Under conditions of high wave exposure, however, the force of the waves can tear the pebbles loose, eroding the beach back to its mobile component parts (Bush, pers. obs.).

Biotic interactions with *S. alveolata* are not well defined, although the reefs themselves are often referred to as biodiversity hotspots (Dubois et al., 2002; Desroy et al., 2011). Predators are largely unknown although *Sabellaria* spp. tubes have been found within fish and crab stomachs (Taylor et al., 1962; Pearce et al., 2011);

both of which are known to live and forage in the reef structures (Wilson, 1971; Gruet, 1972; Bamber & Irving, 1997). Actively growing *S. alveolata* generally out-compete all other intertidal organisms (Cunningham et al., 1984), however following mass *M. edulis* settlement, particularly on stagnating reefs, mussels can out-compete *S. alveolata* (Egerton, 2014; Bush, pers. obs.). The mechanisms of this competition are largely unknown, but during stagnation phase, *M. edulis* juveniles can attach to the reef structures, blocking tube apertures, and smothering reefs in pseudo-faeces (Desroy et al., 2011; Egerton, 2014; Bush & Davies, Chapter 4), whilst additionally competing for food. As filter feeders, *M. edulis* may also passively prey on *S. alveolata* larvae. Competition has also been documented with between *S. alveolata* and both the ephemeral green algae *Ulva armoricana* and the Pacific oyster, *C. gigas*, within Mont Saint-Michel Bay (Dubois et al., 2006).

Although little change in adult *S. alveolata* distribution and abundance were observed in western Britain in the past three decades, the overall health and developmental stage of populations through this time is largely unknown. It has been documented that site-specific successful settlement is sporadic (Wilson, 1971; 1974; Bush & Davies, Chapter 4). However, to the best of the authors' knowledge, there are no broad-scale records of settlement or consideration of successful recruitment years. Unsuccessful settlement could be a result of a decrease in propagule release, increased larval mortality, or altered larval transport. From *in vivo* studies, Slater (2013) demonstrated that larvae are sensitive to temperature, reaching smaller maximum size in low temperatures. Dubois et al., (2007) also noted a larger larval size in warmer temperatures in the field. However, the drivers of recruitment success should be studied further.

3.6. Conclusions

Sabellaria alveolata is a persistent species that is capable of colonising both natural and artificial substrata throughout its biogeographic range. Temperature plays an important role in determining the distribution of *S. alveolata*, particularly near the range edge where colonisations and increases in abundance and reef-forming morphology have occurred with increases in average temperature, and decreases in the magnitude and duration of cold spells, whilst decreases in *S. alveolata* populations have occurred with opposing temperature changes. Under a warming regime, continued increases in abundance and reef-forming morphology and additional colonisations of suitable sites near the range edge are expected. However, wave exposure also plays an important role in determining the distribution of *S. alveolata*. Near the range edge, increases in reef-forming morphology but decreases in abundance occurred with increases in wave exposure, suggesting that elevated reef-forming populations are suppressed whilst populations of lower elevation are facilitated. However, wave exposure changed little near the range edge over the study period, and did not reach the magnitudes of wave exposure within the range, where extirpations and decreases in abundance and reef-forming morphology occurred with large increases in wave exposure, whilst increases in *S. alveolata* populations occurred with decreases in wave exposure.

Whilst this study confirms the importance of temperature in limiting *S. alveolata* populations within the British Isles, and provides an insight into the importance of wave exposure in determining the distribution, abundance, and morphology of *S. alveolata*, the precise mechanisms by which these environmental factors act are unknown, and many other environmental and biotic factors are still to be considered. Decreases in both abundance and the incidence of reef-forming morphology have occurred within the range with increases in wave exposure (e.g. to the 2000s and 2010s), and increases in wave exposure continue to be forecast by climate change models. Such increases may have a direct negative impact on the abundance and morphology of *S. alveolata* within the range, and will act in direct opposition to increased temperature in the north of the range.

3.7. Acknowledgements

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3.8. Appendices

Appendix 3.1: Paired collated *Sabellaria alveolata* records from suitable sites well within the range, paired between the baseline survey of Cunningham et al. (1984) (1980-1984) and contemporary survey (2012-2014). When considering populations well within the range, this dataset is subsequently referred to as baseline to contemporary data. Location data includes site name and OSGB coordinates. Original record identifying codes are included for original data, in addition to identifying codes for each paired area. Presence, abundance and morphological data is given for both the baseline (BL) and contemporary (CT) in addition to the change between datasets (BL -CT).

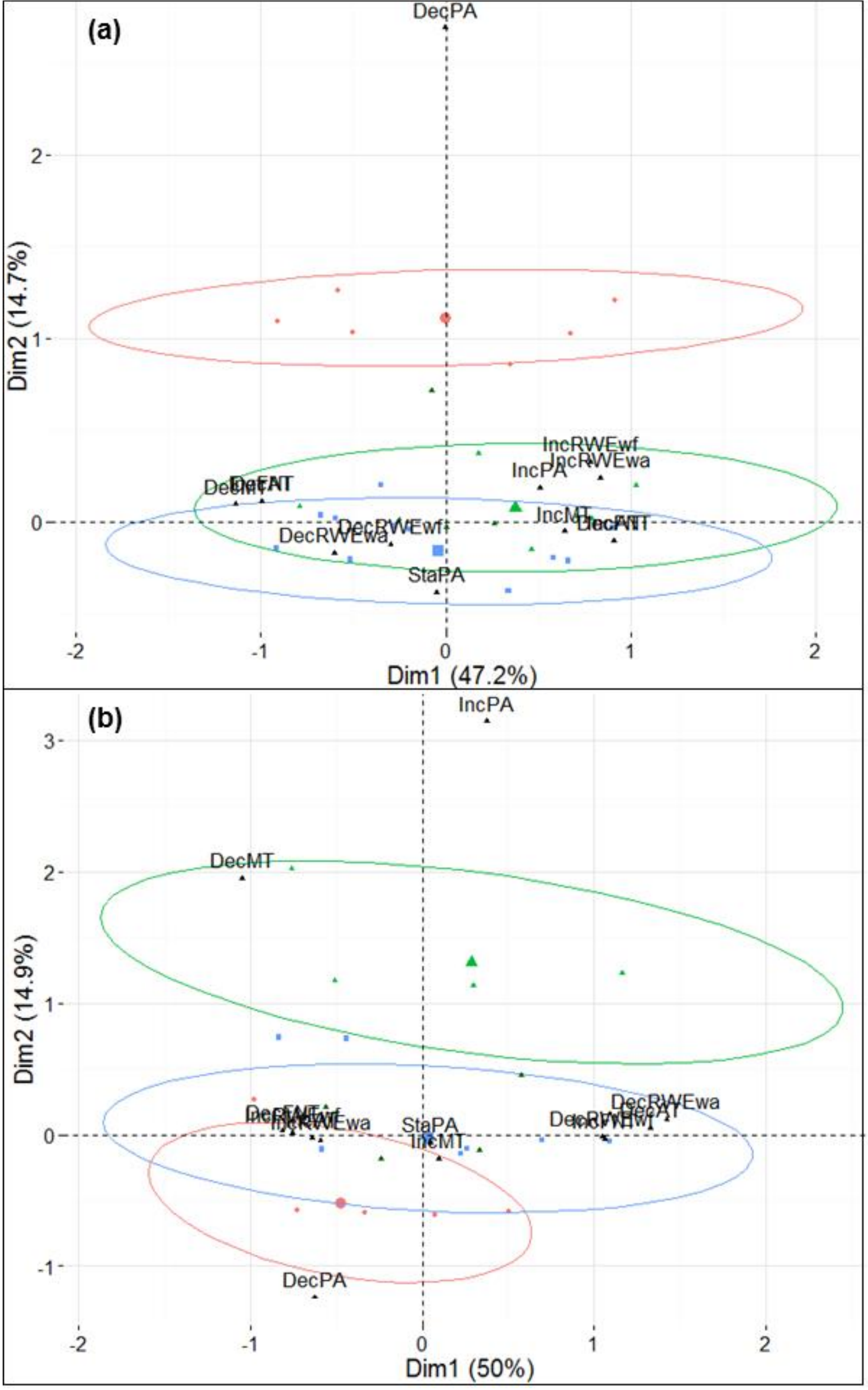
Original record ID	**Paired area ID**	**Site name**	**Eastings**	**Northings**	**Presence**			**Abundance**			**Morphology**		
					BL	**CT**	**BL - CT**	**BL**	**CT**	**BL - CT**	**BL**	**CT**	**BL - CT**
125 - 126	P15	Trebarwith Strand	204000	86000	0	1	1	0	2	1	0	1	1
165 - 166	P26	Crackington Haven N	213000	97000	1	1	0	3	4	1	1	1	0
208 - 211	P27	Millook	218000	100000	1	1	0	7	6	-1	2	2	0
257 - 263	P30	Bude	220000	106000	1	1	0	6	7	1	2	2	0
223 - 248	P32	Duckpool, Coombe	219000	111000	1	1	0	7	7	0	2	2	0
394 - 396	P33	Bucks Mills	235000	123000	1	1	0	5	6	1	2	2	0
280 - 287	P34	Hartland Quay	222000	124000	1	1	0	7	6	-1	2	2	0
379 - 380	P36	Clovelly	232000	124000	1	1	0	5	4	-1	2	1	-1
446 - 449	P39	Westward Ho	242000	129000	1	1	0	5	3	-2	2	1	-1
459 - 462	P40	Downend, Croyde S	243000	138000	1	1	0	4	6	2	1	2	1
1341 - 1342	P46	St Audries Bay, Doniford	310000	143000	1	1	0	6	5	-1	2	2	0
1194 - 1198	P47	Blue Anchor	303000	144000	1	1	0	6	5	-1	2	2	0
550 - /551	P50	Lee Bay, Woolacombe	248000	146000	1	1	0	5	4	-1	2	1	-1
612 - 613	P54	Ilfracombe	251000	147000	1	0	-1	5	0	-5	2	0	-2
1105 - 1109	P55	Minehead	297000	147000	1	0	-1	5	0	-5	2	0	-2
632 - 633	P56	Hele Bay	253000	148000	1	1	0	5	5	0	2	2	0
975 - 976	P58	Porlock Weir	286000	148000	1	0	-1	6	0	-6	2	0	-2
1548 - 1550	P59	Birnbeck, Weston Super Mare	330000	162000	1	1	0	4	4	0	1	1	0
1559 - 1560	P61	Sand Point, Kewstoke	331000	165000	1	0	-1	4	0	-4	1	0	-1
1585 - 1586	P64	Middle Hope Cove, Kewstoke	333000	166000	1	1	0	4	5	1	1	2	1
1081 - 1085	P68	Llantwit Major	295000	167000	1	1	0	3	5	2	1	2	1
1398 - 1401	P69	Lavernock Point	318000	167000	1	1	0	6	6	0	2	2	0
1619 - 1621	P72	Clevedon	340000	172000	1	0	-1	3	0	-3	1	0	-1
1003 - 1008	P75	Dunraven Bay	288000	173000	1	1	0	7	6	-1	2	2	0
918 - 921	P78	Hutchwns Point, Porthcawl	280000	176000	1	1	0	7	6	-1	2	2	0

1668 - 1673	P80	Portishead	346000	177000	1	0	-1	3	0	-3	1	0	-1
592 - 594	P88	Oxwich	250000	185000	1	1	0	4	6	2	1	2	1
781 - 787	P98	Limeslade Bay. The Mumbles, Bracelet Bay	262000	187000	1	1	0	4	6	2	1	2	1
794 - 800	P99	Bracelet Bay, Swansea	263000	187000	1	1	0	7	5	-2	2	2	0
167 - 169	P104	Tenby	213000	200000	0	0	0	0	0	0	0	0	0
173 - 174	P105	Monkstone Point, Saundersfoot	214000	203000	0	1	1	0	2	1	0	1	1
SUMMARY OF CHANGES					6 ↓/23↔/2 ↑			8 ↓/19↔/4 ↑			9 ↓/15↔/7 ↑		

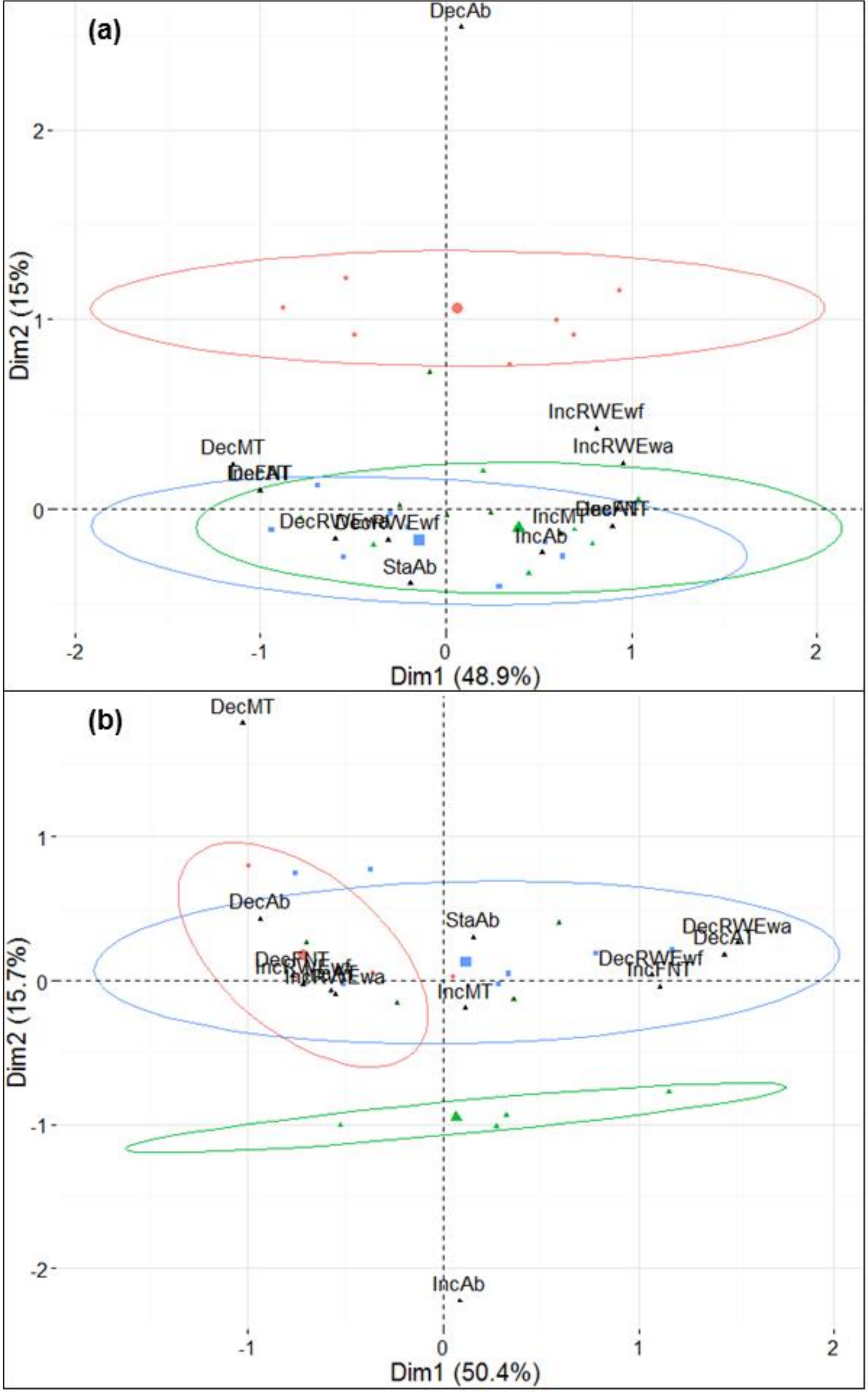
Appendix 3.2: Paired collated *Sabellaria alveolata* records from suitable sites near the range edge, paired between the baseline survey of Cunningham et al. (1984) (1980-1984), the intermediate survey of Frost et al., (2004) (2003-2004) and the contemporary survey (2012-2014). When considering populations near the range edge, this dataset is referred to subsequently as baseline to contemporary data. Location data includes site name and OSGB coordinates. Original record identifying codes are included for original data, in addition to identifying codes for each paired area. Presence, abundance and morphological data is given for the baseline (BL), intermediate (INT) and contemporary (CT) in addition to the change between datasets (BL-INT, BL-CT, INT-CT).

Original record ID	**Paired area ID**	**Site name**	**Eastings**	**Northings**	**Presence**						**Abundance**						**Morphology**					
					BL	**INT**	**CT**	**BL-INT**	**BL - CT**	**INT-CT**	**BL**	**INT**	**CT**	**BL-INT**	**BL - CT**	**INT-CT**	**BL**	**INT**	**CT**	**BL-INT**	**BL - CT**	**INT-CT**
365 - 376	P157	Rhosneigr	231000	372000	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-	0	-
990 - 991	P158	ColwynBay	287000	378000	0	1	-	1	-	-	0	2	-	2	-	-	0	1	-	1	-	-
963 - 966	P162	PenrhynBay_RhosPoint	284000	381000	0	0	-	0	-	-	0	0	-	0	-	-	0	0	-	0	-	-
892 - 895	P165	Great Ormes Head W, Llandudno	275000	383000	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1404 - 1411	P166	Hilbre Island SW	318000	387000	0	1	1	1	1	0	0	6	6	6	6	0	0	2	2	2	2	0
1412 - 1413	P167	North Bay, Hilbre Island	318000	388000	-	1	1	-	-	0	-	6	6	-	-	0	-	2	2	-	-	0
1512 - 1513	P168	Leasowe BW, W of Lighthouse, Wirral Foreshore	324000	391000	-	1	1	-	-	0	-	2	3	-	-	1	-	1	1	-	-	0
1532 - 1533	P169	Leasowe BW Mid, Wirral Foreshore	326000	392000	-	1	1	-	-	0	-	5	5	-	-	0	-	2	2	-	-	0
1546 - 1547	P172	Kings Parade E, Wirral Foreshore	329000	394000	-	1	1	-	-	0	-	5	5	-	-	0	-	2	2	-	-	0
1553 - 1554	P173	N Brighton Lighthouse W, Wirral Foreshore	330000	394000	-	0	1	-	-	1	-	0	5	-	-	5	-	0	2	-	-	2
1563 - 1564	P174	N Brighton Lighthouse E, Wirral Foreshore	331000	394000	-	1	1	-	-	0	-	5	5	-	-	0	-	2	2	-	-	0
1568 - 1570	P175	Rossal Point, Fleetwood	331000	447000	0	1	0	1	0	-1	0	4	0	4	0	-4	0	1	0	1	0	-1
1622 - 1627	P176	Heysham Power Station	340000	460000	0	0	1	0	1	1	0	0	5	0	5	5	0	0	2	0	2	2
1610 - 1615	P177	Foot Skear, Heysham Sands	339000	462000	-	1	1	-	-	0	-	-	7	-	-	-	-	-	2	-	-	-
1337 - 1340	P182	Annaside Bank	309000	484000	1	-	1	-	0	-	6	-	6	-	0	-	2	-	2	-	0	-
1323 - 1325	P183	Annaside Bank	308000	486000	-	1	1	-	-	0	-	6	6	-	-	0	-	2	2	-	-	0
1278 - 1282	P186	Tarn Bay	307000	490000	1	1	1	0	0	0	7	6	6	-1	-1	0	2	2	2	0	0	0
1221 - 1225	P187	Drigg Mid Shore	304000	498000	1	1	1	0	0	0	6	6	6	0	0	0	2	2	2	0	0	0
1203 - 1205	P188	Seascale	303000	500000	-	1	1	-	-	0	-	6	7	-	-	1	-	2	2	-	-	0
1206 - 1208	P189	Seascale	303000	501000	1	-	1	-	0	-	3	-	7	-	4	-	1	-	2	-	1	-
1173 - 1177	P190	Sellafield	301000	503000	1	1	1	0	0	0	3	7	6	4	3	-1	1	2	2	1	1	0
1126 - 1132	P192	Nethertown	298000	507000	1	1	1	0	0	0	6	6	6	0	0	0	2	2	2	0	0	0
1086 - 1090	P194	Saint Bees NE	295000	511000	1	1	1	0	0	0	3	6	6	3	3	0	1	2	2	1	1	0
1134 - 1135	P196	Moss Bay, Harrington	298000	525000	0	-	1	-	1	-	0	-	5	-	5	-	0	-	2	-	2	-
1240 - 1242	P212	Crosscanonby, Allonby Bay	305000	540000	1	-	1	-	0	-	7	-	7	-	0	-	2	-	2	-	0	-
1302 - 1307	P223	Dubmill Scar	307000	545000	1	-	1	-	0	-	4	-	6	-	2	-	1	-	2	-	1	-
1314 - 1316	P237	Beckfoot	307000	550000	0	-	1	-	1	-	0	-	4	-	4	-	0	-	1	-	1	-
293 - 298	P238	Bay at the Cock Inn, Auchenmalg Bay, Luce Bay	223000	551000	1	-	1	-	0	-	6	-	6	-	0	-	2	-	2	-	0	-
657 - 661	P240	Mossyard Bay	255000	551000	1	-	1	-	0	-	6	-	5	-	-1	-	2	-	2	-	0	-
1009 - 1010	P243	Port O Warren Bay	288000	553000	1	-	1	-	0	-	5	-	6	-	1	-	2	-	2	-	0	-
1114 - 1122	P244	Southerness Point	297000	554000	1	-	1	-	0	-	4	-	5	-	1	-	1	-	2	-	1	-
SUMMARY OF CHANGES					BL – INT: 0 ↓/8↔/3 ↑ BL – CT: 0 ↓/16↔/4 ↑ INT – CT: 1 ↓/15↔/2 ↑						BL – INT: 0 ↓/6↔/5 ↑ BL – CT: 0 ↓/12↔/8 ↑ INT – CT: 1 ↓/14↔/2 ↑						BL – INT: 0 ↓/6↔/5 ↑ BL – CT: 0 ↓/11↔/9 ↑ INT – CT: 1 ↓/14↔/2 ↑					

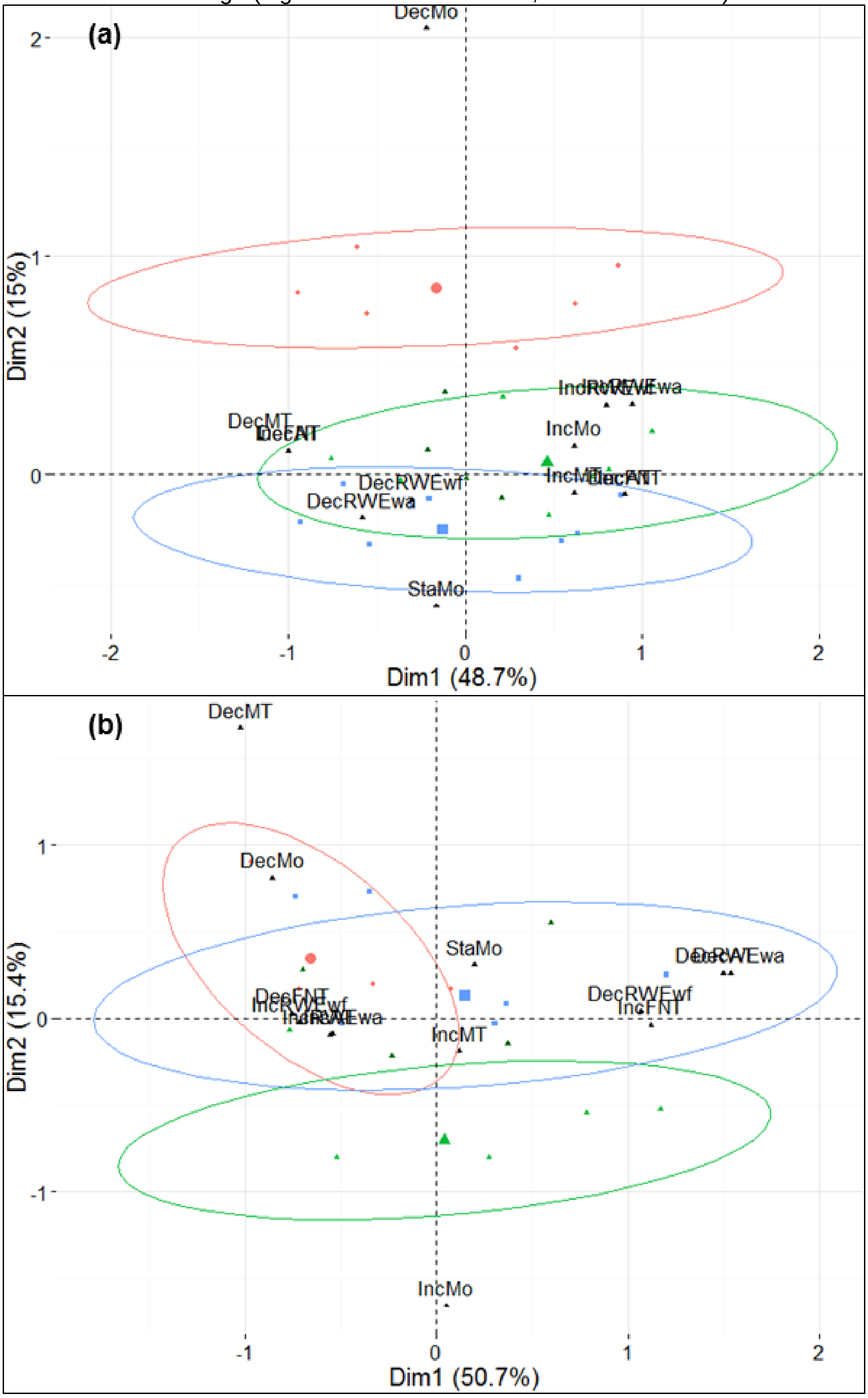
Appendix 3.3: Multiple correspondence analysis biplots of regional changes in *Sabellaria alveolata* distribution (PA) in relation to changes in relative wave exposure (RWEwa = relative wave exposure due to average wind speed, RWEwf = relative wave exposure due to frequency of wind events) and air temperature (AT = average temperature, MT = minimum temperature, FNT = Frequency of negative temperature events). 'Inc' = increase, 'Dec' = decrease, 'Sta' = Stable. Ellipses represent 95% of individuals. (a) Populations near the range edge (eigenvalues: 0.551 for dimension 1 (D1); and 0.171 for dimension 2(D2)). (b) Populations well within the range (eigenvalues: 0.584 for D1; and 0.174 for D2).



Appendix 3.4: Multiple correspondence analysis biplots of regional changes in *Sabellaria alveolata* SACFOR abundance (Ab) in relation to changes in relative wave exposure (RWEwa = relative wave exposure due to average wind speed, RWEwf = relative wave exposure due to frequency of wind events) and air temperature (AT = average temperature, MT = minimum temperature, FNT = Frequency of negative temperature events). ‘Inc’ = increase, ‘Dec’ = decrease, ‘Sta’ = Stable. Ellipses represent 95% of individuals. (a) Populations near range edge (eigenvalues: 0.571 for dimension 1 (D1); and 0.175 for dimension 2 (D2)). (b) Populations well within the range (eigenvalues: 0.589 for D1; and 0.183 for D2).



Appendix 3.5: Multiple correspondence analysis biplots of regional changes in *Sabellaria alveolata* morphology in relation to changes in relative wave exposure (RWEwa = relative wave exposure due to average wind speed, RWEwf = relative wave exposure due to frequency of wind events) and air temperature (AT = average temperature, MT = minimum temperature, FNT = Frequency of negative temperature events). ‘Inc’ = increase, ‘Dec’ = decrease, ‘Sta’ = Stable. Ellipses represent 95% of individuals. (a) Populations near range edge (eigenvalues: 0.568 for D1; and 0.176 for D2). (b) Populations well within the range (eigenvalues: 0.591 for D1; and 0.179 for D2).



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4. Site-specific conditions trigger switch between alternative states in temperate intertidal reefs

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Declaration

I declare that this manuscript is entirely my own work. A.J.D. provided supervision.

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4.1. Abstract

Sabellaria alveolata biogenic reefs are largely stable and persistent habitats over national and regional scales within Britain. However, some changes in both abundance and distribution have been reported, particularly near the north of the biogeographic range. This study aimed to assess reef stability on smaller spatial scales, through site-specific long-term monitoring near the northern range edge. In direct contrast to broad-scale trends, high within-site variability was demonstrated. Some populations decreased from reef-forming to absent within a year (e.g. MB2 in 2013), whilst others increased from spatially isolated hummocks to homogenous reefs (e.g. MB3 in 2013), and others remained stable with respects to reef extent and/or condition (e.g. in Llan in both years). Decreases in spatial cover of reef were associated with increases in *Mytilus edulis* cover (e.g. at MB1 in 2014; $R^2 = 0.83$) and physical disturbance (e.g. at MB2 in 2013), whilst increases were associated with *S. alveolata* settlement (e.g. at MB3 in 2013; $R^2 = 0.67$). This study provides evidence that the ecosystem engineers *S. alveolata* and *M. edulis* are alternative stable state communities in Britain. A transition was demonstrated from *S. alveolata* to *M. edulis* dominated community in poor settlement years that may be facilitated by the substrate stabilising ability of *S. alveolata*. It is suggested the alternative *M. edulis* state persists in part as a result of habitat modification (e.g. an increase in fine particulates). However, following physical removal and failed settlement of *M. edulis*, domination by *S. alveolata* was observed (e.g. Llan in 2014). State is modified by physical disturbance (either natural or anthropogenic), and partially dependent on successful secondary settlement. As *S. alveolata* is a Lusitanian species, and *M. edulis* a boreal species, *S. alveolata* can be expected to gain a competitive advantage in temperate waters under warming conditions.

4.2. Introduction

Biogenic reefs are often considered biodiversity hotspots, with rich and varied associated flora and fauna (Holt et al., 1998), and consequently, they are protected on European coastlines (e.g. Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora–Annex 1: Reefs). Within the northeast Atlantic, intertidal biogenic reefs are generated by several species of invertebrate (e.g. the honeycomb reef worm, *Sabellaria alveolata*; the sand mason worm, *Lanice conchilega*; the common mussel, *Mytilus edulis*; and the invasive Pacific oyster, *Crassostrea gigas*; amongst others; Holt et al., 1998; Smyth & Roberts, 2010; Lejart & Hily, 2011; De Smet et al., 2015). Whilst these ecosystem engineers can occur in dense homogeneous aggregations, they often coexist as alternative community states: *S. alveolata* has been reported adjacent to *L. conchilega* reefs (Larsonneur, 1994); *C. gigas* have overgrown native *M. edulis* beds within the Wadden Sea (Markert et al., 2013); whilst *C. gigas* and *M. edulis* have been reported in high abundance attached to *S. alveolata* reefs (Cunningham et al., 1984; Allen et al., 1999; 2002; Dubois et al., 2006; Desroy et al., 2011).

Gruet (1986) reported a natural cycle of reef development within *S. alveolata* populations from initial recruitment through to reef destruction. This cycle is initiated and sustained by settlement, which has been observed on both artificial and natural hard substrata (Firth et al., 2015), with settlement to existing populations or reef remains preferred (Wilson, 1968 b; 1970). Settlement is gregarious with larvae generally recruiting in high abundance. Rapid tube growth occurs, particularly following dense recruitment, likely due to competition for space, with Wilson (1976) documenting maximum growth of ~40 cm in 15.5 months post settlement. A decline in growth rate has been reported with age. Following initial rapid growth, over 15.5 months, Wilson (1976) observed only a few centimetres of growth in the following 8 months. Similarly Gruet (1986) suggested a growth phase of 2-3 years, subsequent to which the reef enters a stagnation phase and little or no growth occurs. Secondary settlement onto stagnation phase reef can restore the population back to growth phase but in the absence of this, the reef will enter a destruction phase, although total destruction is rare (Gruet, 1986; Bush et al., Chapter 2; 3). Settlement is highly variable, and dense settlements do not occur every year, even at highly abundant sites. Wilson (1971; 1974; 1976) observed settlement in nine out of 12 years of observation; however, settlement was sparse in three of those years, with dense settlement only observed in two. The timing of settlement is also unpredictable: Wilson (1971) reported some settlement in any month from August to June, generally in 1-3 months of each year, with months inconsistent between years (although dense settlement was only reported from September to December).

Sabellarian reef morphology is the result of a delicate balance between biological and physical factors, a balance that changes as the reef grows and develops. Whilst wave action initially plays a positive role suspending sediment and making it available for tube construction, as elevated reef structures are formed, wave action can become a negative force eroding the resultant tubes (Gruet, 1986; Bush et al., Chapter 3). Wilson (1976) observed that dense settlement and rapid growth did not necessarily equate to longevity: following moderate settlement, growth of the reef was relatively slow, and the reef was physically removed by wave action after approximately 3 years; following dense settlement, rapid growth occurred with the reef reaching an equivalent height within just 2 years, when it too was removed by wave action, indicative that maximum morphology is site-specific. Persistent populations are composed of several generations of worms, with individuals surviving typically for 3-5 years (Gruet, 1986). Wilson (1976) observed that within a developed reef, the distribution of young and old worms was very uneven. Some sections were composed entirely of older worms, whilst others were composed entirely of young worms, and still others are a mosaic of both. Consequently, spatial variability in developmental phase is prolific within a persistent population.

The mechanisms governing the ecosystem dynamics of reef-forming species are largely not understood, although positive and negative species interactions have been identified (Irving & Bertness, 2009). Facilitation, through the creation of solid biogenic habitat, is a common positive interaction (Irving & Bertness, 2009). Within the predominantly sedimentary Wadden Sea, *M. edulis* aggregations provided a suitable substratum for *C. gigas*, facilitating the successful spread of this invasive species throughout the region (Markert et al., 2013). *Sabellaria alveolata* has been observed to provide a similar function, through the binding of loose sand grains into cohesive reef structures, providing suitable substrata for both episammic and epilithic organisms (Naylor & Viles, 2000; Dubois et al., 2006; Fournier et al., 2010).

Models of alternative community states are often used to explain how assemblages of different species coexist in a spatial mosaic within the same environment (Petraitis & Latham, 1999; Beisner et al., 2003). In theory, alternative species assemblages are generated by differences in the original environmental conditions, or from community disturbance. Alternative states may or may not be stable, with a switch between states the result of a change in species density, pushing one state beyond equilibrium. Either an influx of recruits or a disturbance event has a negative impact on the original community, such that recruits of an alternative community can establish (Petraitis & Latham, 1999; Beisner et al., 2003; Petraitis et al., 2003). The alternative assemblage may physically alter the environment to promote the establishment of a more competitive species (negative feedback), whilst the succession species may alter the environment to support its own persistence (positive feedback). Subsequent disturbances may disrupt maintenance mechanisms, either returning the system to the original assemblage or amplify the secondary assemblage (Petraitis & Latham, 1999).

Cunningham et al. (1984) suggested a natural "*Sabellaria/Mytilus* succession" may exist within the British Isles, with *M. edulis* reported in high abundance on old reef, and reef remains, at many sites. However, when in growth phase, *S. alveolata* is the dominant competitor for space, forming homogenous, largely monospecific platforms over large areas (Wilson, 1971; Porras et al., 1996; Dias & Paula; 2001; La Porta & Nicoletti; 2009). Reduced growth, and ultimately the initiation of the destruction phase may be triggered by extreme temperature (Crisp, 1964; Wilson, 1971) or wind (Wilson, 1971), smothering (Wilson, 1971; Strachan, 2013), trampling (Cunningham et al., 1984; Strachan, 2013), competition (Cunningham et al., 1984; Perkins, 1988; Allen et al., 2002), predation (Wilson, 1971; Bamber & Irving, 1993; 1997), changes in the sedimentary or hydrodynamic regime (Allen et al., 2002) or simply age of *S. alveolata* (Gruet, 1986). Secondary settlement can restore the system to an actively growing *S. alveolata* reef; however settlement of *M. edulis* may tip the balance in favour of *M. edulis* reef. Both species demonstrate high fecundity, a semi-continuous larval supply, gregarious settlement and initial rapid growth (Wilson, 1968 a, b; Rodhouse et al., 1984; Bush et al., 2015). However, whilst *S. alveolata* potentially facilitates settlement of both by stabilising the substratum (Cunningham et al., 1984), *M*. *edulis* may have a negative impact on *S. alveolata* by increasing the concentration of fine particulates, decreasing the particle clearance rate of individuals, and potentially inducing smothering (Dubois et al., 2009).

Petraitis & Latham (1999) highlight the importance of scale when considering alternative community assemblages, as natural populations are not at equilibrium and are susceptible to disturbance dependent change. If the spatial or temporal scale of the original disturbance event is substantial, and post disturbance recruitment is sufficiently rapid and abundant, then an alternative assemblage may establish. Scale is also important when considering the longevity of assemblage changes. Long-term broad-scale studies of *S. alveolata* distribution and abundance have suggested stability and persistence on British coastlines (Bush et al., Chapter 2), with the exception of near the range edge where increases in abundance have been reported (Bush et al., Chapter 3; Frost et al., 2004; Firth et al., 2015). However, large temporal site-specific variability has also been demonstrated. For example, in Morecambe Bay, Jones reported a population of Occasional abundance in 1959, Frequent in 1960, Rare in 1961 but Absent in 1984 (data within Cunningham et al., 1984). Subsequently Haley reported a Common population in 1997, and Abundant in 1999 (data held by MBB), whilst Allen at al. (2002) reported Abundant reef in 2002. Superabundant populations were present in 2012-2014 (Bush et al., Chapter 2, 3). Large site-specific spatial variability has also been demonstrated. For example, Allen et al. (2002) reported 5 different “types” of reef covering a total of 0.02 km^2 categorised by morphology, coverage, area, height and health.

The aim of this study was to establish the dynamics of local occurrences of *S. alveolata* reefs, in particular with respects to variability in developmental phase, reef morphology and extent, and competition with other species such as *M. edulis*. This addressed two hypotheses: 1) Persistent *S. alveolata* reefs would be morphologically diverse, featuring multiple stages of reef development and individuals from multiple periods of settlement at any one time. In contrast, transient and declining reefs would largely reflect a lack of developmental diversity, featuring limited recurrent settlement (i.e. composed of individuals of similar ages). 2) Successful settlement of *M. edulis* onto stagnating reef populations, would result in an alternative stable state, but physical disturbance (e.g. removal of the reef structure, substrate upheaval) can interrupt this process, returning to a *S. alveolata* dominated community.

4.3. Study Area and Methods

4.3.1. Study area

Observations focused on four distinct transects at two localities within the Irish Sea. Three transects were situated within an extensive area of biogenic reef in Morecambe Bay, northwest England, and one in a smaller area of reef at Llanddulas, north Wales. The reef at Llanddulas was not large enough for more than one transect, however transects within Morecambe Bay were considered distinct sites as they were more than 100 m apart, and exhibited very different patterns of change (Figure 4.1). The transect at Llanddulas will subsequently be referred to as *Llan* (Figure 4.1 c) whilst those as Morecambe Bay will be referred to as *MB1*, *MB2*, and *MB3* (Figure 4.1 b). Each transect contained a *S. alveolata* population that featured Abundant reef during at least one sampling period over the three years of surveillance. Similarly each transect featured an Abundant *M. edulis* population during at least one sampling season. Biogenic reefs overlaid pebble scar at all transects, with *S. alveolata* physically binding the pebbles together with sand and self-excreted biomineralised cement (Fournier et al., 2010). *Mytilus edulis* were physically attached to each other, to pebbles scar and to existing *S. alveolata* populations. Seaward of the biogenic reefs, the substratum was principally composed of sand, with substantial sediment loading within the water.

4.3.2. Sampling methodology

Fieldwork was carried out at low spring tides in 2012-2014. At *Llan*, seasonal sampling was carried out in spring (April), summer (August) and autumn (October), whilst due to logistical constraints, sampling was carried out annually in summer (August) at Morecambe sites. In each sampling period, SACFOR abundance of *S. alveolata* was assessed within each site, with reef-forming populations categorised as Common abundance or greater (See Bush et al., Chapter 2) for complete SACFOR methodology). A fixed vertical transect (50 m long, by 10 m wide) was positioned through the *S. alveolata* reef-forming population at each site, perpendicular to the low water spring tide line, inshore from the seaward edge of live

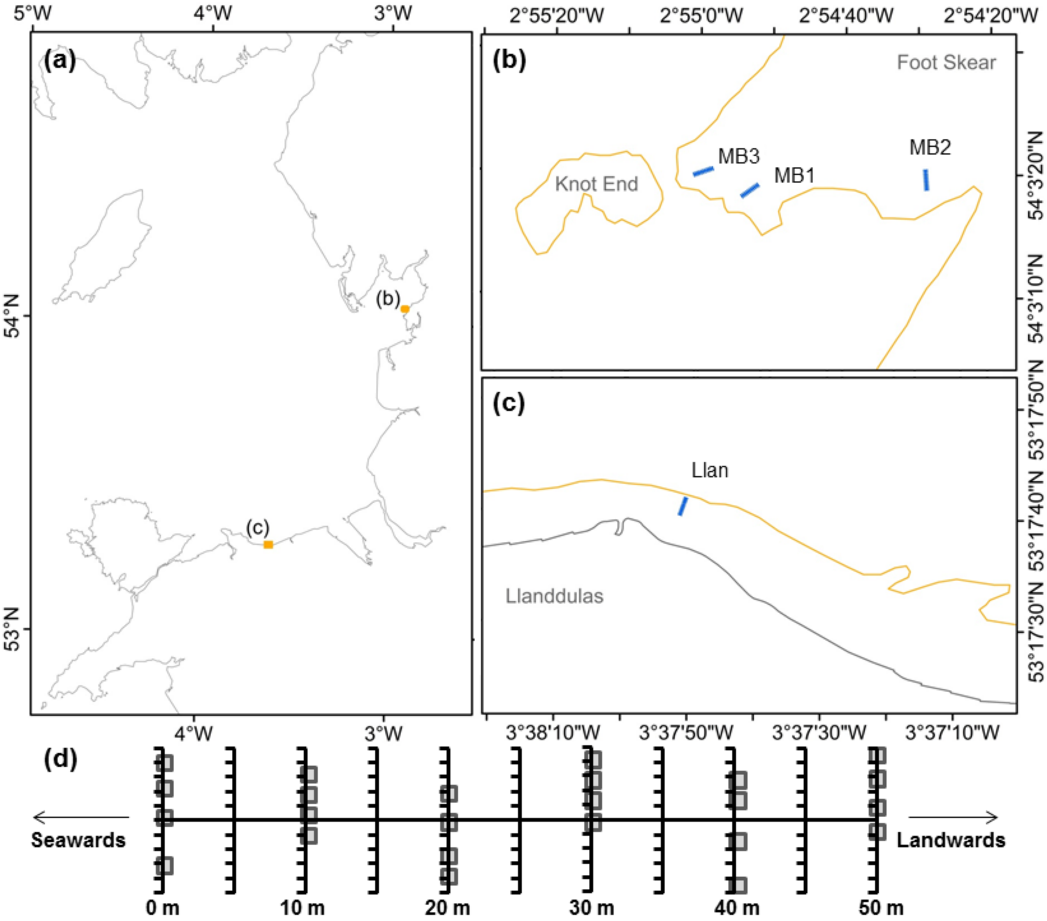
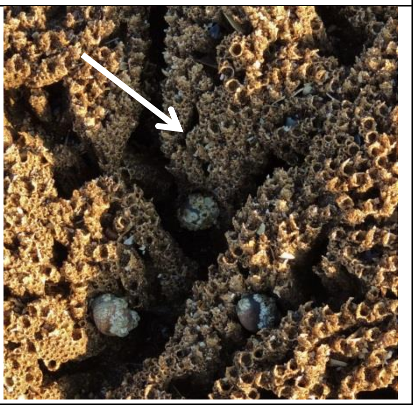


Figure 4.1: Long term monitoring sites for *Sabellaria alveolata*. (a) location of sites within the central Irish Sea. (b) location of transects in Morecambe Bay. (c) location of transects in Llanddulas. Coastline demarked in grey, low water spring in orange, 50 x 10 m transects in blue. (d) sampling methodology schematic for 50 m by 10 m transect. Every 5 m up the shore, at every dash, *S. alveolata* presence, height and health were recorded. Every 10 m up the shore, *S. alveolata* and *Mytilus edulis* percentage cover (total and recruits) were recorded in four 1 m^2 quadrats (☐, not to scale).

S. alveolata reef (Figure 4.1 b, c). Within each vertical transect, horizontal transects were positioned perpendicular to the main vertical transect, every 5 m up the shore (i.e. at 0, 5, …, 45 and 50 m). Within each horizontal transect, *S. alveolata* presence (present or absent), height from the substrata (measured with a skewer pushed through the reef; Wilson, 1971), and developmental phase, including the presence of secondary settlement (Table 4.1), was recorded at 1 m intervals (within 15 cm of the 1 m mark). Within every 10 m up the shore four 1 m^2 quadrats were randomly sampled and percentage cover of *S. alveolata*, *M. edulis* and other hard substrate

Table 4.1: Visual examples of the condition of *Sabellaria alveolata* populations (modified from Gruet, 1982; 1986; Images copyright Laura Bush).

Condition	Diagnostics	Photograph
Destruction	No living worms observed. No porch growth. Reef scar/remains dark brown to grey in colouration. May feature episammic organisms.	
Stagnation	Many inactive worms with limited porch growth. Reef dark brown in colouration. Signs of reef erosion in places Often featuring episammic organisms	
Growth	Living worms dominate. Active porch growth. Hummocks to reefs with uniform aspect Surface of reef of similar colour to surrounding sediment (i.e. sand/"fawn-yellowed")	
Secondary Recruitment	Small tubes of recruits present (aperture <2.5 mm).	

(e.g. bare rock, gravel, sand and dead shell) was recorded (Figure 4.1 d). Presence of *M. edulis* juveniles (defined as individuals with height less than 1.5 cm) within quadrats was recorded.

4.3.3. Data analysis

Stability and persistence of biogenic reefs on short-term small scales:

Summer SACFOR abundance, average percentage cover of *S. alveolata* and *M. edulis*, average reef height, and condition (i.e. developmental phase, settlement success, and percentage cover of bare substrata) were compared between sites and years. Additionally, at *Llan*, parameters were compared inter-annually (e.g. spring to summer, summer to autumn, and autumn to spring). In each comparison, average percentage cover of *S. alveolata* and *M. edulis* and reef height were compared statistically with Kruskal-Wallis (KW) tests due to the high variability and lack of normality in both datasets.

Sabellaria alveolata: Mytilus edulis *dynamic*:

Annual change in percentage cover of *S. alveolata* was compared with annual change in the percentage cover of *M. edulis* at all sites. Both were compared with settlement success (i.e. for *S. alveolata*, the change in the proportion of the horizontal transect from which juveniles were reported, and for *M. edulis*, the change in the proportion of quadrats from which juveniles were reported). Data from all sites were pooled for regional comparison and on a site specific basis using regression analysis.

4.4. Results

4.4.1. Overall site classification using SACFOR

At *Llan*, reef-forming *S. alveolata* was present in all seasons in all years. Little change in SACFOR abundance was observed with Abundant abundance reported throughout, with the exception of autumn 2013 when sections of the reef reached 66 cm in height, and thus Superabundant abundance (Table 4.2). In contrast to the relative stability at *Llan*, within Morecambe Bay large annual changes in SACFOR abundance were observed at all sites, although the direction and magnitude of these changes was not consistent between sites. Overall decreases in abundance were observed at both *MB1* and *MB2*. *MB1* deteriorated from Superabundant to Occasional in year 1 (i.e. from 2012 to 2013), and continued declining in year 2 (i.e. from 2013 to 2014) with only Remains reported in 2014. Similarly *MB2* deteriorated from Abundant to Occasional in year 1, with some recovery to Frequent in year 2. In contrast, *MB3* increased in abundance in year 1 (i.e. from Common to Abundant), but by 2014 complete reef destruction had occurred, with no *S. alveolata* observed (Table 4.2). Despite small-scale variability and the deterioration of all three sites within Morecambe Bay during the period of observation, populations located outside of the transects (e.g. between *MB1* and both *MB2* and *MB3*, on Knot End, and north of *MB3*; Figure 4.1 b) thrived throughout the period of observation with expansion of S*. alveolata* reefs northward on Foot Scar in 2014. Consequently, despite high variability on a small spatial scale, the maximum abundance of *S. alveolata* within Morecambe Bay demonstrated broad-scale stability.

4.4.2. Percentage cover of *Sabellaria alveolata*

No significant differences in cover were demonstrated between years (Figure 4.2 a) or seasons (Figure 4.3 a) at *Llan* (KW $\chi^2 \leq 3.49$, df = 1, p-value >0.05). In contrast, significant differences in cover were demonstrated between years at sites within Morecambe Bay, however the magnitude and direction of annual change in cover was not consistent between sites. For example, at *MB1* a significant decrease in

Table 4.2: Variability of *Sabellaria alveolata* from 2012 to 2014 within transects. Percentage of presence, maximum height and patch size are reported within each transect (*= No living worms, just reef remains present). Colour coded to SACFOR abundance with Superabundant highlighted in dark blue, Abundant in pale blue, Common in turquoise, Frequent in yellow, Occasional in orange, Remains in maroon, and Not Seen in white.

Site	Season	2012			2013			2014		
		Pres-ence (%)	Max Height (cm)	Max Patch size (m^2)	Pres-ence (%)	Max Height (cm)	Max Patch size (m^2)	Pres-ence (%)	Max Height (cm)	Max Patch size (m^2)
Llan	Spring	46.28 ± 4.55	45	>1	50.41 ± 4.56	45	>1	80.17 ± 3.64	50	>1
	Summer	64.46 ± 4.37	49	>1	69.42 ± 4.21	55	>1	77.69 ± 3.80	50	>1
	Autumn	42.15 ± 4.51	50	>1	64.46 ± 4.37	66	>1	75.83 ± 3.91	55	>1
MB1	Summer	95.87 ± 1.82	120	>1	0.83 ± 0.83	60	<0.11	0.00 ± 0.00	30*	<0.11*
MB2		99.17 ± 0.83	40	>1	0.83 ± 0.83	10	<0.11	2.48 ± 1.42	15	<0.11
MB3		18.18 ± 3.52	15	>0.11	66.12 ± 4.32	55	>1	0.00 ± 0.00	0	0.0

cover was demonstrated from 2012 to both 2013 and 2014, whilst at *MB2* a significant decrease was demonstrated in year 1 but a subsequent increase in year 2, and at *MB3* a significant increase was observed in year 1 followed by an opposing decrease in year 2 (KW $\chi^2 \geq 7.97$, df = 1, p-value <0.01; Figure 4.2 a).

4.4.3. Reef Height

Significant differences in average reef height between years were demonstrated within all transects, however the magnitude and direction of annual change in average reef height was also not consistent between sites (Figure 4.2 e). For example, at *Llan* significant increases in summer height were demonstrated from both 2012 and 2013 to 2014, whilst at *MB3* an increase was demonstrated in year 1, followed by a decrease in year 2 to levels significantly less than in 2012. At *MB1* and *MB2* decreases in height were demonstrated from 2012 to both 2013 and 2014, however at *MB1* continual decreases in cover were demonstrated in both years, whilst at *MB2*, an increase was demonstrated in year 2 (KW $\chi^2 \geq 7.69$, df = 1, p- value

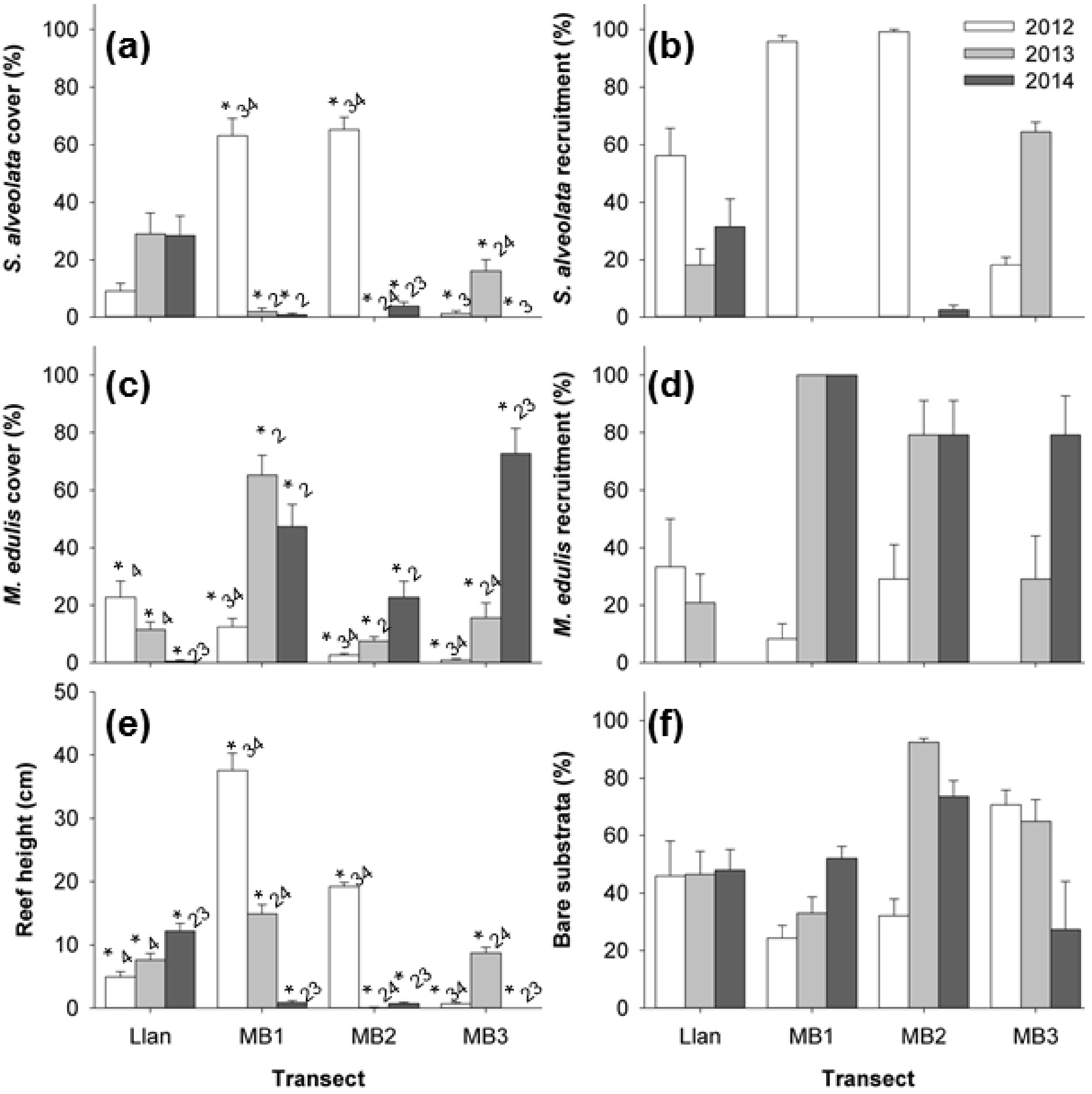


Figure 4.2: Site-specific summer morphology and abundance of *Sabellaria alveolata* reefs and associated *Mytilus edulis* at *Llan*, *MB1*, *MB2* and *MB3*, from 2012 to 2014. (a) Percentage of quadrats occupied by *S. alveolata* (n = 24). Significant differences between years were assessed with KW tests (df = 1, p-value < 0.05), and are demarked with an asterisk (i.e. significantly different to 2012 as $*_2$, to 2013 as $*_3$, and to 2014 as $*_4$). (b) Percentage of the site where *S. alveolata* recruitment was observed (n = 121). (c) Percentage of quadrats occupied by *M. edulis* (n = 24). Significant differences were assessed and denoted as a. (d) Percentage of quadrats where *M. edulis* recruitment was observed (n = 24). (e) Average height of *S. alveolata* reef (n = 121). Significant differences were assessed and denoted (as a). (f) Percentage of quadrats composed of bare substrata (n = 24).

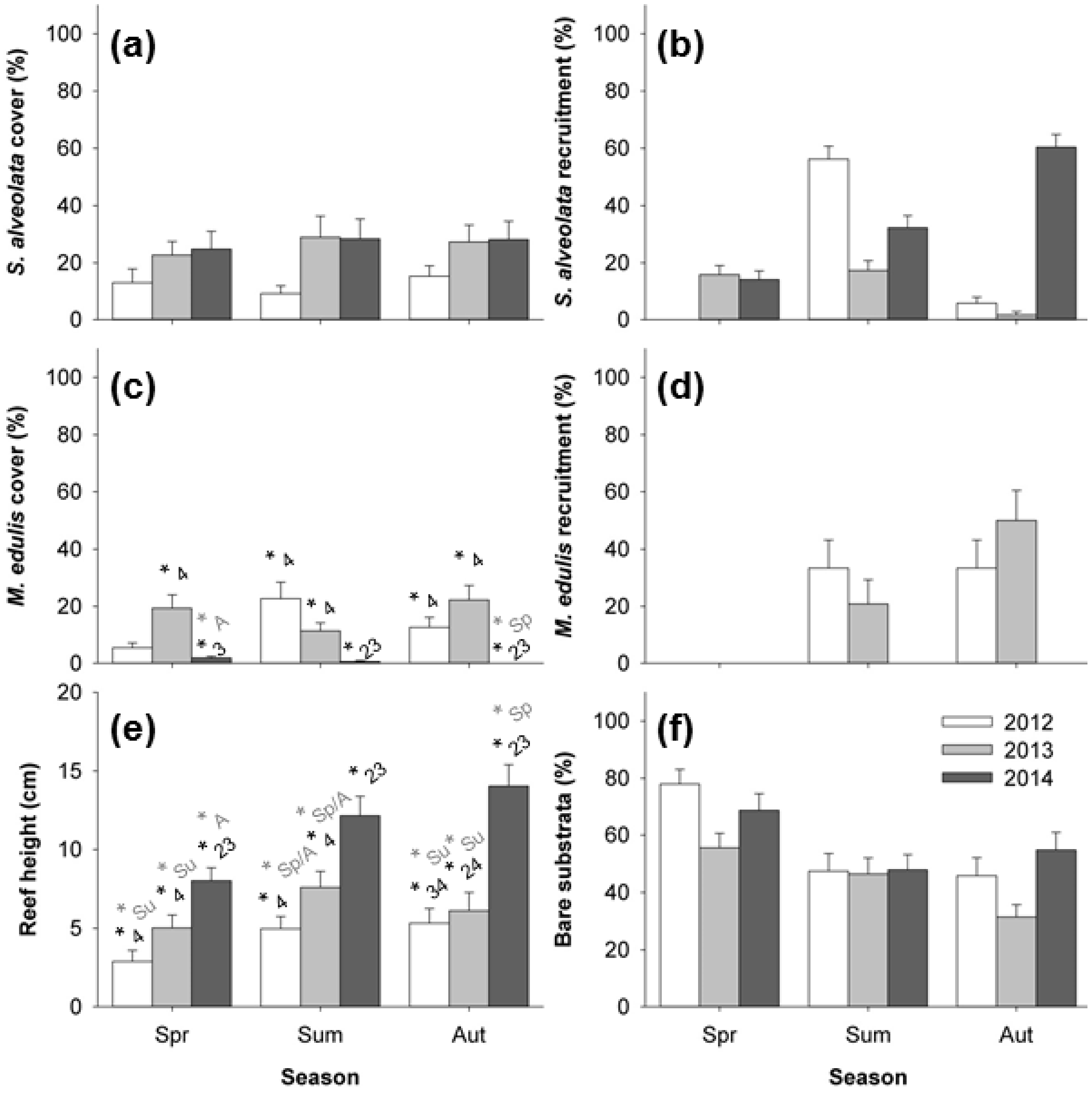


Figure 4.3: Site-specific seasonal morphology and abundance of *Sabellaria alveolata* reefs and associated *Mytilus edulis* at *Llan* from 2012 to 2014*.* (a) Percentage of quadrats occupied by *S. alveolata* (n = 24). No significant differences between years or seasons were demonstrated with KW. (b) Percentage of the site where *S. alveolata* recruitment was observed (n = 121). (c) Percentage of quadrats occupied by *M. edulis* (n = 24). Significant differences (df = 1, p-value < 0.05) were assessed with KW tests, and are demarked with an asterisk, black between years (i.e. significantly different to 2012 as *$_2$, to 2013 as *$_3$, and to 2014 as *$_4$), grey between seasons (i.e. significant different to spring as *$_{Sp}$, to summer as *$_{Su}$, and to autumn as *$_A$). (d) Percentage of quadrats where *M. edulis* recruitment was observed (n = 24). (e) Average height of *S. alveolata* reef (n = 121). Significant differences were assessed and denoted (as c). (f) Percentage of quadrats composed of bare substrata (n = 24).

<0.01; Figure 4.2 e). At *Llan*, significant differences in height were also observed between seasons in all years. For example, in both 2012 and 2013, height was significantly less in spring than summer, and in 2014, in spring than autumn). However, seasonal changes in height were not consistent between years. For example, height in summer was significantly less than in autumn in 2012, but significantly greater in 2013 (KW $\chi 2 \geq 4.25$, df = 1, p-value ≤0.03; Figure 4.3 e).

4.4.4. ***Sabellaria alveolata*** **condition**

Several stages of development were observed in persistent reef populations. For example, at *Llan* a mosaic of actively growing and stagnating reef was observed in all sampling seasons (Figure 4.4 a). Whilst actively growing reef was the dominant developmental phase, stagnating reef was initially locally restricted to the lower reef, only reported throughout the site as the reef aged (e.g. in the summer and autumn of 2014). Similarly, both actively growing and stagnating reef were observed at *MB1* in 2012, although stagnating reef dominated. In subsequent years reef destruction was reported at *MB1*, and reef remains dominated (Figure 4.4 b). In contrast, in transient populations (i.e. *MB2* and *MB3*), when present, reefs were dominated by active growth (Figure 4.4 a, d). Bare substrata was present throughout all transects, the percentage of which remained relatively constant at *Llan* between years (Figure 4.2 f), with decreases from spring to autumn suggested in all years (Figure 4.3 f). In contrast, the percentage of bare substrata increased at *MB1* and *MB2* (particularly in year 1 at *MB2*), and decreased at *MB3* (Figure 4.2 f).

Settlement also demonstrated spatial and temporal differences. At *Llan*, semi-continuous recruitment was observed with settlement reported in all years of observation (Figure 4.2 b), in almost all sampling seasons (with the exception of spring 2012; Figure 4.3 b) but annual variability was observed in the density and location of this settlement (Figure 4.2 b). For example, in 2012 some settlement was observed throughout *Llan* particularly in the summer, in 2013 low density settlement was observed in the reef interior, whilst in 2014 settlement was confined to the lower margins of the reef in spring and summer but was again observed throughout the reef in autumn (Figure 4.2 b; 3 b). Within Morecambe Bay, settlement demonstrated

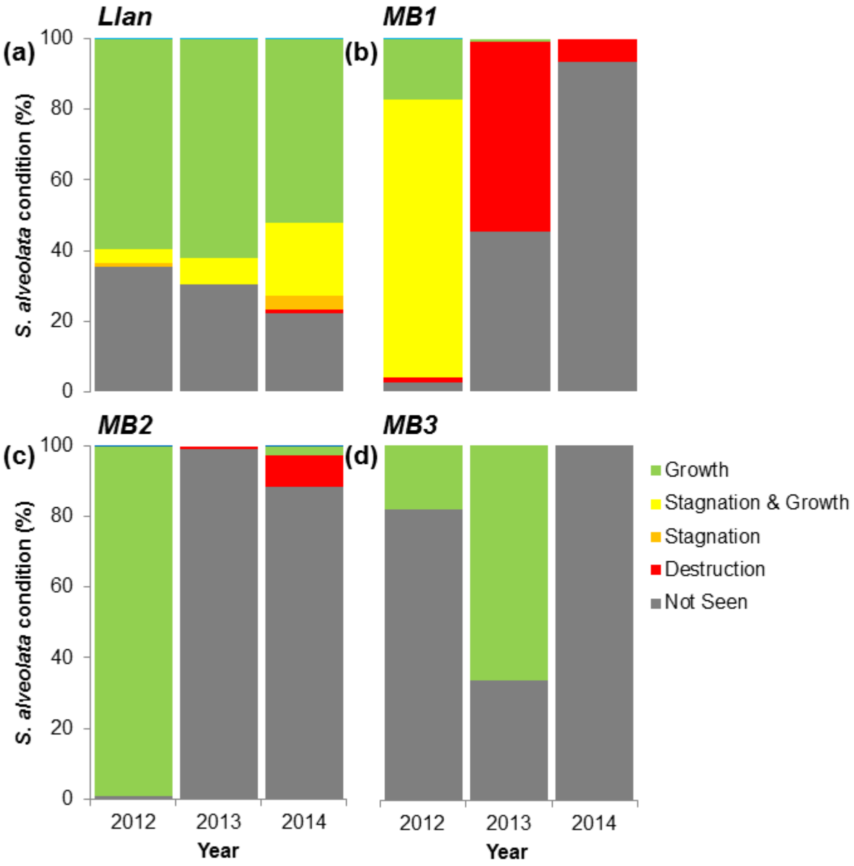


Figure 4.4: Proportion of transect featuring each developmental phase of *Sabellaria alveolata*, in addition to absence, in summer of 2012, 2013 and 2014. Developmental phases are colour coded. (a) *Llan*. (b) *MB1*. (c) *MB2*. (d) *MB3*.

a boom-bust pattern. Summer settlement was observed at all sites in 2012, in high density across the entirety of *MB1* and *MB2*, and low density at *MB3* (Figure 4.2 b). However, in 2013 settlement was only observed at *MB3* at high density throughout the majority of the reef (Figure 4.2 b), and in 2014 settlement was only observed at *MB2*, spatially restricted and in low density (Figure 4.2 b). Within Morecambe Bay, dense settlement was only observed on *MB2* and *MB1* in 2012, and *MB3* in 2013, but in all years recruits were observed in high densities out with the transects. For example, in 2014 recruits were observed in high densities to the north on Foot Scar.

4.4.5. Percentage cover of *Mytilus edulis*

As with *S. alveolata*, the magnitude and direction of change in *M. edulis* cover through time was not consistent between sites. For example, from 2012 to 2014, a significant decrease was demonstrated at *Llan* in contrast to a significant increase at all transects in Morecambe Bay (KW $\chi^2 \geq 8.14$, df = 1, p-value <0.01; Figure 4.2 c). Differences were also demonstrated within Morecambe Bay with a significant increase demonstrated at all sites in year 1, but at *MB3* only in year 2 (KW $\chi^2 \geq 8.80$, df = 1, p-value <0.01; Figure 4.2 c). When considered seasonally, no change in overall cover at *Llan* was demonstrated between seasons in either 2012 or 2013 (KW $\chi^2 \leq 2.42$, df = 1, p-value >0.05), but a significant decrease in cover were demonstrated from spring to autumn in 2014 (KW $\chi^2 = 9.37$, df = 1, p-value <0.01; Figure 4.3 c).

Differences were also observed in settlement of *M. edulis* within years at Llan, and between transects between years. At *Llan*, no *M. edulis* settlement was observed in the spring of any year, additionally, whilst juveniles were observed in both summer and autumn of 2012 and 2013, no settlement was observed in 2014 (Figure 4.3 d). Within Morecambe Bay, settlement had occurred by summer of all years. However, despite dense homogeneous settlement across Foot Scar inshore of the *S. alveolata* reefs, settlement on the reefs themselves was temporally and spatially variable, increasing from 2012 to 2014 at all sites (Figure 4.2 d).

4.4.6. *Sabellaria alveolata*: *Mytilus edulis* dynamic

When all sites were considered, a weak negative relationship was suggested between annual change in *M. edulis* percentage cover and annual change in *S. alveolata* percentage cover (Figure 4.5 a). This relationship was not consistent at all sites, with a negative relationship only suggested at *MB1* (Figure 4.5 c) and *MB3* (Figure 4.5 e) where a shift in state from *S. alveolata* dominated to *M. edulis* dominated reef was demonstrated (Figure 4.2 a, c). No clear relationship was observed at *MB2* (Figure 4.5 d) where *S. alveolata* initially dominated but was physically removed exposing a substrate of muddy sand with little available hard

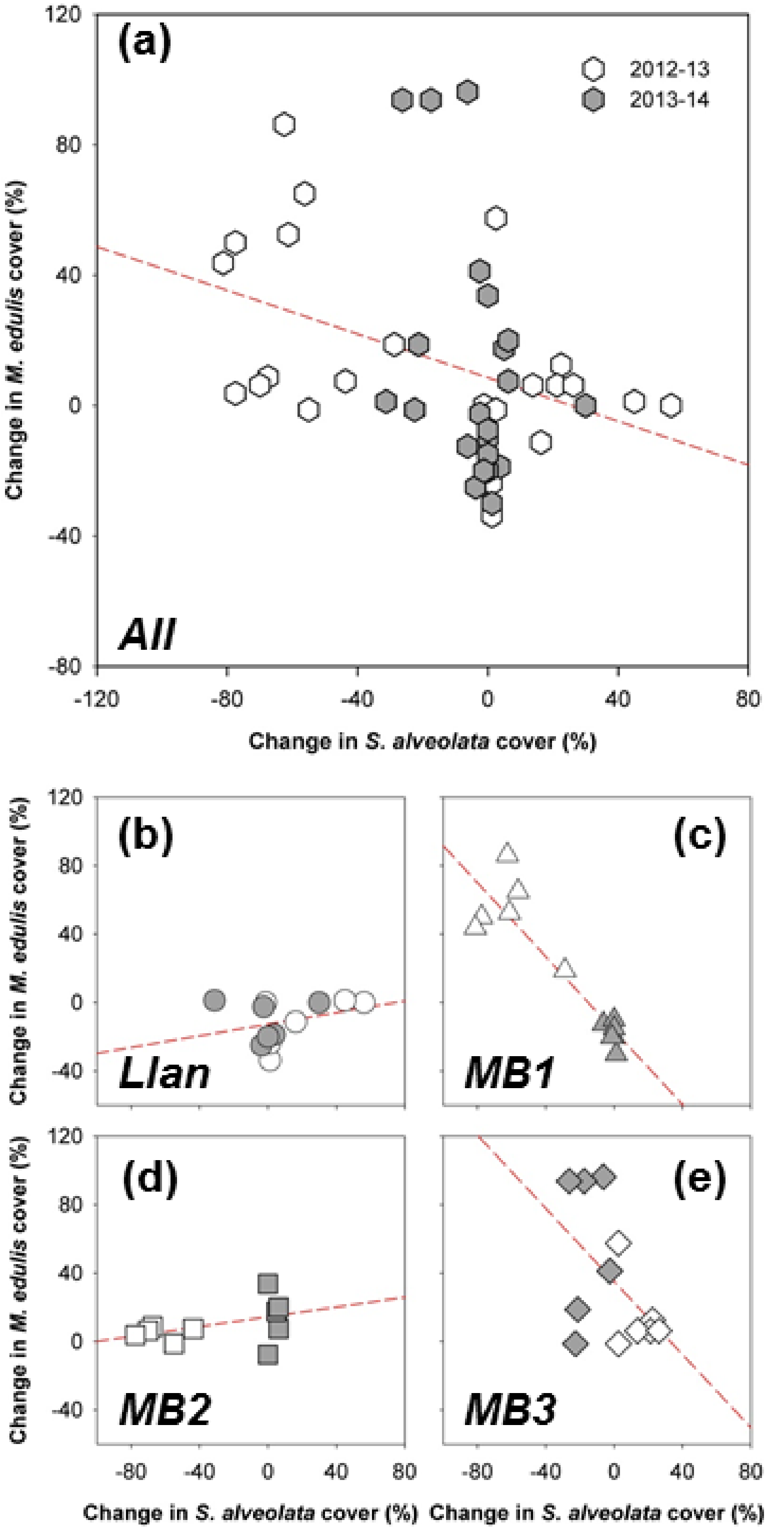


Figure 4.5: Changes in *Sabellaria alveolata* and *Mytilus edulis* percentage cover. Years are colour coded. Regression lines are displayed (- - -). (a) All transects combined (R^2 = 0.12). (b) *Llan* (R^2 = 0.10). (c) *MB1* (R^2 = 0.83). (d) *MB2* (R^2 = 0.23). (e) *MB3* (R^2 = 0.26). Refer to Appendix 4.1 for regression parameters.

substrate for secondary settlement. Additionally, no clear relationship was observed at *Llan* (Figure 4.5 b) where both *S. alveolata* and *M. edulis* were reported as Abundant in the summer of all years (with the exception of *M. edulis* in 2014), and the percentage cover of bare substrata also remained relatively constant through time (Figure 4.2 f).

4.4.7. *Mytilus edulis* cover: settlement success

When all sites were considered, a positive relationship was suggested between annual change in *M. edulis* percentage cover and recruitment success (Figure 4.6 a). A positive relationship was observed at all sites (Figure 4.6 b-e), although little change in *M. edulis* cover was observed at *MB2* in the period of observation (Figure 4.6 d). At *Llan*, the proportion of quadrats containing juvenile *M. edulis* decreased through time, as did the percentage cover of *M. edulis*. In contrast within Morecambe Bay, the proportion of quadrats containing juvenile *M. edulis* increased through time, as did the percentage cover of *M. edulis*.

4.4.8. *Sabellaria alveolata* cover: settlement success

As for *M. edulis*, a positive relationship was suggested between annual change in *S. alveolata* percentage cover and recruitment success, when all sites were considered (Figure 4.7 a). This was observed at all sites within Morecambe Bay (Figure 4.7 c-e), but not at *Llan* (Figure 4.7 b). At *Llan*, little change in *S. alveolata* cover was observed through time, with some settlement observed in each summer sampling period. In contrast, within Morecambe Bay, large changes in *S. alveolata* percentage cover and settlement were observed at all sites.

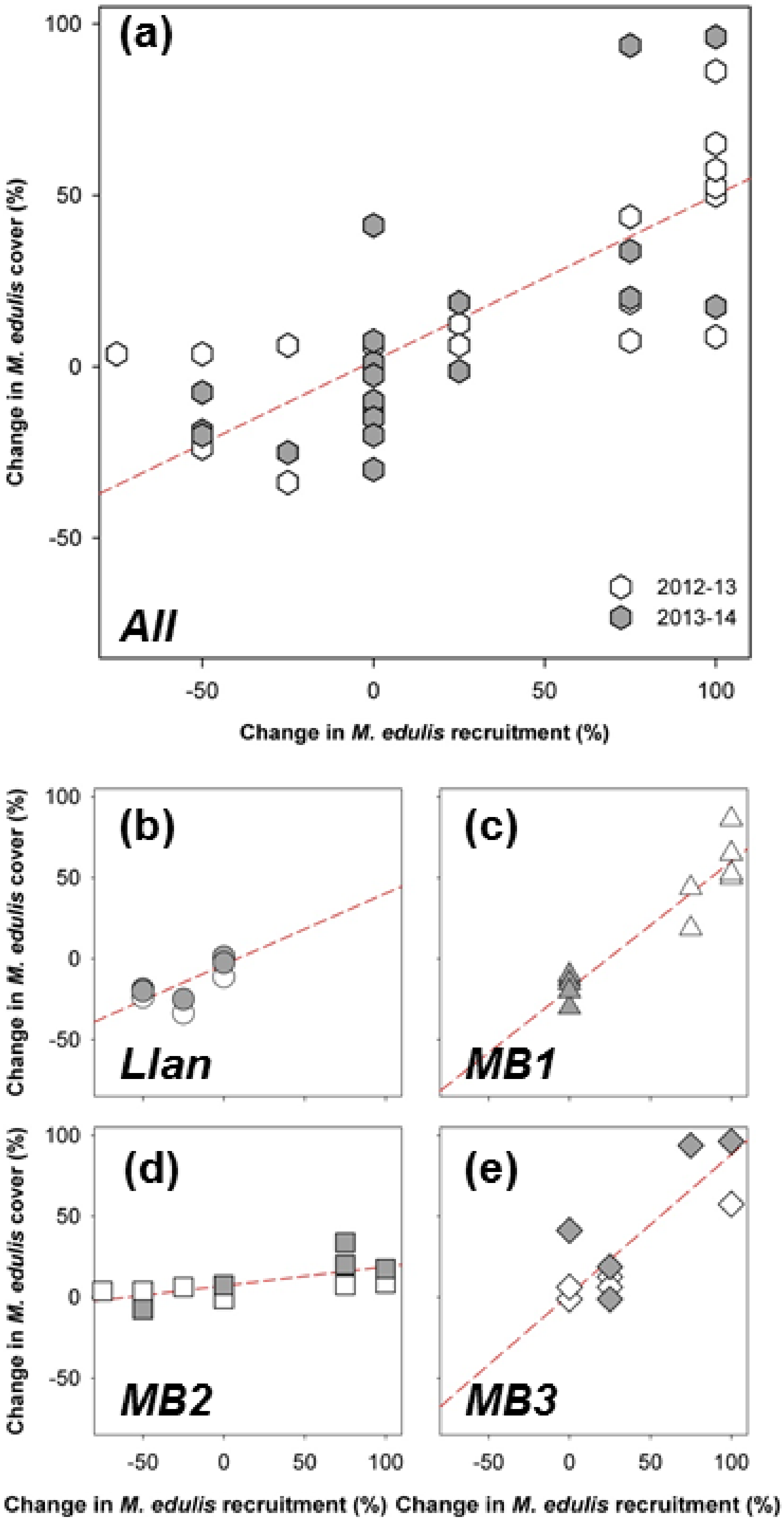


Figure 4.6: Changes in adult *Mytilus edulis* percentage cover related to recruitment success. Years are colour coded. Regression lines are displayed (- - -). (a) All transects combined (R^2. = 0.55). (b) *Llan* (R^2 = 0.60). (c) *MB1* (R^2 = 0.91), (d) *MB2* (R^2 = 0.48), (e) *MB3* (R^2 = 0.68). Refer to Appendix4.2 for regression parameters.

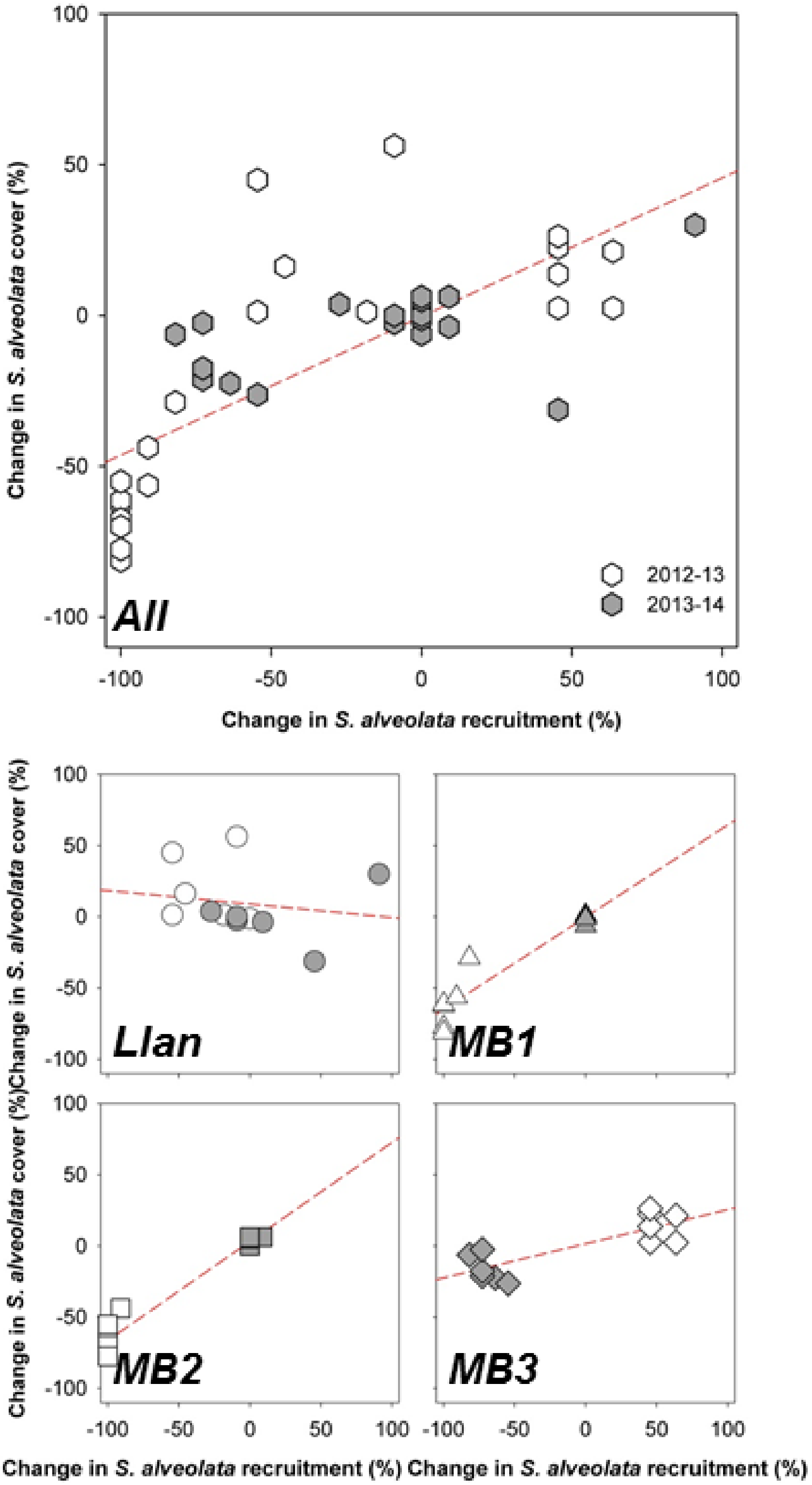


Figure 4.7: Changes in adult *Sabellaria alveolata* percentage cover related to recruitment success. Years are colour coded. Regression lines are displayed (- - -) . (a) All transects combined (R^2 = 0.57). (b) *Llan* (R^2 = 0.03) . (c) *MB1* (R^2 = 0.91), (d) *MB2* (R^2 = 0.95), (e) *MB3* (R^2 = 0.67). Refer to Appendix 4.3 for regression parameters.

4.5. Discussion

Intertidal ecosystem engineers of pebble shores demonstrated substantial short-term variability on small spatial and temporal scales. Persistent *S. alveolata* reef-forming populations demonstrated high morphological variability, with many stages of development present at any time point (e.g. active growth and stagnating reef), whilst a lack of developmental diversity was observed in transient populations. For example, just actively growing reef was observed in newly established potentially short-lived, reef-forming populations, and stagnating reef in degrading populations. It is suggested that reefs persist through time as a result of reoccurring settlement. On British coastlines, short-term small-scale changes in *S. alveolata* percentage cover on pebble shores were negatively related to those of *M. edulis*. Within Morecambe Bay, a succession was observed from the original *S. alveolata* dominated community to a *M. edulis* dominated community, with *S. alveolata* and *M. edulis* functioning as alternative community states. Succession in *M. edulis* dominated reef was also largely driven by settlement success, with complete state switch observed within a year at some sites, however sites exhibited variable periods of succession, with state change from *S. alveolata* to *M. edulis* dominated reef potentially interrupted by overly strong environmental conditions.

4.5.1. Stability and variability in *Sabellaria alveolata* reef

High spatial variability in cover, abundance, and morphology was observed within biogenic reef-forming populations at any point in time. For example, on a scale of tens of metres, within a single transect, reef height varied from 0 – 120 cm, and percentage cover of *S. alveolata* and *M. edulis* varied from 0 – 100 %. Additionally, high temporal variability was observed with local colonisation and extirpation of *S. alveolata* reef observed within consecutive years (i.e. at *MB3*). Large natural variability in *S. alveolata* populations is well documented (Wilson, 1971; 1976; Cunningham et al., 1984; Gruet, 1986; Allen et al., 2002; Frost et al., 2004), and a natural cycle of development from settlement stage to stagnation and potential destruction is recognised (Gruet, 1986). It is suggested that the natural cycle of reef development can occur in spatially distinct populations, offset in time, within a single reef system, initiated by patchy settlement, and representative of the age and health of the population. In support of this, recurrent settlement and developmental diversity were observed within persistent reef, whilst in the absence of secondary settlement, a lack of developmental diversity, and ultimately reef destruction occurred.

Stable persistent reef was observed at *Llan* in all sampling seasons. This population was first reported in 2008, and subsequently, reef-forming populations have consistently been reported (Firth et al., 2015; Bush, pers. obs.). It is suggested that this reef was not fully developed in 2012 as an increase in the proportion of stagnation phase reef (i.e. individuals ≥ 3 years old; Gruet, 1986) was observed during the sampling period, in conjunction with increases in overall reef height. Recurrent successful secondary settlement was observed at *Llan* in all seasons throughout the sampling period (with the exception of spring 2012). By 2014, *Llan* was covered in a relatively homogeneous sheet of *S. alveolata*, with stagnation phase reef intermixed with actively growing reef. Gruet (1986) reported that following completion of such a platform, or 2-3 years post settlement, the growth phase ends and the stagnation phase begins. However, successful secondary settlement was again observed by autumn 2014. Consequently, it is likely the reef at *Llan* will persist for at least another 3 years.

In contrast to the persistence of *S. alveolata* reef at *Llan*, reef-forming populations within Morecambe Bay were more transient in time and space. Despite the relatively close proximity of these transects, the magnitude and direction of change in average *S. alveolata* cover or reef height was not consistent through time, although a decrease from reef-forming populations to absent was observed during the sampling period within all transects. The existence of reef-forming populations within Morecambe Bay coincided with dense secondary settlement events, but in the absence of reoccurring settlement, extirpation occurred. Although not monitored individually through time, reef-forming populations were present upon both Foot Scar and Knot End, outside the sites of interest, in all years of observation, and secondary settlement was observed in all sampling seasons. This highlights the spatial variability of this habitat on a small scale (i.e. tens of metres), but also the overall stability of this habitat on a larger scale. Such stability was also reported by Bush et al., (Chapter 2) with little change in abundance observed at the majority of sites within the British Isles on decadal timescales.

4.5.2. ***Sabellaria alveolata*: *Mytilus edulis* dynamic**

The coexistence of the ecosystem engineers *S. alveolata* and *M. edulis* is well documented, particularly in stagnating reefs (Cunningham et al., 1984; Perkins, 1988; Holt et al., 1998; Woombs, 1999; Allen et al., 2002; Desroy et al., 2011), with both present within Llanddulas and Morecambe Bay in all years of study, and *M. edulis* often observed episammic on *S. alveolata* reefs. Similarly to *S. alveolata*, significant differences in overall *M. edulis* cover were observed at all sites through time. Within Morecambe Bay, increases in *M. edulis* cover occurred at all sites during the sampling period, associated with decreases in overall *S. alveolata* cover and reef height, whilst at Llanddulas, decreases in *M. edulis* were observed in association with an increase in reef height. *Mytilus edulis* populations within Morecambe Bay are ephemeral and annually removed on large spatial scales, either anthropogenically or naturally by weather (Egerton, 2014). Consequently, populations in all years were predominantly composed of seed mussels, with adult *M. edulis* in the minority. In contrast, at Llanddulas, adult *M. edulis* were observed in all sampling seasons, and little change in *M. edulis* cover was observed in 2012 and 2013. However following the exceptionally windy winter of 2013-2014 (Matthews et al., 2014), *M. edulis* were almost completely removed from the system, with local extirpation by the end of the sampling period, coupled with an increase in *S. alveolata* reef height.

Persistence of *S. alveolata* is partly determined by settlement success, with a positive relationship demonstrated between annual change in cover and recruitment success overall. Within Morecambe Bay, *S. alveolata* populations demonstrated a boom-bust cycle of existence with the presence of reef-forming populations associated with successful settlement, and subsequent decreases in cover associated with failed recruitment. In contrast, no relationship was observed for *S. alveolata* at Llanddulas where little change in *S. alveolata* cover was observed through time, in conjunction with continuous recurrent secondary settlement. Annual and seasonal variability in *S.*

alveolata recruitment has been widely reported (Wilson, 1971, 1976; Gruet, 1986; Dubois et al., 2006). Wilson (1971; 1976) only reported dense settlement twice, in 12 years of observation at Duckpool, UK (in autumn to winter). Similarly, *S. alveolata* recruitment demonstrated variability in time and space within the central Irish Sea in the present study. Whilst some recruitment was observed at Llanddulas in the majority of sampling seasons, dense settlement was only observed in two of nine sampling seasons (in summer and autumn), and in Morecambe Bay, dense settlement was only observed once at each site.

Succession by *M. edulis* is also partly determined by settlement success. Similarly to *S. alveolata*, a positive relationship was demonstrated between annual change in *M. edulis* cover and recruitment success overall. At Llanddulas successful *M. edulis* recruitment (i.e. high abundance of juveniles on the reef in summer and autumn of 2012 to 2013) initially maintained populations at high abundance, however failed recruitment in 2014 (i.e. no juveniles observed on the reef), following an exceptionally stormy winter, and the physical removal of the majority of the established *M. edulis* population, resulted in local extirpation. Within Morecambe Bay, increased *M. edulis* recruitment success throughout the sampling period was associated with an increase in *M. edulis* cover at most sites, with the exception of *MB2* where *M. edulis* recruitment and cover remained low in all sampling periods. *Mytilus edulis* populations within Morecambe Bay are generally of high abundance. However, Egerton (2014) noted that *M. edulis* recruitment failed within Morecambe Bay in 2011, and although dense *M. edulis* recruitment was observed in 2012, it was localised and predominantly out with the *S. alveolata* beds. Consequently, it is likely that *M. edulis* populations were suppressed within Morecambe Bay in 2011, and that they remained suppressed in *S. alveolata* reefs in 2012, at the initiation of this study.

A negative relationship was demonstrated between *M. edulis* and *S. alveolata* cover, with *S. alveolata* populations decreasing in Morecambe Bay in association with increases in *M. edulis*. Conversely, at Llanddulas, *S. alveolata* populations increased following decreases in *M. edulis.* It is theorised that in 2011, when *M. edulis* populations were reportedly suppressed within Morecambe Bay (Egerton, 2014), *S.*

alveolata populations thrived. At the initiation of this study, it is likely that the *S. alveolata* population observed within Morecambe Bay was elevated. However, as the settlement success of *M. edulis* increased, that of *S. alveolata* decreased. Cunningham et al., (1984) suggested a *Sabellaria: Mytilus* succession and this was observed within this study. The complete switch from a *S. alveolata* to a *M. edulis* dominated ecosystem at both *MB1* and *MB3* is strong evidence that these are alternative stable states. The increase in *S. alveolata* in conjunction with a decrease in *M. edulis* at *Llan* supports this. The variable responses to successful settlement are likely the result of changing environmental conditions (e.g. increased unsuitable substrata, increased wave action), with physical disturbance capable of disrupting this natural progression. For example, following complete removal of *S. alveolata* reefs and all associated episammic organisms at *MB2*, the remaining substrata was predominantly mud and fine sand, with limited availability of hard substrata for settlement by either ecosystem engineer. At this site, exposed substrata remained largely uncolonised by ecosystem engineers throughout the remainder of the sampling period. In contrast, physical removal of *M. edulis* at *Llan* during the extremely stormy winter of 2013-2014 and a resultant release from competition, coincided with a subsequent increase in reef height.

Whilst physical disturbance can be detrimental to both ecosystem engineers, dependent on the magnitude and type of this physical disturbance, and the success of subsequent *S. alveolata* and *M. edulis* settlement, one species may achieve dominance. Within Morecambe Bay, *M. edulis* seed beds are harvested annually by hand, and the majority of remaining *M. edulis* are naturally scoured by autumn and winter storms leaving bare mud and rock scar (Egerton, 2014). *Sabellaria alveolata* settlement has been reported in winter months within the British Isles (Wilson, 1971, 1976). Consequently, annual removal of *M. edulis* in late summer will provide bare substrata for *S. alveolata* settlement, potentially facilitating annual escapes from *M. edulis* competition, and maintaining the highly abundant and persistent *S. alveolata* population on Foot Scar. In contrast to populations within Morecambe Bay, Llanddulas is located on a region of sloping coast where wave energy on shore, and thus wave exposure are inherently greater (Burrows et al., 2008). During the period of observation, complete dominance by *M. edulis* was not observed at *Llan*. Succession to a *M. edulis* dominated ecosystem may constantly be hindered by physical environment at this site.

It has been suggested that *S. alveolata* reefs stabilise the substrata, with stagnating *S. alveolata* reefs forming a suitable substratum for *M. edulis* recruitment (Cunningham et al., 1984). Through gregarious settlement and rapid growth, *S. alveolata* can generate a large area of hard substrata (e.g. binding loose pebbles into a cohesive reef), potentially suitable for settlement by *S. alveolata* and *M. edulis* larvae. Additionally, it is theorised that *M. edulis* implement negative feedback to establish and maintain an alternative community state. Episammic *M. edulis* have been observed to break up the surface structure of *S. alveolata* reefs as they grow. Dense aggregations compete physically for space, and by altering the environment (e.g. reducing water flow and increasing the proportion of fine sediments) they potentially render it unsuitable for adult *S. alveolata* inhabitation (Ragnarsson & Raffaelli, 1999; Dubois et al., 2009; Desroy et al., 2011, Egerton, 2014). Additionally, *M. edulis* may predate on *S. alveolata* larvae inhibiting secondary settlement (Cowden et al., 1984; Lehane & Davenport, 2004). Whilst in growth phase *S. alveolata* are reported to be a dominant competitor for space, but unless secondary settlement occurs, less competitive stagnation phase reef will develop as the original polychaetes age (Gruet, 1986). Previous studies have suggested that stagnation phase reef is particularly susceptible to competition for space (e.g. Cunningham et al., 1984). However, dense *M. edulis* recruitment onto *S. alveolata* reefs in both active growth and stagnation phase was observed in this study, with complete shift to the alternative *M. edulis* dominated state within a year.

Rapid phase shifts are facilitated by lifecycle strategy with both *S. alveolata* and *M. edulis* demonstrating r-selected traits (e.g. high fecundity, semi-continuous larval supply, rapid population growth). Whilst *S. alveolata* predominantly spawn bimodally in spring - summer and autumn (Wilson, 1971; Gruet & Lassus, 1983; Dubois et al., 2007; Bush et al., 2015), trickle spawning has been observed throughout the year (Dubois et al., 2007; Bush et al., 2015). *Sabellaria alveolata* larvae can develop to settlement stage within one month in optimal conditions (Dubois et al., 2007; Newstead & Davies, unpub.; Bush et al., 2015) but metamorphosis to settlement stage can be delayed by a further up to 7.5 months dependent on environmental conditions and availability of suitable substrata (Cazaux, 1970; Wilson, 1968a; 1986b; Dubois et al., 2007). Similarly *M. edulis* also displays bimodal spawning in spring and summer (Seed, 1969). Under optimal conditions larvae can develop to settlement stage within 20 days (although 1 month is typical in natural conditions) and can delay metamorphosis for up to 6 months (Bayne, 1965; Bayne, 1976; Beaumont & Budd, 1982; Lane et al., 1985). When settlement circumstances are ‘suitable’, *M. edulis* can development to settlement stage before *S. alveolata.* In years with failed *M. edulis* success, but successful *S. alveolata*, the latter will expand, however in years of successful *M. edulis* settlement, *S. alveolata* may only settle on substrata free from *M. edulis.*

4.5.3. Future Considerations

Mytilus edulis is a cold-temperate species native to North Atlantic coastlines (Fly & Hilbish, 2013), historically extending from the English Channel to Norway and Iceland within the north-eastern Atlantic (Jansen et al., 2007), whilst *S. alveolata* is a Lusitanian species, extending from Morocco to the south of Scotland. Whilst range overlap is substantial, larvae and adults are likely to have contrasting favourable conditions. *Mytilus edulis* range retractions poleward have been observed within the Atlantic (Jones et al., 2009; 2010), whilst increases in abundance of *S. alveolata* have been observed in the north of its range within the Irish Sea (Firth et al., 2015). Consequently, the impact of climate change must be considered further. Competition with other episammic organisms should also be considered, but whilst other species were observed attached to the reef (e.g. *Actinia equina*, *Sagartia elegans*, *Nucella lapillus*, *Lanice conchilega*, *Gibbula umbilicalis*, *Littorina littorea, Ulva lactuca* and *Fucus serratus*), these were present in low density. Both *Fucus* spp. and *Ulva* spp. have been reported on *S. alveolata* reefs elsewhere (Cunningham et al., 1984; Allen et al., 2002; Dubois et al., 2006; Bush, pers. obs.), with the sweeping of *Ulva* spp. fronds implicated in reduced *S. alveolata* settlement success (Dubois et al., 2006).

4.6. Conclusions

Reef-forming *S. alveolata* populations are highly morphologically variable when considered on small spatial scales, with variability in both cover and reef height observed at all sites. Whilst some reef-forming populations exhibited annual persistence and stability, others were more transient in nature with large changes in *S. alveolata* cover and reef height observed through time. Secondary settlement was observed on all reef-forming populations, with decreases to encrusting populations, reef remains or complete extirpation associated with failed recruitment. Both *S. alveolata* settlement and physical disturbance are unpredictable in time and space, and within a well-developed *S. alveolata* reef, many growth phases can be observed suggesting the cycle of reef development is occurring at small spatial scales within a persistent reef offset in time.

A negative relationship exists between *S. alveolata* and *M. edulis* cover, with a natural progression from unstable pebble scar, to *S. alveolata* dominated, to *M. edulis* dominated ecosystems observed at the north of the *S. alveolata* range. This can occur within two years, under optimal conditions, with changes in *M. edulis* cover positively related to recruitment success. It is suggested that negative feedback by *S. alveolata* stabilises the substrata, facilitating *M. edulis* settlement whilst positive feedback by *M. edulis* maintains the alternative assemblage with the build-up of fine mud and pseudofaeces associated with dense aggregations detrimental to *S. alveolata* populations (Dubois et al., 2009). Additionally, it is theorised that physical disturbance (e.g. increases in wave exposure, *M. edulis* harvesting etc.) can disrupt natural succession allowing continual recolonisation of *S. alveolata.* Consequently, at exposed sites, *S. alveolata* may have a competitive advantage, as it actively stabilises the substrata, whilst *M. edulis* aggregations are physically removed by wave action. The impact of climate change on the *S. alveolata: M. edulis* dynamic should be considered further as *M. edulis* has demonstrated range retractions, whilst *S. alveolata* has demonstrated increases in abundance in the north of its range in association with warming temperatures.

4.7. Acknowledgements:

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4.8. Appendices

Appendix 4.1: Annual change in *Mytilus edulis* cover related to annual change in *Sabellaria alveolata* cover from 2012 to 2014. Parameters of the regression line. Highlighted in red if negative relationship suggested ($R^2 > 0.5$).

Regression	**Linear relationship**	**All**	**Llan**	**MBO**	**MBN**	**MBC**
2012-2013	**R^2**	0.20	0.39	0.17	0.00	0.19
	Gradient	-0.29	0.37	-0.49	0.01	-0.91
2013-2014	**R^2**	0.12	0.00	0.24	0.01	0.02
	Gradient	-1.01	-0.03	-1.30	0.48	0.70
2012-2014	**R^2**	0.12	0.10	0.83	0.23	0.26
	Gradient	-0.34	0.17	-1.08	0.14	-1.07

Appendix 4.2: Annual change in *Mytilus edulis* cover related to change in recruitment success from 2012 to 2013. Parameters of the regression line. Highlighted in red if negative relationship, and in blue if positive relationship suggested ($R^2 > 0.5$).

Time	**Linear relationship**	**All**	**Llan**	**MB1**	**MB2**	**MB3**
2012-2013	**R^2**	0.61	0.60	0.55	0.31	0.94
	Gradient	0.41	0.54	1.29	0.03	0.57
2013-2014	**R^2**	0.55	0.71	NA	0.74	0.70
	Gradient	0.60	0.40	NA	0.21	0.93
2012-2014	**R^2**	0.55	0.60	0.91	0.48	0.68
	Gradient	0.48	0.44	0.79	0.12	0.87

Appendix 4.3: Annual change in *Sabellaria alveolata* cover related to change in recruitment success from 2012 to 2013. Parameters of the regression line. Highlighted in red if negative relationship, and in blue if positive relationship suggested ($R^2 > 0.5$).

Time	**Linear relationship**	**All**	**Llan**	**MB1**	**MB2**	**MB3**
2012-2013	**R^2**	0.62	0.00	0.80	0.62	0.05
	Gradient	0.55	-0.09	2.2	2.83	-0.24
2013-2014	**R^2**	0.31	0.09	NA	0.13	0.56
	Gradient	0.18	0.13	NA	0.30	-0.76
2012-2014	**R^2**	0.56	0.03	0.91	0.95	0.67
	Gradient	0.46	-0.09	0.65	0.70	0.24

4.9. References

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5. Linking larval dispersal to adult persistence in the ecosystem engineer *Sabellaria alveolata*

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Declaration

I declare that this manuscript is entirely my own work, with the exception of the biophysical modelling which was conducted by P.E.R.. I researched *S. alveolata* ecology, and subsequently defined the model parameters. I also interpreted model outcomes (with supervision from P.E.R. and A.J.D.). It is acknowledged that S.J.B. conducted the larval behaviour studies, with L.E.B input. Additionally, S.J.B., S.N., E. S., and E.S.L. amongst others provided laboratory and fieldwork assistance. Supervision was provided throughout by A.J.D.

The work in this Chapter has not been previously submitted or presented, either in part or whole, for a degree at this or any other University or institution.

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5.1. Abstract

Through a combination of traditional monitoring and laboratory techniques with state of the art modelling approaches, insights are provided into *Sabellaria alveolata* population connectivity patterns, within the British Isles. The model species is highly persistent on a long-term broad-spatial scale, however little is known with regards spawning patterns, larval behaviour, and population connectivity. A negative phototactic response in latter stage *S. alveolata* larvae was observed *in vivo* (ANOVA, df = 2, SS ≥ 363.46, F ≥ 4.49, P ≤ 0.02), in addition to a semi-continuous poorly seasonally synchronised spawning pattern with peak summer spawning *in situ* (e.g. early stage larvae present in all sampled months at Aber, but increased by three orders of magnitude in Jul-Aug; Kruskal Wallis, H ≥ 11.20, df ≥ 3, P ≤ 0.05). Combining ecological data with larval dispersal modelling, this study provided evidence of the existence of sub-populations of intertidal species of sheltered to moderately exposed shores within the British Isles, with larval connectivity within, but not between, subpopulations. Larval dispersal distance was site-dependent, with some sites acting as source sites to many other reefs (e.g. Criccieth), some demonstrating high self-recruitment (e.g. Dunraven), and others acting as sink sites for larvae from elsewhere (e.g. Aberarth). This study highlights the importance of a holistic approach to understanding pelagic larval dispersal, and thus the distribution and long-term persistence of marine species.

5.2. Introduction

In the marine environment, external fertilisation is common amongst benthic invertebrates, with geographically distinct adult populations (i.e. metapopulations) linked by a dispersive larval stage (Jolly et al., 2009). Many intertidal species rely on self-recruitment (larval retention and thus recruitment to the natal population) or connectivity (dispersal of larvae to other populations within the metapopulation) for population replenishment, and thus long-term persistence (Levin, 2006; Robins et al., 2013). Species distributions are ultimately determined by the dispersal capacity of the mobile phase (Johnson et al., 2001). However, understanding the links between larval dispersal and environmental parameters remains a fundamental challenge in population connectivity studies, with hydrodynamic and biological processes influencing larval success. Both vary at different spatial and temporal scales, influencing larval dispersal patterns (Pineda et al., 2007; Ayata et al., 2009; 2011; Jolly et al., 2009). Asymmetric larval dispersal patterns are common (Levin, 2006), and can be monodirectional (Bode et al., 2006) with sites acting as sinks for larvae from other source sites, or bidirectional with larval exchange between reefs (Ayata et al., 2009).

Hydrodynamic factors that affect pelagic larvae include wind induced and tidal currents, coastal upwellings, river plumes, eddies and gyres (Wilson, 1971; Cunningham et al., 1984; Thiebaut et al., 1998; Bradbury & Snelgrove, 2001; Dubois et al., 2007; Ayata et al., 2009; Jolly et al., 2009). Robins et al. (2013) reported that transport in shelf seas is predominantly dependent on tidal parameters (e.g. range, phase and local bathymetry), residual currents (e.g. circulations patterns that fluctuate with variations in weather and climate), and the interaction of non-random larval behaviour (e.g. diel or tidal vertical migration, morphogenic depth changes) with these circulation patterns. Additional biological processes that influence larval dispersal include adult fecundity at source sites, spawning season and larval development time (Ellien et al., 2004; Pineda et al., 2007; Ayata et al., 2009; 2011). Consequently, species-specific regional scale analysis of the scale of both connectivity and self-recruitment is crucial in understanding metapopulation dynamics (Robins et al., 2013; Bush et al., 2015).

Three-dimensional (3D) hydrodynamic models can be used to predict larval dispersal, as passive particles or with inclusive of behaviour, within Lagrangian particle tracking frameworks (e.g. Paris et al., 2007; Robins et al., 2013; Etter & Bower, 2015). Modelling passive particles may limit the effectiveness of recruitment estimations (Roberts, 1997; Cowen et al., 2000; Leis, 2002; Knights et al., 2006), but inclusion of simplified larval behaviour may also lead to unrealistic predictions (Siegel, 2003; Almany, 2007, Corell et al., 2012). Whilst larval behaviours are known to play an important role in influencing larval dispersal, species-specific larval behaviours (e.g. vertical migrations) have often not been investigated, and the drivers (e.g. tide, daylight, developmental stage) are often not known (Pineda et al., 2007). Additionally, larval behaviour characteristics observed in the laboratory, whilst indicative of potential behaviour mechanisms, may not be expressed in the natural environment (Knights et al., 2006). Confidence in model predictions can only be achieved through extensive validation of a range of variables. Within the Irish Sea, several hydrodynamic models exist (e.g. Xing & Davies, 2001; Horsburgh & Hill, 2003; Hartnett et al., 2007; Robins et al., 2013) against which current hydrodynamic model prediction can be validated (Robins et al., 2013), in addition to hindcast data. Within the Irish Sea, larval oceanographic distance rather than geographic distance appears to be related to population connectivity, dependent on tidal velocities and the presence of oceanographic features. For example, larvae from source populations located near strong tidal currents travel a greater oceanographic distance with high population connectivity, whilst those from sheltered populations travel less far, with potentially greater self-recruitment (Robins et al., 2013). Validation of particle tracking models on a shelf scale with real observations is rare, as robust measurements of *in situ* larval dispersal are inherently difficult (Pineda et al., 2007).

Larval dispersal is particularly important in species with a fragmented habitat (Robins et al., 2013). Consequently, the intertidal polychaete, *Sabellaria alveolata*, is a potential model organism for investigations of the role of larval dispersal (i.e.

connectivity and retention) in populations dynamics as populations are strongly dependent on the distribution of suitable substrata (i.e. hard substrata such as bedrock, pebble scars and artificial sea defences), and wave exposure regimes (i.e. wave energy sufficient to suspend suitable sediment, but not to cause physical damage) and consequently, this species exhibits a highly fragmented distribution on rocky shores from Morocco to Scotland within the northeast Atlantic (Cunningham et al., 1984; Firth et al., 2015). Populations are highly persistent, and have been consistently reported from some sites through time. For example, in Mont Saint Michel Bay, France (Audouin & Edwards, 1832; Galaine & Houlbert, 1916; Renaud, 1917; Lucas, 1959; Dollfus, 1960; Mathieu, 1967; Le Rhun & Mathieu, 1982; Gruet, 1982,1986; Dubois et al., 2006; 2007; Fournier et al., 2010; Noernberg et al., 2010; Desroy et al., 2011), and at Seascale, UK (Cunningham et al., 1984; Frost et al., 2004; Firth et al, 2015; Bush et al., Chapter 2), presence has been reported for a century or more. However, on a short-term small-scale, such populations are highly dynamic, and partially dependent on successful larval recruitment for persistence (Bush & Davies, Chapter 4), which is reportedly highly variable year-to-year (Wilson, 1971; 1974; 1976; Gruet, 1986; Bush & Davies, Chapter 4). Within the British Isles, historical population fragmentation through local extirpations has occurred (Crisp, 1964; Cunningham et al., 1984; Frost et al., 2004). Such fragmentation can result in low connectivity between sub-populations of marine organisms and a loss of marine larval recruitment (Levin; 2006).

Sabellaria alveolata is a long lived species (i.e. generally 3 – 5 years, but up to 10; Wilson 1971; Gruet, 1986), and reef structures generally persist beyond individual life times, as the biogenic material is highly attractive to settlement stage larvae, with gregarious settlement often observed on both live and dead reef (Wilson, 1968b; 1970; 1976; Pawlik, 1988; Bush et al., Chapters 2; 3; Bush & Davies, Chapter 4). However, little is known about many of the determining biological parameters of the larvae. The spawning pattern (Wilson, 1971; Gruet & Lassus, 1983; Dubois et al., 2007; Culloty et al., 2010), larval development time and thus planktonic larval duration (PLD; Wilson, 1968b, 1970, 1971; Cazaux, 1970; Dubois et al., 2007) are highly variable, whilst few studies have investigated other biological parameters (e.g.

adult fecundity or larval behaviour). Consequently, little is known with regards larval dispersal.

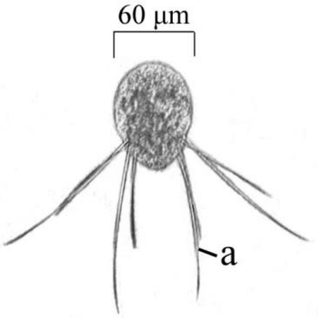
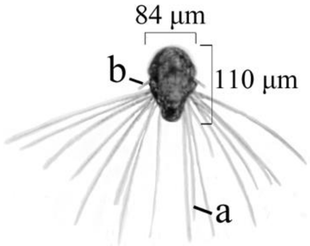
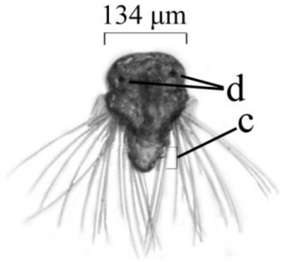
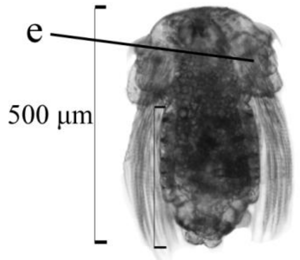
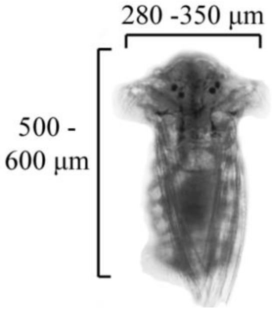
5.2.1. *Sabellaria alveolata* life cycle

Sabellaria alveolata is a gonochoric broadcast spawning species (Ayata et al., 2009), that may display site-dependent, poorly seasonally synchronised, semi-continuous spawning (Dubois et al., 2007), however there is conflicting information regarding spawning season. For example, Wilson (1971) reported a short spawning event in Jul in the UK. In contrast, Culloty et al. (2010) reported extended spawning from Jun - Sep in Ireland, whilst studies in France suggested a longer, potentially bimodal, spawning pattern (Gruet & Lassus, 1983; Dubois et al., 2007). Mature ripe adults have been reported in all months (Gruet & Lassus 1983; Dubois et al., 2003; 2007; Culloty et al., 2010), and Davies & Newstead (2013) reported successful fertilisation throughout the year, providing evidence that semi-continuous spawning is possible.

Gametes are fertilised externally, with rapid development to free swimming trochophore larvae (Wilson, 1929; Pawlik, 1988). Trochophore larvae develop into obligate metatrochophore larvae, and then facultative erpochete larvae that are ready to settle (Table 5.1; Dubois et al., 2007, Elkin & Marshall, 2007). There is conflicting information regarding PLD with larvae reported to reach settlement stage within as little as 1 month (Dubois et al., 2007; Davies & Newstead, 2013), but capable of delaying metamorphosis for up to a further 7.5 months (Cazaux, 1970; Dubois et al., 2007; Wilson, 1970). Such variability may be attributed to temperature, food availability or substrata (Reitzel et al., 2004; Qian & Chia, 1991). For example, Dubois et al. (2007) reported slower development in spring than autumn associated with lower temperatures, and Pawlik (1988) reported increased development with increasing temperature.

The timing and success of settlement are also highly variable. Wilson (1971; 1974) reported settlement predominantly in autumn - winter in the UK, although some settlement was observed in spring and summer. Gruet (1986) reported settlement

Table 5.1: A summary of *Sabellaria alveolata* larval developmental stages with descriptions and size classes. The age at which larvae achieved each developmental stage within the laboratory is also noted (Wilson, 1929; Cazaux, 1964; Dubois et al., 2007).

Larval stage	Description	Size (µm)	Age (days)	Representative image
Young trochophore (Stage 0 = S^0)	Very little elongation with no segmentation. Chaetae evident (a).	<90	2-5	
Trochophore (Stage 1 = S^1)	Some elongation, no segmentation, chaetae prominent, cilia forms (b)	90-120	5-12	
Young metatrochophore (Stage 2 = S^2)	Elongation, segmentation has begun, formation of first abdominal segments (c), ocellus present (d).	120-350	13-20	
Old metatrochophore (Stage 3 = S^3)	Further elongation, segmentation has continued with an increase in abdominal segments, darker pigmentation, formation of 2 tentacular buds (e)	350-500	20-30	i.e. 
Erpochete (Stage 4 = S^4)	Ready for settlement, larger abdominal segments, intensification of dark pigment, elongation of tentacular palps, formation of future palae of the adult worm.	≥500	≥30	

from spring to summer in France, and Bush & Davies (Chapter 4) observed settlement in spring, summer and autumn in the UK. Wilson (1971, 1974) only observed dense settlement in two of twelve years of study, on both occasions in autumn - winter, but Bush & Davies, (Chapter 4) observed site-dependent dense settlement in spring and autumn in up to two of three years of study.

This study aimed to develop an understanding of how distinct reefs interact, not just within their local environment but also within regional hydrodynamics. Ultimately I aimed to understand their population connectivity. Current literature exposed the gaps in knowledge in this area, specifically with regards spawning strategy, larval behaviour and subsequently larval dispersal. The objectives of this study were to provide consistent long term gamete and larval density data from natural populations, investigate phototactic responses and swimming speeds of larvae at different development stages, produce estimates of connectivity of abundant reef-forming populations on the west coast of the British Isles, and to identify major source and sink sites. These objectives provided the opportunity to test two hypotheses. Firstly, that reproductively active individuals will be observed throughout the sampling period and consequently, that British *S. alveolata* will display semi-continuous spawning with a synchronised summer peak in larval abundance. Secondly, that larvae will be dispersed rapidly from their source reefs in regions of open coastline, with substantial connectivity between neighbouring populations.

5.3. Study Area and Methods

5.3.1. Study area

Surveys were carried out at *S. alveolata* sites of high abundance on a latitudinal gradient: Dunraven Bay in South Wales, Aberarth in mid Wales and Llanddulas in North Wales (Figure 5.1), subsequently referred to as *Dun*, *Aber* and *Llan* respectively. At all three sites, biogenic structures varied from encrusting veneers of a few centimetres in height, to reefs of more than 50 cm tall, with a spatial extent of > 200 m^2. Reef populations at *Llan* were spatially contained (i.e. extended < 500 m parallel to the coast), however at *Dun* and *Aber* populations were present semi-continuously, on hard substrata, throughout the lower intertidal, adjacent to the selected site. Populations at *Aber* were predominantly encrusting, rarely reaching more than 30 cm in height. Differences regarding larvae production, dispersal abundances and recruitment are expected associated with differences in reef size and quality and location.

5.3.2. Fecundity of *Sabellaria alveolata* adults

Monthly sampling of *S. alveolata* was carried out from Feb - Sep 2014 (survey dates are listed in Appendix 5.1). In each sampling period, a small hummock (~10 cm^3) of actively growing adult worms were collected from within a 20 m^2 area of reef at each site (i.e. near the upper edge of the reef, adjacent to the access point). Individual worms were physically removed from their tube *in situ*, placed in vials containing 9 ml filtered seawater, agitated and left for 1 hour, before the addition of 1 ml buffered 39% formalin solution (i.e. made up to 10 ml of 4.0% formaldehyde). All worms spawned under this treatment (Wilson, 1968b). Donor worms were sexed by gamete morphology (i.e. small white sperm or large pink eggs), and five representative vials for each sex were retained. Retained worms were removed from vials and mass recorded. The spawning solution of each worm was diluted (*d*) to 20 ml (solutions with an exceedingly high concentration of gametes were diluted further, up to 60 ml,

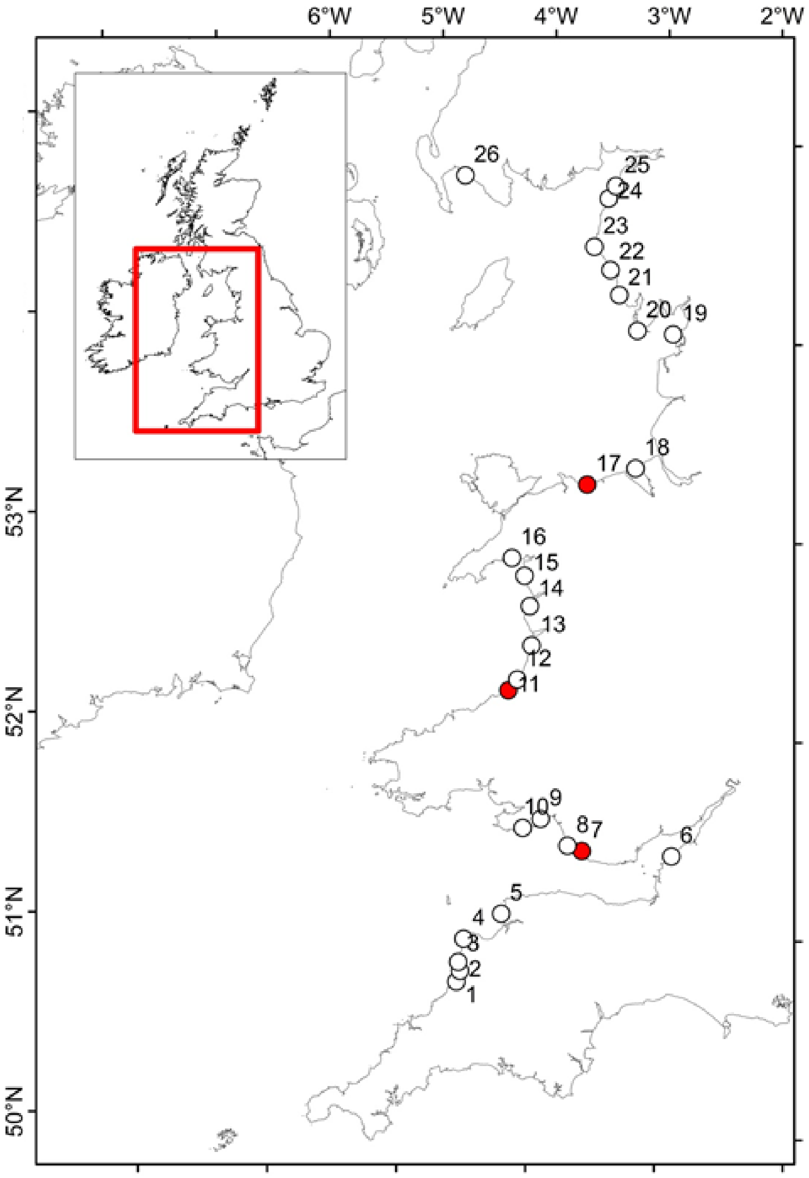


Figure 5.1: Location of persistent abundant *Sabellaria alveolata* reef sites on the west coast of the British Isles (○),.according to data collected and collated in Bush et al. (Chapter 2; 3). Fieldwork sites are highlighted in red (i.e. site 7 = Dunraven, site 11 = Aberarth and site 17 = Llanddulas; other site names in Table 5.2).

to facilitate accurate enumeration), and homogenised by repeated inversion. The number of gametes in a 1 ml subsample was enumerated in a *Neubauer Haemocytometer (*constructed of nine large grid squares, each divided into sixteen small grid squares). Gametes were enumerated in four diagonally connected small grid squares, in three randomly selected large grid squares, under a compound microscope (*c*). The number of gametes produced by each individual was estimated, and normalised by mass (m) of the donors (Equation 1, where *N* is the normalised gamete count, and 11.9 is the dilution factor in this case):

$$N = (11.9d.c)/m \qquad (1)$$

Additionally, the size of ten randomly selected eggs was determined using an inverted compound microscope (240x magnification). Significant temporal variability in egg size, egg count and sperm count between months and sites were assessed with Kruskal-Wallis tests (KW).

5.3.3. Spawning and rearing *Sabellaria alveolata* larvae

Adult *S. alveolata* were collected from *Llan*, transported in seawater within an insulated cool-box, and retained within aquaria supplied with a continuous flow of 0.2 µm filtered seawater prior to shock-induced spawning (methodology described above; Wilson, 1968a). Adult worms were physically removed undamaged from tubes. Donors were placed in individual vials with 5 ml of ambient temperature 0.2 µm filtered seawater. Within five minutes, gamete expulsion was observed in most individuals. Vials containing gametes of same sex were combined into separate 200 ml vials. Gamete concentration was determined with a *Neubauer Haemocytometer*. Sperm was added to eggs at a ratio of 5:1, reducing the risk of polyspermy. The resultant solution was left for 20 minutes to allow fertilisation to occur. Following fertilisation, eggs were rinsed through a 50 µm mesh to remove redundant sperm and reduce risk of bacterial infection before being transferred to 1 L of aerated ambient temperature seawater. After 18 hours most viable eggs had developed to trochophore stage larvae (e.g. Wilson, 1970; Pawlik, 1986), and initial larval concentration was determined by Neubauer haemocytometer. Larval solution was then transferred into aerated 12 L buckets of 0.2 µm filtered seawater at a concentration of approximately 1 larvae ml^{-1}. Larvae were fed daily with a 1:1 mixture of phytoplankton (*Pavlova lutheri* and *Tahitian isochrysis)* to larvae (e.g. Pawlik, 1988). Larvae development buckets remained in a thermostatically controlled room at

18 ˚C, under a florescent light setting of 13:11 hour light to dark cycle (mimicking summer sunlight exposure). Twice-daily partial water changes were made via reverse filtration through a 50 µm mesh. Approximately 500 ml of larval solution was retained in each water change and resuspended in an additional 11.5 L of filtered seawater of the same temperature. On alternate days, larval solution was transferred to a clean bucket (e.g. Pawlik, 1988). Larvae were sampled from development buckets at different stages post fertilisation for behaviour experimentation, and speed and length measurements: day 5 (trochophore), day 15 (young metatrochophore), and day 30 (erpochete) for all, in addition to day 20 and 25 (old metatrochophore) for the speed and length measurement. Speed and length measurements were estimated by video recording and imagery respectively, using the same methodology as egg size in the fecundity study.

5.3.4. *Sabellaria alveolata* larval behaviour in vivo

The response of larvae to light was monitored within both vertical and horizontal chambers. Horizontal phototaxis experiments were carried out in acrylic chambers (20 cm x 2 cm x 2 cm) following a protocol similar to Miller & Hadfield (1986). One half of each chamber was coated in opaque black paint and lidded to prevent light penetration, whilst the opposite side remained exposed to light. Chambers were filled to 1.5 cm depth with 0.2 µm filtered seawater containing 20-70 larvae. Larval chambers were acclimated in a dark room for 10 minutes (e.g. Marsden 1984). Following acclimation, the exposed end of treatment chambers were illuminated from above by cold source light at an intensity of 0.6 x 1016 quanta s^{-1} cm^{-2} (KL 1500 LCD halogen) for 20 minutes. Subsequently, a central partition was inserted between shaded and exposed ends of the chamber to prevent subsequent larval migration. Larvae within a 10 ml of subsample from each end were enumerated under a dissection microscope.

Vertical phototaxis trials were also conducted. Vertical cylindrical chambers (50 cm x 7 cm) were coated with opaque black paint, and filled with 20 ml of 0.2 µm filtered seawater, containing 20-70 larvae as previously. Following 10 minutes of acclimation, cold source light was directed up the treatment cylinders from the base for 20 minutes, resulting in a light gradient that opposed gravity, thus larvae would have to actively swim away from the light to exhibit a negative phototactic response. The tubes had graduations every 10 cm, with each graduation equating to a volume of 4 ml. 5 sequential 4 ml subsample were released from the tube, and larvae in each enumerated. Significant differences in the proportion of larvae present were assessed using ANOVA.

5.3.5. Temporal and spatial variability in concentration of *Sabellaria alveolata* larvae

Monthly sampling of *S. alveolata* larvae were carried out offshore on a monthly basis from Apr - Sep 2014 (Survey dates are listed in Appendix 5.1). Offshore sampling was not possible at *Aber* or *Dun* in Apr, or *Dun* in Aug due to unavailability of boat or crew. At *Llan*, offshore sampling for Jun was delayed until Jul 1st due to poor weather conditions. Larval samples were collected with plankton tows, to allow estimates of larval abundance offshores. At each site 50 µm plankton net samples (aperture 50 cm) were collected at constant speed (~2 knots), at two distances offshore (i.e. ~100 m and ~1 km), at three different locations (i.e. ~500 m either side of the reef, and directly in front of the reef), and at two different depths (e.g. 1 m and 5 m). Sample volume was measured with a calibrated Hydro-Bios digital flowmeter (model 438 110). Retained samples were filtered (i.e. 50 µm sieve) immediately and preserved in 10% borax-buffered formosaline solution.

Subsequently larval abundance, life-history stage and size (i.e. length and width) were determined under a binocular microscope. Preserved larvae samples were refiltered, cleaned, and resuspended in 500 ml of filtered seawater immediately prior to analysis. 5 ml subsamples were transferred to *Bogorov* Modified Counting Chambers with a *Hensen-Stempel* Pipette. Methylene blue dye was added to facilitate larval identification. Larval abundance was assessed under a binocular microscope. All larvae were removed and retained in 70% ethanol solution. In general three replicate subsamples were processed, but if the initial count was greater than 250 larvae per 5 ml, a 1 ml subsample was counted for the remaining two subsamples. This methodology was validated and each subsample was consistent with the original count. All subsamples were rescanned under the binocular microscope until no further larvae were found. Ten percent of all subsamples analysed, selected at random across all sites and time periods, and were quality controlled by another analyst.

Larval developmental stages of *Sabellaria alveolata* were characterised into size ranges following Dubois et al. (2007) (Table 5.1). Images were captured of ten randomly selected larvae (or all larvae in samples of less than 10), and lengths measured as previously, facilitating an estimate of the abundance of each larval stage within each sample. Significant differences in larval concentration in relation to depth, distance offshore from the reef, and direction along shore from the reef at each site were assessed overall and monthly. Statistical analysis was carried out in R in the same procedure as fecundity (i.e. KW).

5.3.6. Biophysical modelling of *Sabellaria alveolata* larvae

The transport of virtual 'larvae' particles (i.e. planktonic *S. alveolata* larvae) was simulated within the Irish Sea, facilitating predictions of the proportion of *S. alveolata* larvae that contribute to self-recruitment at larval source sites, and to connectivity within the metapopulation (methodology originally described in Coscia et al., 2013). The model domain extends from 50 to 56° N, and from the British coastline to -9° W (see Robins et al., 2013). Larvae particles were released from 26 known reef sites (Table 5.2), identified from historical data sources (Cunningham et al., 1984; Frost et al., 2004), that were revisited in the summers of 2012-2014 (Bush et al., Chapter 2) and so known to be persistent through time (Table 2.5). Modelling was based on a hydrodynamic model in addition to a Lagrangian particle tracking model (PTM) (Robins et al., 2013; Bush et al., 2015). Once released from natal sites, larvae particles were exposed to shelf sea currents, and transported either locally within their natal habitat (self-recruitment), to similar habitat elsewhere (connectivity) or were transported offshore or to assumed unsuitable habitat (unsuccessful).

The hydrodynamics were simulated using a three-dimensional (3D) Princeton Ocean Model (Robins et al., 2013; Gormley et al., 2015). Detailed information on the

Table 5.2: Particle Tracking Model release locations for *Sabellaria alveolata*.

Reef site	Name and location	Reef site	Name and location
1	Millook	14	Barmouth Bay
2	Bude	15	Shell Island
3	Duckpool	16	Criccieth
4	Hartland Quay	17	Llanddulas
5	Croyde	18	Hilbre Island
6	Clevedon	19	Morecambe Bay
7	Dunraven	20	Cross Dyke Scar
8	Porthcawl	21	Annaside Bank
9	Swansea Bay	22	Drigg
10	Limeslade Bay	23	St. Bees
11	Aberarth	24	Maryport
12	Aberystwyth	25	Dubmill Point
13	Borth	26	Auchenmalg Bay

development and validation of this model, and its application for this process have been reported in Robins et al. (2013) and Bush et al. (2015). The standard predictive variables (e.g. 3D velocity, salinity, temperature, turbulence, and elevation) were given by terrain-mapping sigma layers in the vertical plane, and finite-difference discretisation on a staggered, orthogonal grid in the horizontal plane (Robins et al., 2013; Bush et al., 2015). The model grid covered the previously mentioned domain, where the horizontal cell size was 1/30˚ (longitude) by 1/60˚ (latitude), providing a ~1.85 km resolution (Robins et al., 2013; Gormley et al., 2015). Twenty equally segmented vertical layers gave the average and minimum resolutions at mean sea level (Robins et al., 2013).

To validate the hydrodynamic model, a typical year (i.e. not an extreme weather year) was simulated; namely 1990, which was selected based on an analysis of bed shear stress, significant wave heights and temperature records from a decadal simulation (1989-1998) (Neill et al., 2010). A six-month simulation was made from 01 Apr 1990 (following a one month simulation to allow baroclinic currents to fully develop; Robins et al., 2013; Bush et al., 2015). The simulation was forced with six tidal properties including the semi-diurnal solar (S_2) and lunar (M_2) constituents (Robins et al., 2013; Bush et al., 2015). Synoptic meteorological fields were sourced from ‘the European Centre for Medium-Range Weather Forecasts-Interim reanalysis’

(Simmons et al., 2006), available 3 hourly, at a resolution of 1.5° (Robins et al., 2013; Bush et al., 2015).

Lagrangian PTMs were used to predict likely dispersal of *S. alveolata* larvae in space and time, based on 3D advection and turbulent mixing. The site-specific dispersal probabilities of larvae were mapped, and population connectivities estimated. Simulated 3D velocities and diffusivities were output from the hydrodynamic model for use in the PTMs (Detailed information on this process has been described in Robins et al., 2013). This 'off-line' technique is sufficiently accurate, since the transport of larvae does not affect the hydrodynamics, and has the added advantage that a large number of PTMs can be performed from one hydrodynamic simulation, which is computationally more efficient (Robins et al., 2013; Bush et al., 2015).

Particles were simulated both as (i) neutrally buoyant and passive, and (ii) with daytime vertical downward migration. Whilst larval behaviour in the laboratory demonstrated a response to light, the results of larval dispersal in the field were not conclusive. Over-dispersal of larvae is often predicted by including laboratory witnessed behaviour traits (Knights et al., 2006). Larval mortality was not considered, because a mortality function reduces the number of particles in the analysis. Additionally, although mortality rates will affect overall connectivity, unless mortality varies spatially, they will not affect connectivity patterns (Paris et al., 2007). Larvae that encounter a coastline were reflected back into the water column to their position at the previous iteration time step, rather than 'washed-up' on land, so that maximum dispersal was investigated (Robins et al., 2013; Bush et al., 2015).

Cohorts of 10,000 larvae were released simultaneously from each of the 26 natal sites, which is sufficient so that the trajectories were not polluted by statistical outliers (Robins et al., 2013). Development to erpochaete stage was observed within 1 month in the laboratory (Bush, pers. obs.) and reported in the field (Dubois et al., 2007). Ayata et al. (2009) suggested most larvae were competent to metamorphose within 6 weeks, however highly variable rates of development have been reported due to the ability of larvae to delay metamorphosis in unsuitable conditions (e.g. Wilson, 1929; 1968b, 1970, 1971; Cazaux, 1970, Dubois et al., 2007). Consequently, larvae were tracked for a PLD of 60 days. The initial footprint of each reef (within which 10,000 particles were randomly positioned) was 1 km^2 at a point closest to the reef location. The above procedure was repeated at 4 different times throughout the summer; 01 May, 01 Jun, 01 Jul, and 01 Aug (Bush et al., 2015).

This study analysed the sensitivity of larval dispersal distances, retention and connectivity, to the following variables: release location, release time (i.e. seasonal effects). This study used oceanographic dispersal distances (i.e. the total distance travelled by each larvae) and release time as proxies for variations in tidal energy and residual currents, respectively. Using source distribution matrices, quantitative parameterisations of population connectivity have been produced. This process is detailed in Ayata et al. (2010), and Robin et al. (2013). Population connectivity was quantified as the proportion of larvae that successfully settle in a sink population, after the 60 day PLD, which originated in a different source population. Conversely, larval retention at the source site was quantified as the proportion of larvae that remained at the source site. Larvae were deemed successful, and thus to settle, if located within 10 km of one of the 26 release sites at the end of the 60 days (Cowen et al., 2006; Robins et al., 2013; Bush et al., 2015). Conversely, larvae were deemed unsuccessful if they were located outwith 10 km of one of the 26 natal reefs at the end of 60 days. This distance is similar to the tidal excursion of a passive particle in the Irish Sea (Xing & Davies, 2001). This methodology resulted in connectivity being based on just a sub-set of possible environments, however, only the comparative outputs were considered (e.g. between release locations and seasons; Robins et al., 2013; Bush et al., 2015).

5.3.7. Validation of vertical *Sabellaria alveolata* larval migration with *in situ* observations

Following larval behaviour experiments, the predicted patterns were compared with *in situ* observations of larval concentration. For instance, if diel vertical migration occurred, a greater concentration of latter stage larvae (i.e. S^2-S^3) would be expected at 5 m depth than at 1 m depth. Monthly concentrations for latter stage larvae were pooled and compared with depth (df = 1) with KW.

5.3.8. Validation of horizontal *Sabellaria alveolata* larval dispersal with *in situ* observations

Following larval dispersal modelling, the predicted patterns were again compared with *in situ* observations of larval concentration. For instance, if the model predicted that larvae were rapidly transferred offshore, a greater larval concentration would be expected 1 km offshore than 100 m offshore. Similarly, if the model predicted larvae were transported southward down the coast, a greater larval concentration would be expected to the south than the middle or north. Monthly larval concentrations were compared with distance offshore from reef (df = 1), and direction alongshore from reef (df = 2), with KW.

5.4. Results

5.4.1. Fecundity of *Sabellaria alveolata* adults

A significant decrease in egg size was demonstrated from Feb – May to Jun – Aug at all three sites (KW, H ≥ 3.94, P ≤ 0.05; Appendix 5.2; Figure 5.2 a). Where significant differences in monthly mean egg size were demonstrated between sites, egg size was greater in the southern population (e.g. Dun than Llan in Apr, Jun, Aug and Sep; KW, H ≥ 3.94, P ≤ 0.05; Appendix 5.2; Figure 5.2 a). A summer peak in both raw and normalised egg count was observed at all three sites, however this peak was temporally offset between sites (Figure 5.2 c, d). Monthly variation in donor weight occurred (Figure 5.2 b), and when egg count was normalised by weight, summer peaks were reinforced (Figure 5.2 d). For example, normalised egg counts were significantly greater at *Llan* in May - Jun than Feb – Apr and Jul – Sep (KW, H = 5.77, P ≤ 0.02; Appendix 5.2; Figure 5.2 d), at *Aber* in Jun – Sep than Feb – Apr (KW, H ≥ 4.81, P ≤ 0.03; Appendix 5.2; Figure 5.2 d), and at *Dun* in Jul than Jun, Aug – Sep (KW, H ≥ 4.81, P ≤ 0.03; Appendix 5.2; Figure 5.2 d). In contrast to northern sites, normalised egg counts also demonstrated a spring peak at *Dun* where counts were significantly greater in Feb – Mar than Jun and Aug – Sep (KW, H ≥ 5.31, P ≤ 0.02; Appendix 5.2; Figure 5.2 c, d). A summer peak in raw and normalised sperm count was also observed at all three sites (Figure 5.2 e, f). Normalised sperm counts were significantly greater at *Llan* in May – Jul than Feb – Apr and Aug – Sep, with the exception of May to Mar (KW, H ≥ 3.94, P ≤ 0.05; Appendix 5.2; Figure 5.2 f), at *Aber* in May – Jun than Feb – Apr and Jul – Sep (KW, H ≥ 4.81, P ≤ 0.03; Appendix 5.2; Figure 5.2 f), and at *Dun* in May than Feb – Apr and Jun – Aug (KW, H ≥ 3.94, P ≤ 0.05; Appendix 5.2; Figure 5.2 f). Whilst the peaks in opposing gamete counts were temporally correlated at *Llan* (i.e. May – Jun), temporal mismatches were demonstrated at both *Aber* and *Dun* (Figure 5.2 d, f). At *Aber*, a partial mismatch occurred with the peak in sperm count was initiated 1 month prior to the peak in egg count although both normalised gamete counts remained elevated in Jun, whilst at *Dun*, complete mismatch occurred with peak normalised sperm count intermediate to spring and summer egg count peaks (Figure 5.2 d, f).

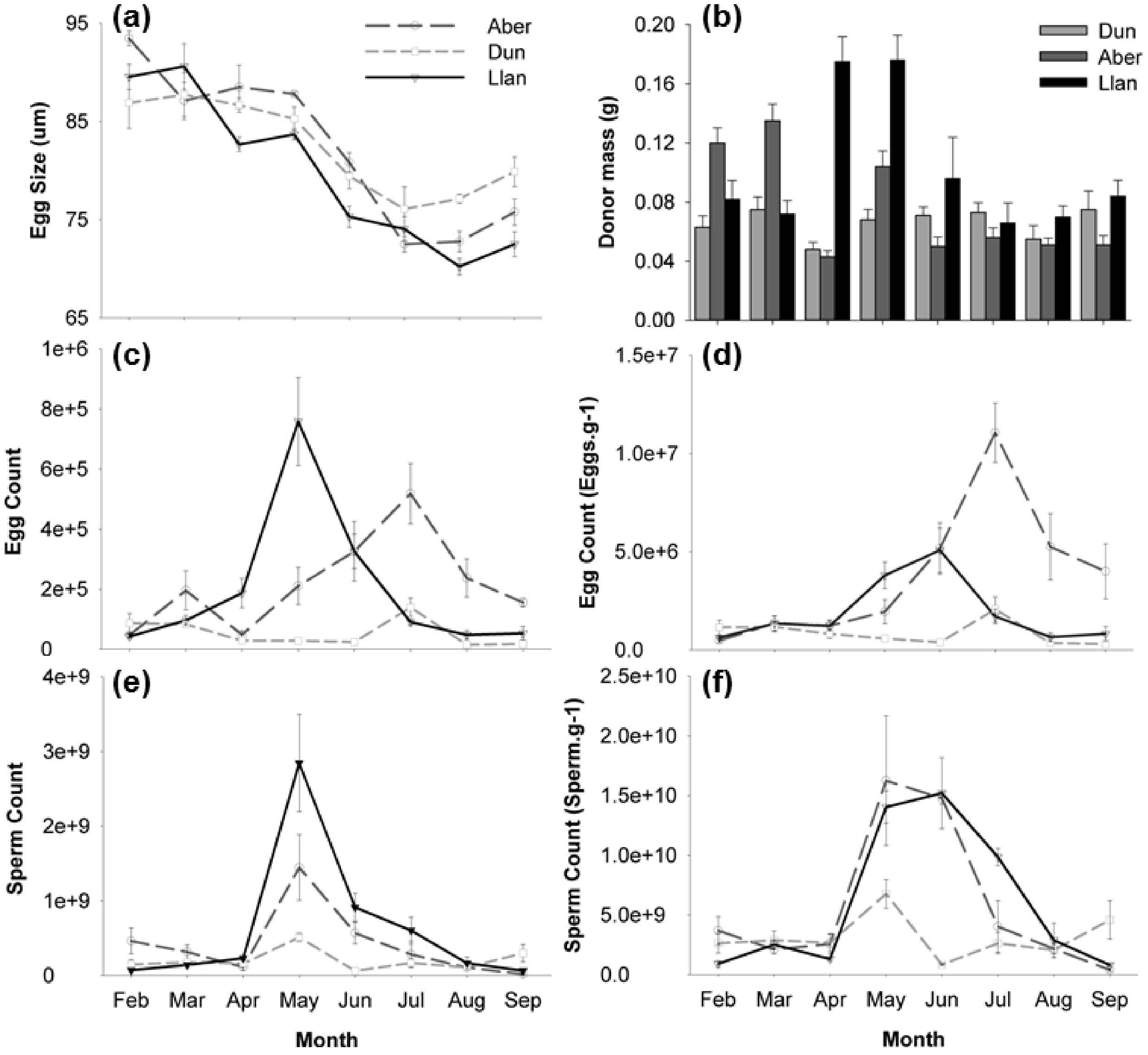


Figure 5.2: Monthly fecundity data, with gamete counts related to weight of 5 donor *Sabellaria alveolata* individuals collected at 3 different sites, from February to September 2014. Mean fecundity and weight data are colour coded to site. Error bars represents 1 standard error. (a) Egg size. (b) Donor weight. (c) Egg count. (d) Egg count normalised by weight of donor females. (e) Sperm count. (f) Sperm count normalised by weight of donor males.

5.4.2. *Sabellaria alveolata* larval behaviour in vivo

A significant interaction was demonstrated between light exposure and larval age in both horizontal and vertical experiments (ANOVA, df = 2, SS ≥ 363.46, F ≥ 4.49, P ≤ 0.02). In horizontal chambers, no phototaxis was observed 5 days post fertilisation, with no significant difference in larval concentration demonstrated between the shaded/covered and exposed half of the horizontal chamber (Figure 5.3 a). In contrast, 15 and 30 days post fertilisation larvae demonstrated negative phototaxis, favouring the shaded half of the horizontal chamber (ANOVA, df = 1, SS ≥ 4868, F ≥ 54.45 , P < 0.01; Figure 5.3 a). Similarly, the effect of vertical light exposure on larval phototaxis was dependent on age, with a significantly different proportion of both day 5 and 30 larvae present dependent on light intensity (ANOVA, df = 1, SS ≥ 2208, F ≥ 14.44, P < 0.01). For example, significantly more day 5 larvae where present at high light intensity, near the bottom of the vertical chamber (e.g. at 20 cm; ANOVA, df = 2, SS = 1278, F = 4.38.44, P <0.01), and significantly more day 30 larvae at lower light intensity, near the top of the chamber (e.g. at 50 cm; ANOVA, df = 2, SS = 6972, F = 29.61, P < 0.01), despite having to actively swim up in the water column to maintain this position (Figure 5.3 b).

A significant difference was demonstrated in larval swimming speeds with age (ANOVA, df = 4, SS = 1.22 x10^{-7}, F = 65.04, P <0.01). A significant increase in swimming speed occurred from day 5 to day 20, with a significant decrease in swimming speed to from day 25 to day 30 (Tukeys HSD, P < 0.01; Figure 5.3 c). No significant difference was demonstrated between days 20 and 25 when larvae reached maximum swimming speed (Tukeys HSD, P = 1.00), or days 15 and 30 due to a reduction in swimming speed as larvae develop towards settlement stage (Tukey HSD, P = 0.94). Larvae demonstrated significant growth (ANOVA, df = 4, SS = 8.10 x10^{-5}, *F* = 160.98, P <0.01; Figure 5.3 c), with a significant increase in length from day 5 to 20 (Tukey HSD, P < 0.01) with no significant difference from day 20 to 30 (Tukey HSD, P ≥ 0.06; Figure 5.3 c).

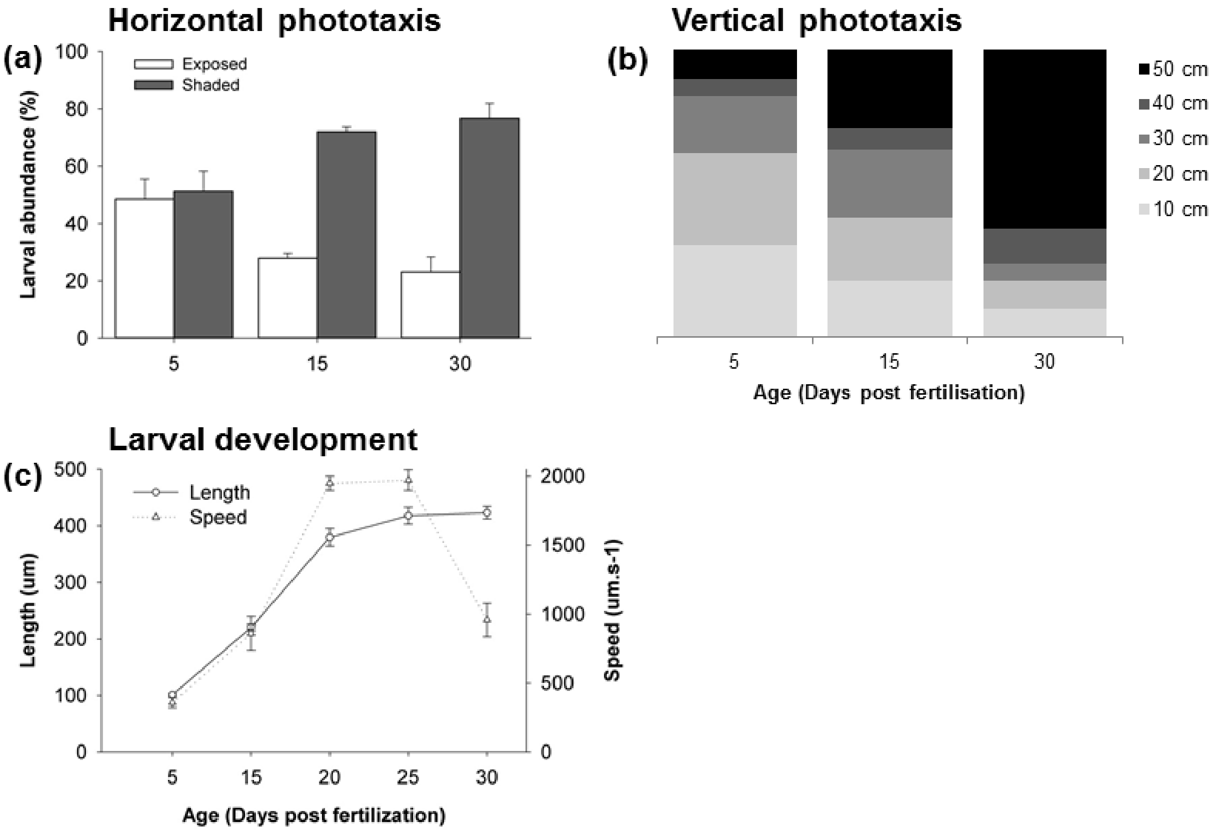


Figure 5.3: Temporal changes in *Sabellaria alveolata* larval behaviour and size with increased age (i.e. 5 to 30 days post fertilisation). (a) Altered phototactic response of larvae to horizontal light exposure. The percentage of larvae found in the exposed and shaded half of the chamber are colour coded. (b) Altered phototactic response of larvae to a vertical light gradient. The percentage of larvae found in each 10 cm vertical depth fraction, from the bottom (exposed to the highest light intensity) to the top (exposed to the lowest intensity) of a chamber are colour coded. (c) The change in mean larvae swimming speed and size. Error bars ±1 standard error.

5.4.3. Temporal and spatial variability in concentration of *Sabellaria alveolata* larvae

Larvae were present in all sampled months at all sites; however mean larval concentrations demonstrated substantial variation (Figure 5.4). Significant differences in overall larval concentration were demonstrated between sites (KW, $H \geq 6.08$, df = 2, $P \leq 0.05$), with maximum larval concentrations reported from *Aber*, and minimum from *Llan* (Figure 5.4). Significant differences in overall larvae concentration were also demonstrated between months (KW, H= 10.13, df = 3, P = 0.02), with a summer larval bloom observed at all sites (KW, $H \geq 11.20$, $df \geq 3$, $P \leq 0.05$; Figure 5.4 a), however the magnitude and timing of this bloom was site

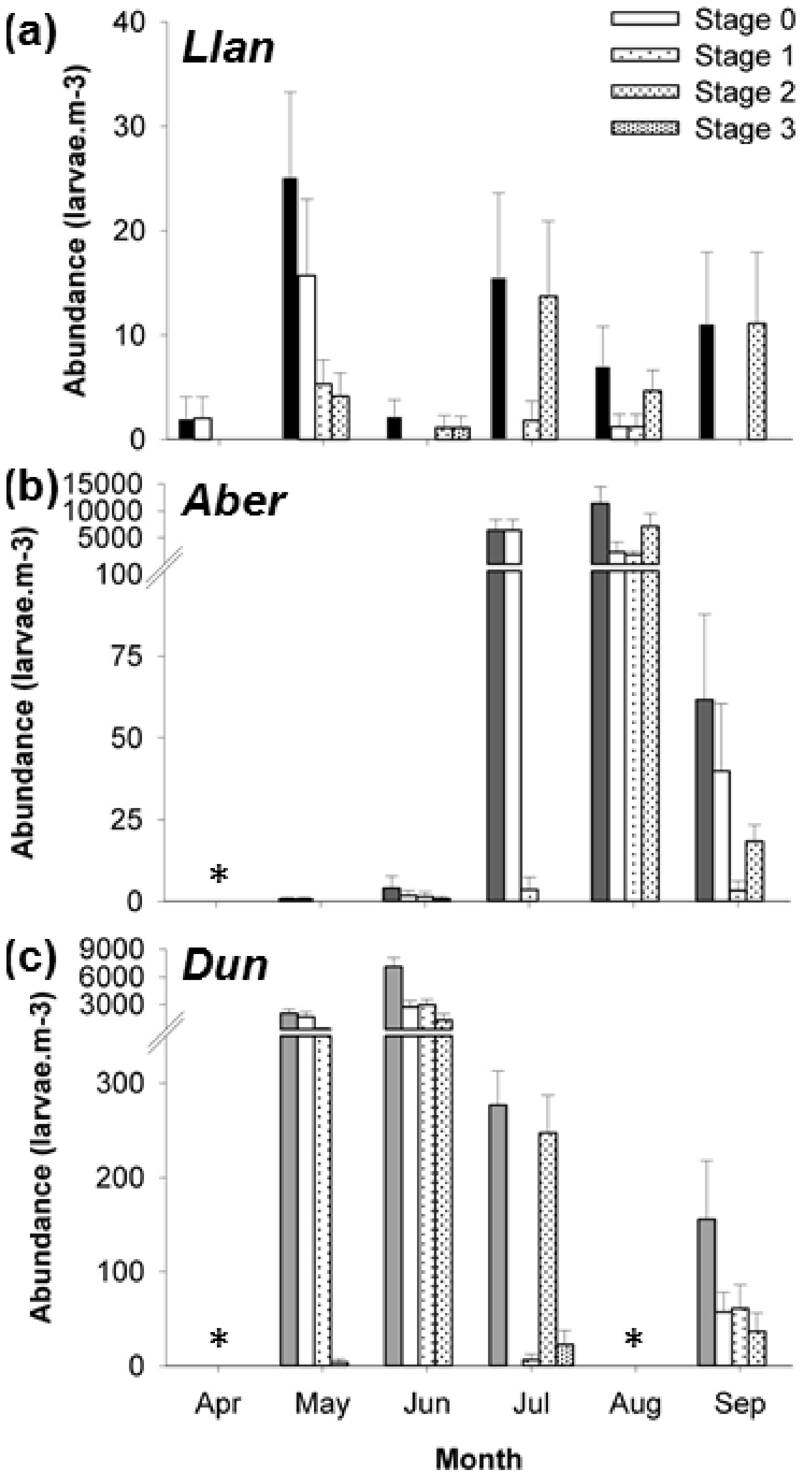


Figure 5.4: Mean abundance of *Sabellaria alveolata* larvae collected from twelve plankton tows offshore from the reef monthly at 3 sites. The overall proportion of larvae at each stage of development has also been depicted. Larval abundance is colour coded. Error bars represent 1 standard error. (a) Llanddulas, (b) Aberarth and (c) Dunraven. No sampling occurred in either Aberarth or Dunraven in April, or Dunraven in August (highlighted by *).

dependent. Despite the relatively low larval concentrations observed at *Llan* in all months (Figure 5.4 a), a significant temporal difference was demonstrated (e.g. a peak in larval concentration was demonstrated in May in comparison with all other months; KW, H= 11.20, df = 5, $P < 0.05$; Figure 5.4 a). Similarly significant differences in larval concentrations were demonstrated at both southern sites between months (KW, H≥ 38.08, df ≥ 3, $P < 0.01$), with a ≥2 month peak in total mean larval concentration observed (Figure 5.4 b, c). For example, at *Aber*, a larval bloom was observed from Jun – Aug in comparison with other months (Figure 5.4 b), whilst at *Dun*, a larval bloom was observed from May – Jun (Figure 5.4 c).

When larval stage was considered, significant differences in the overall concentration of S^1 to S^3 larvae were demonstrated with month (KW, H≥ 9.13, df = 3, P ≤ 0.03). Although no significant difference in the overall concentration of S^0 larvae was demonstrated between months, maximum S^0 concentrations were observed in Jul, a month prior to maximum concentrations of S^1 and S^2 larvae. S^3 larvae were only reported in Jul. When considered on a site specific basis, significant differences in the concentration of S^0 to S^1 larvae were demonstrated with month at *Llan*, of S^0 to S^2 larvae at *Aber*, and of S^0 to S^3 at *Dun* (KW, H ≥9.39, df ≥ 3, P ≤ 0.02). For example, at *Llan* S^0 and S^1 larvae were greater during the larval bloom in May than any other month (Figure 5.4 a). At *Aber* the vast majority of larvae recorded in Jul were S^0. By Aug, S^1 larvae were recorded in equivalent concentrations but S^2 larvae were in the majority, whilst in Sep S^0 were again the dominant developmental stage (Figure 5.4 b). At *Dun*, the majority of larvae recorded in May were S^0, with a relatively large concentration of S^1 larvae also present. By Jun the concentration of S^0 larvae had increased but S^1 larvae were present in similar concentrations, in addition to a smaller proportion of S^2 larvae. By Jul S^2 larvae dominated, although S^1 and S^3 larvae were also present. No S^0 larvae were present in Jul suggesting a progression of the main larval bloom through time. In Sep, some S^0 larvae were again detected suggesting secondary spawning had occurred (Figure 5.4 c).

5.4.4. Biophysical modelling of *Sabellaria alveolata* larvae – Passive particles

Simulated passive larvae were advected with tidal oscillations, and generally did not travel far from their natal reef (i.e. located within 150 km of their natal reef after a 60-day PLD; Figure 5.5 a, b; see Appendix 5.3 for additional simulations), despite larval mean oceanographic dispersal distance (LODD) of up to approximately 2500 km (Figure 5.6). In the majority of simulations most larvae cohorts remained close to one another throughout their 60-day PLD, as a singular patch or splitting to form two patches (bi-modal distribution). Bi-modal distribution usually resulted in one patch travelling a short distance, entrained in weak coastal currents, and another patch travelling offshore with larger LODD (e.g. sites 8, 17, 21 and 22; Figure 5.6; Appendix 5.4).

The LODD of cohorts in Cardigan Bay (i.e. Sites 11 – 16) were similar between sites, with patch-averaged LODD of between 600 and 800 km over their 60-day PLD (Figure 5.6), however within the British Isles, wide variation was suggested from hundreds or thousands of kilometres (Figure 5.6). For example, an LODD of approximately 200 km was simulated from Site 19 (i.e. Morecambe), but approximately 2500 km from Site 7 (i.e. *Dun*). Consistently, in all monthly release scenarios, simulated LODD was greatest from *Dun*. However, at this site, no significant residual current was encountered, and final stage larvae were similarly close to the release location as elsewhere (i.e. within 100 km from the release reef). Seasonal variability in LODD was suggested, with overall increases from May to Aug (Figure 5.7 a), but this was site specific. Simulated LODD from *Llan* in May was less than in Jun – Aug, whilst LODD from site 10 (i.e. Limeslade Bay) demonstrated a reverse pattern, greatest during May and lowest during Aug (Figure 5.5 a, b).

Larval connectivity between populations was only predicted between neighbouring reefs, less than 150 km apart (Figure 5.8 a). Subpopulations formed of several neighbouring populations were suggested, between which larvae may travel from the source reef and settle at other reefs, dependent on controls such as atmospheric conditions and larval release date. For example, *S. alveolata* reefs in Cardigan Bay formed a sub-population, isolated from all other modelled reefs following a 60-day

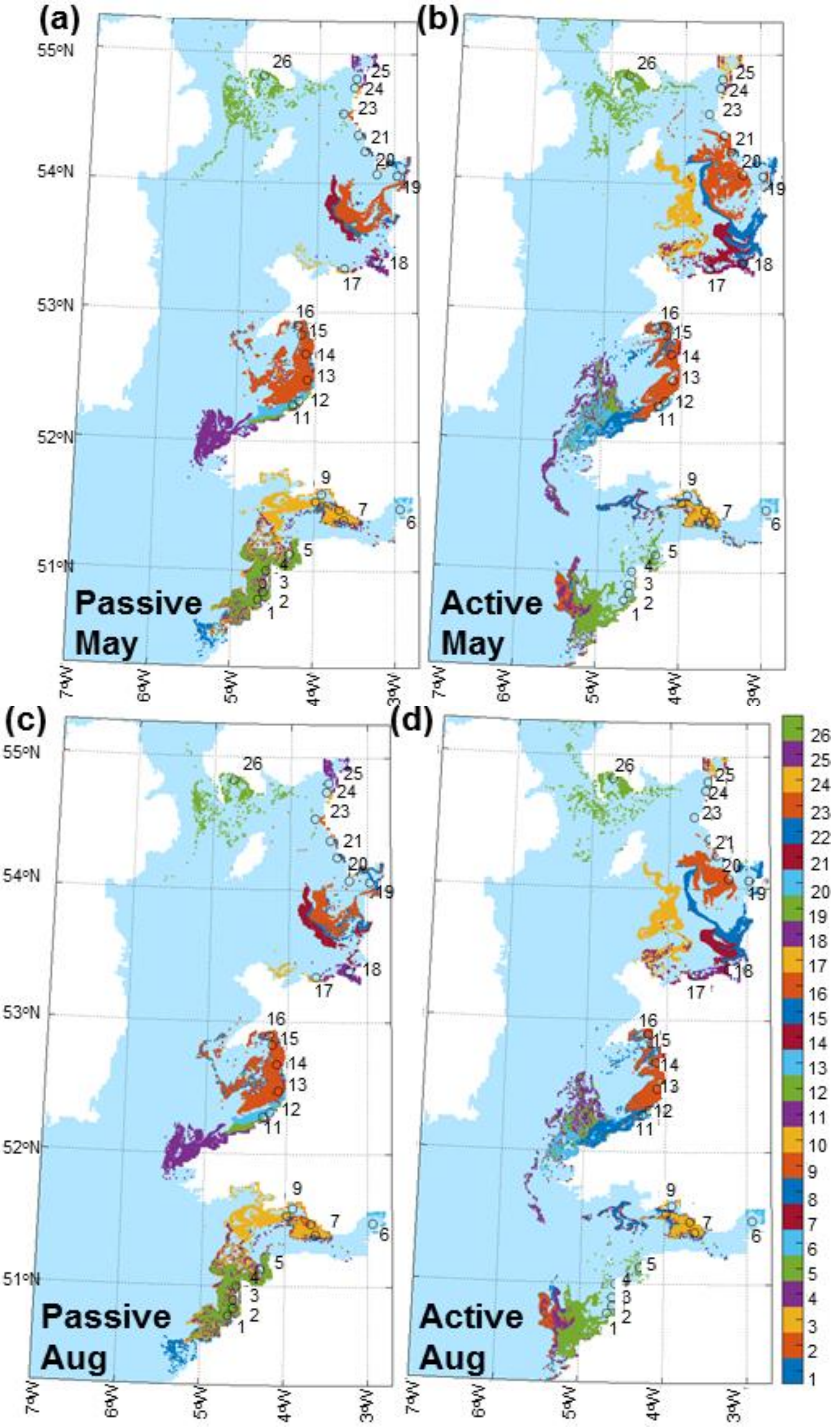


Figure 5.5: Particle Tracking Model (PTM) simulations of larval dispersal for *Sabellaria alveolata*, representing the potential dispersal of cohorts of larvae released ('spawned') from 26 selected reefs around the eastern Irish Sea. Each cohort of 10,000 particles is colour-coded to numbered release reef locations (○). Site 17 is Llanddulas (yellow), Site 11 is Aberarth (purple) and Site 7 is Dunraven (maroon). Each map depicts dispersal after a typical 60-day pelagic larval duration, for (a, b) passive particles, and (c, d) active particles. Monthly particle releases on: (a, c) 01 May, (b, d) 01 Aug.

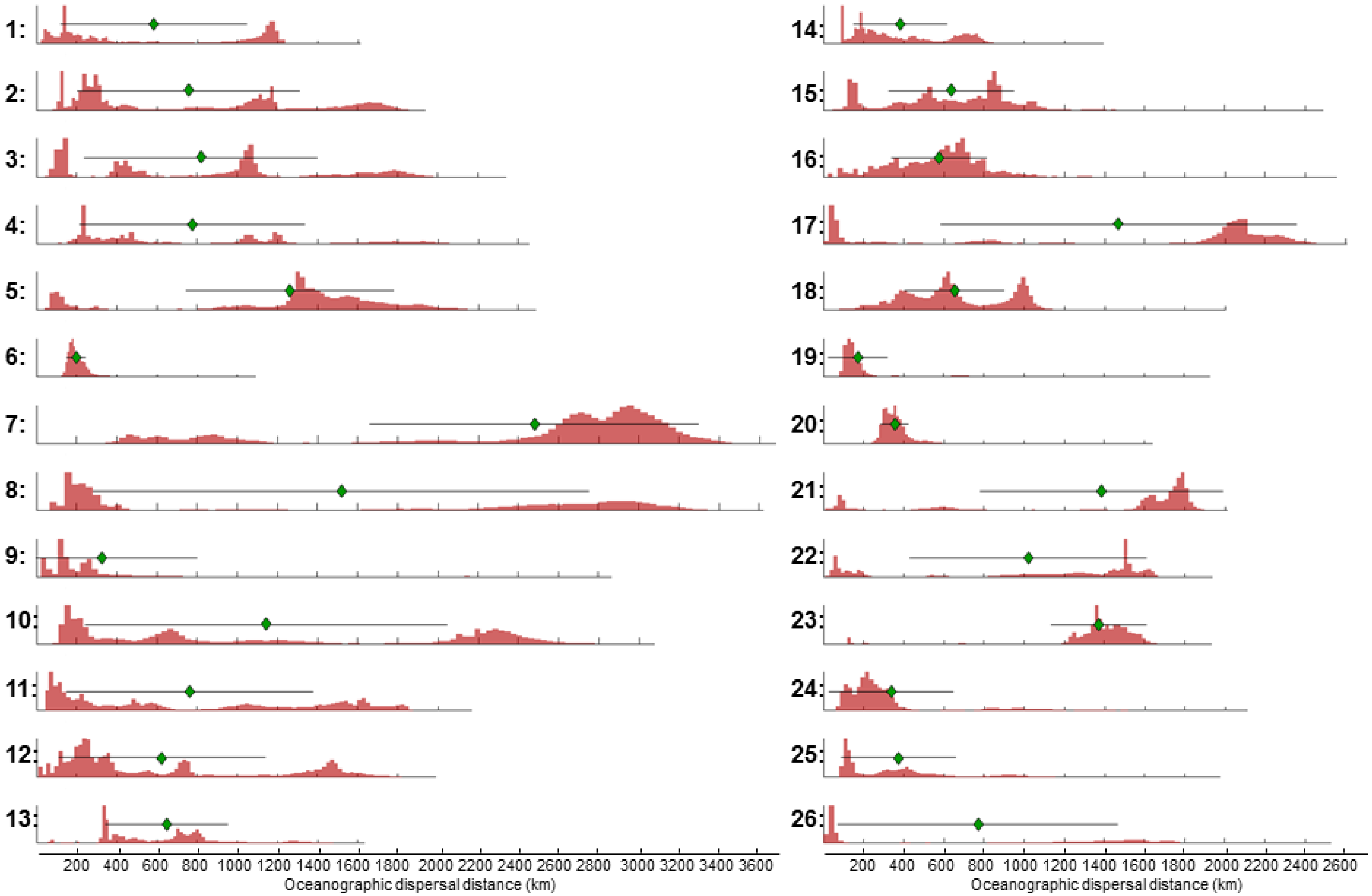


Figure 5.6: Histogram plots of oceanographic larval dispersal distance, for all passive particles, released for all release dates (oceanographic larval dispersal distances for active particles are displayed in Appendix 5.3). Each histogram shows the normalised distribution of oceanographic dispersal for 40,000 particles released from the numbered site. The patch-mean (green diamond) and standard deviation (black line) are also plotted.

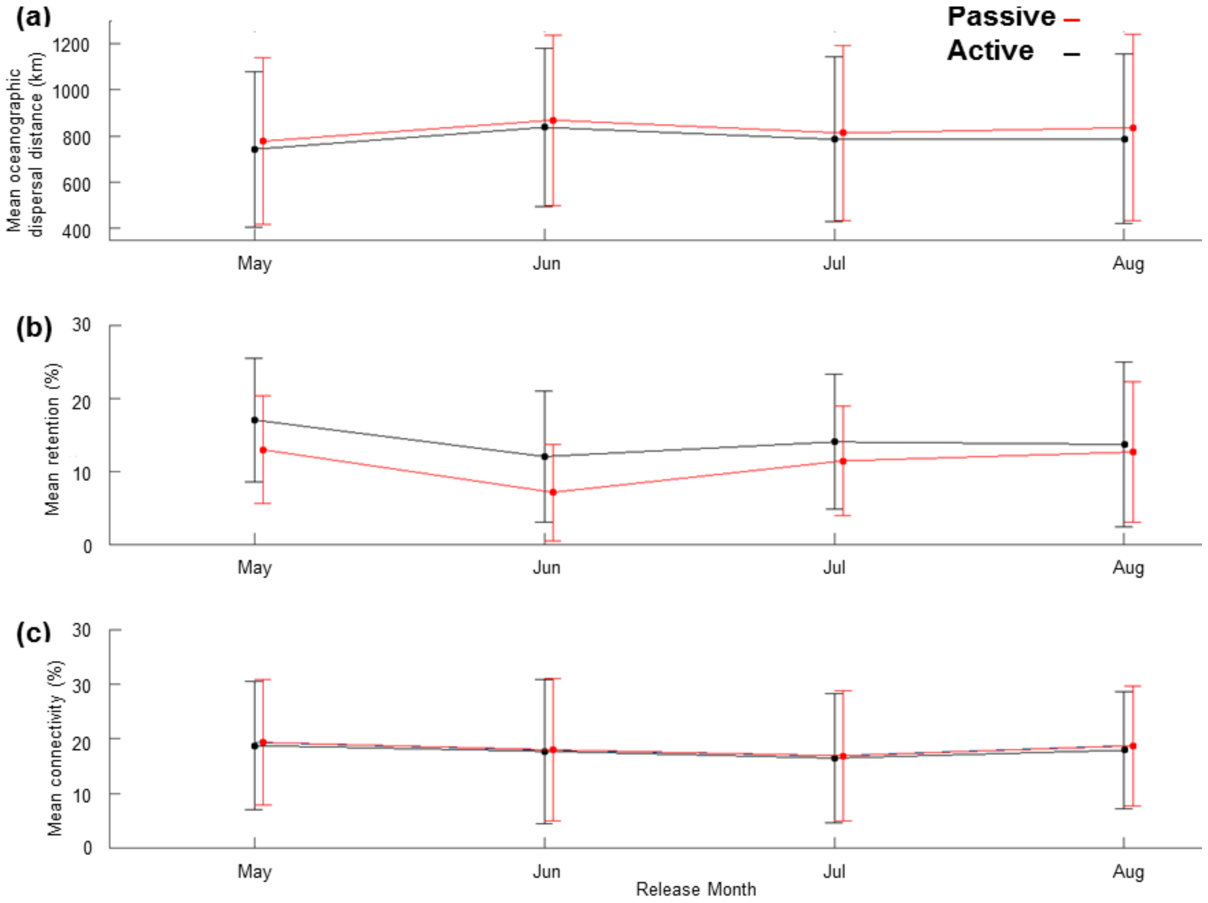


Figure 5.7: Predicted seasonal variability from simulated PTMs of both passive particles (red) and active particles (black), in terms of (a) mean oceanographic dispersal distance, (b) mean retention, and (c) mean connectivity. In all cases, each population cohort of 10,000 particles was averaged, and then the 26 population averages were averaged to give the overall ean. The error bars signify one standard deviation from the mean.

PLD (Figure 5.8 a), as did populations in north Wales, northwest England and Scotland (i.e. Sites 17 – 26). From Scotland to Cardigan Bay, larvae were predominantly dispersing from north to south, partially due to residual coastal currents that develops during summer months. It was also suggested that reefs in South Wales (i.e. Sites 7 – 10) formed a sub-population (Figure 5.8 a); although a low percentage of larvae dispersed south connecting with a subpopulation along the north coasts of Cornwall and Devon (i.e. Sites 1 – 5), indicating these sub-populations are not entirely distinct.

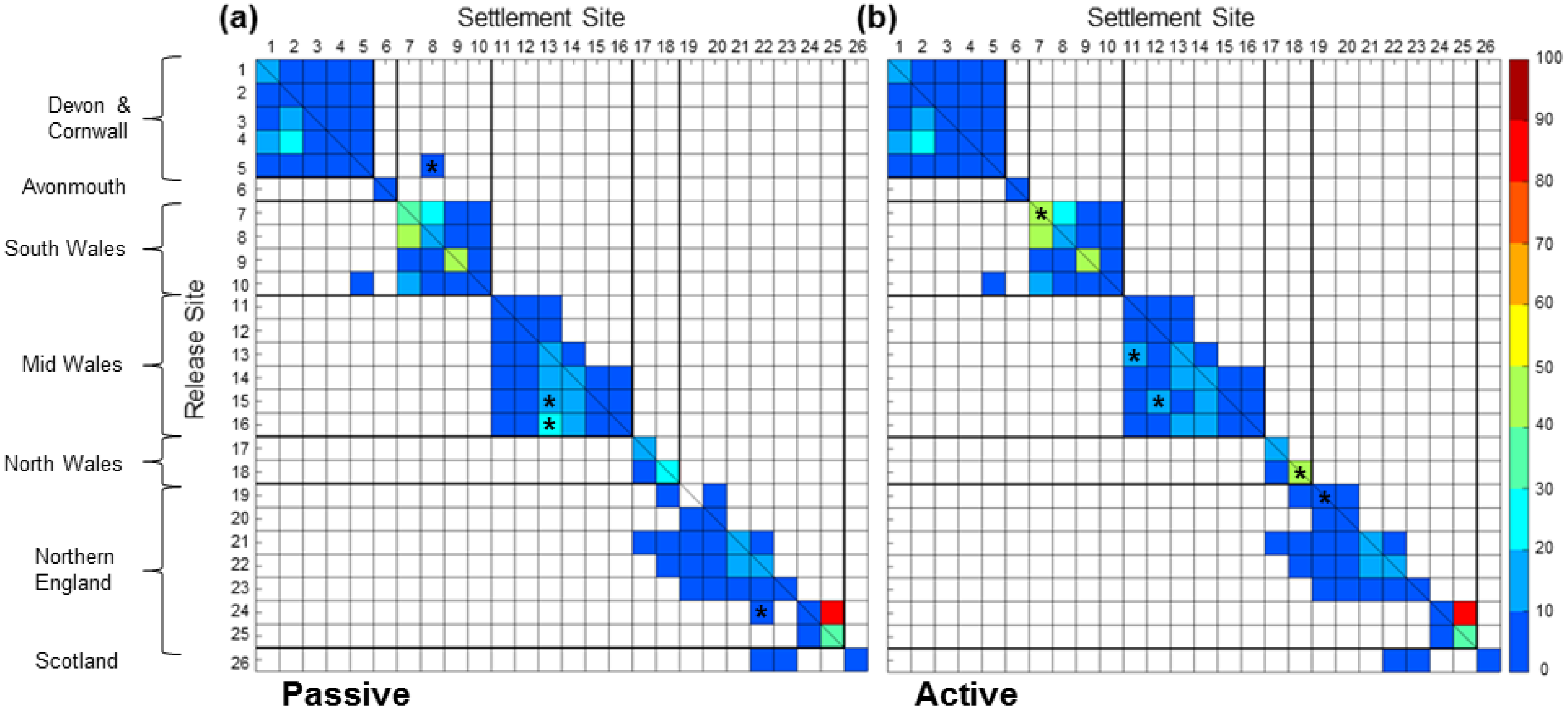


Figure 5.8: Connectivity matrices, depicting mean simulated predictions of larval retention and larval connectivity after a 60-day PLD. Larval retention is depicted in the diagonal cells with a diagonal black line through. Larval connectivity is depicted by the other cells. The colour scale signifies the percentage of retention or connectivity of the population at each settlement site, where white cells indicate no connectivity. (a) passive particles, (b) active particles. (* represent differences, where the simulated connectivity or self-recruitment is greater in the highlighted cell).

Little difference in connectivity was predicted with month of larval release (Figure 5.7 c). In most cases, there is some retention at each natal reef after a 60 – day PLD. Despite a short LODD, Morecambe is the exception, with no self-recruitment of passive larvae simulated in any month (Figure 5.8 a). Simulated larvae were transported north and east away from the source reef but retained within Morecambe Bay. In contrast, at *Dun*, despite a large LODD, due to the oscillatory nature of local tidal currents, approximately 35 % of larvae were present at the source site after 60-days, indicative of high self-recruitment. High self-recruitment was also observed at Sites 9, 18, and 25 (Figure 5.8 a). In all PTMs, self-recruitment only was suggested at site 6 (i.e. Avonmouth) within the Severn Estuary, and at site 26 (i.e. Auchenmalg Bay) in the far north of the range. A seasonal element existed to larval retention with a greater proportion of larvae released in May predicted to be retained near the source reef than in latter months (Figure 5.7 b).

5.4.5. Biophysical modelling of *Sabellaria alveolata* larvae – Diel vertical migration

Incorporation of vertical migratory behaviour into the PTM resulted in broadly similar monthly simulated larval dispersal patterns (Figure 5.5 c, d), and connectivity (Figure 5.7 c, 5.8) but reduced LODD from all natal reefs in all months (Figure 5.7 a; Appendix 5.4). For example, simulated LODD from *Dun* decreased by approximately 400 km (Figure 5.6; Appendix 5.4). Consequently, incorporation of vertical migratory behaviour increased larval retention and thus self-recruitment (Figure 5.7 b; 5.8). For example, whilst no self-recruitment was simulated in any month for passive particles from Morecambe, retention was simulated in Jun for active larvae. Similarly at *Dun*, retention was increased by approximately 5 % and at site 18 (i.e. Hilbre) retention was increased by more than 10 % (Figure 5.8). As with passive PTMS, active PTMs predicted that larval connectivity between populations was only possible between neighbouring reefs, and provided further evidence of the existence of subpopulations (Figure 5.7).

5.4.6. Validation of vertical *Sabellaria alveolata* larval migration with *in situ* observations

Little difference in phototactic larval concentration (i.e. larvae ≥ S^2) was demonstrated with depth at any site in any month, with the exception of *Aber* in Aug when a significantly greater mean concentration of S^2 larvae was demonstrated at 5 m depth than 1 m depth (KW, $H = 8.31$, $df = 1$, $P < 0.01$). In further support of laboratory findings, in Jun, at both *Aber* and *Llan*, phototactic larvae were only recorded from 5 m depth, and in both Aug and Sep, at *Llan*, more phototactic larvae were reported from 5 m depth than 1 m depth. However, little difference in phototactic larval concentration was observed with depth at *Llan* in May, any site in Jul, or *Aber* in Sep, and in contrast to laboratory findings at *Dun*, all phototactic larvae observed in May were at 1 m, and more phototactic larvae were reported from 1 m than 5 m in Jun and Sep.

5.4.7. Validation of horizontal *Sabellaria alveolata* larval dispersal with *in situ* observations

Monthly PTMs simulated larvae released at *Llan* predominantly moving offshore to the north and west (Figure 5.5 a, b), with limited self-recruitment (Figure 5.8 a). Minimal connectivity was suggested with larvae from sites to the north and west (i.e. Hilbre; and site 21, Annaside Bank). In support of this, observed larval concentration at *Llan* was minimal in all sampling months (Figure 5.4 a). When considered on a month by month basis, no significant differences in larval concentration (overall or stage dependent) were demonstrated with position along shore (i.e. to the east, middle or west of the reef), or distance offshore (i.e. 100 m or 1 km), with the exception of Jul when a significantly greater mean larval concentration of all larvae and S^2 was demonstrated 100 m offshore of the reef than 1 km offshore (KW, $H= 5.23$, $df = 1$, $P =0.02$). No significant differences were observed in earlier stage larvae. The PTMs simulated larvae being transported in cohorts, however the natal source of observed larvae is unknown. For example, larvae may have originated at *Llan* and been retained near source, or they may have originated in northern England, and *Llan* may be acting as a larval sink.

Within Cardigan Bay, PTMs simulated north to south larval transport, with larvae from *Aber* dispersed south around Pembrokeshire, but larvae from sites further north being present at *Aber* in all simulations (Figure 5.5 a, b; 5.8 a). In support of this, larvae, particularly S^0 larvae, were present at this site in all sampling months (Figure 5.4 b). Additionally, in Jul, a significant difference in the mean concentration of S^0 larvae was demonstrated with direction along the shore (KW, H = 6.5, df = 2, P = 0.04), with mean S^0 larval concentration to the north an order of magnitude greater than in the mid or south of the reef.

In south Wales, PTMs suggested a high larval retention at *Dun* after 60-day PLD, with connectivity with all other simulated sites in this region (Figure 5.8 a). In support of this, larvae were present in relatively high abundance in all sampling months (Figure 5.4), although the natal source of larvae cannot be determined. Larval transport oscillated to the west before returning east in all simulations, with some southern transport (Figure 5.5 a, b). In support of this, in both May and Jun, a significant difference in overall larval concentration was demonstrated with distance from the reef (KW, H $^{=}$ 4.33, df = 1, P = 0.04) with mean larval concentration greater at 1 km offshore. When stage was considered, a significant difference in the concentration of S^0 larvae was demonstrated in May, and in S^1 larvae in Jun, with distance from reef (KW, H $^{\geq}$ 5.77, df = 1, P ≤ 0.02).

5.5. Discussion

From a combination of long-term monitoring *in situ*, larval experiment *in vivo* and larval dispersal modelling, this study provides insights into larval dynamics and population connectivity of *Sabellaria alveolata* in the British Isles. Through long-term monitoring of both adult fecundity and larval concentrations, this study confirms the existence of semi-continuous and poorly seasonally synchronised spawning in an intertidal ecosystem engineer at the north of its range. Larval dispersal modelling of passive particles suggested that sub-populations of intertidal species may exist in British waters, with consistent connectivity between sites within sub-populations, but little to no connectivity out with distinct sub-populations. *In vivo* larval behaviour experiments provided evidence of the development of a negative phototactic larval response with age, and whilst inclusion of a diel vertical migration into the larval dispersal model had little impact on connectivity reinforcing the sub-population concept, such behaviour increased larval retention near source sites, acting as a mechanism for increased population self-recruitment, facilitating long-term persistence of natal sites.

5.5.1. Spawning strategy in *Sabellaria alveolata*

Semi-continuous, or trickle spawning is not uncommon in marine invertebrates (e.g. Seed & Brown, 1977; McQuaid & Phillips, 2006), and has been previously reported by *S. alveolata*. Ripe adults have been reported previously within populations at several sites, in many months of the year (e.g. Wilson, 1971; Gruet & Lassus, 1983; Culloty et al., 2010). Additionally, Wilson (1968a) observed larval settlement in most months of the year. Long term monitoring supports semi-continuous spawning as ripe individuals of both sexes were present at all sites throughout the sampling period, indicative that spawning was possible, and larvae were detected in the water column throughout the sampling period, with early stage recently spawned larvae present in the majority of months at all sites.

A summer synchronised spawning pattern has also been suggested. A peak in gametogenesis in summer months was reported by Culloty et al. (2010) in the Republic of Ireland, with some overlap between sexes, and Wilson (1971) reported a summer spawning event at Duckpool, North Cornwall. Similarly, this study demonstrated a summer peak in both gamete production and larval concentration; however both were poorly seasonally synchronised with differences between maximum gamete count in opposing sexes at some sites, and in both the timing and magnitude of gamete and larval concentrations between sites. For example, near the north of the range (e.g. at *Llan*), elevated egg and sperm counts were temporally correlated in early-summer over a period of 2 months, further south (e.g. at *Aber*) sperm counts peaked prior to egg counts, with a 1 month overlap in mid-summer. In contrast, in the south of the British Isles (e.g. at *Dun*) both sperm and egg counts were suppressed throughout the summer, with maximum sperm count in early-summer preceded maximum egg count in mid-summer with no temporal overlap.

A bimodal spawning pattern has also been reported at populations within the range, with the summer larval bloom followed by a secondary autumn bloom (Gruet & Lassus, 1983; Dubois et al., 2007). Similarly, at *Dun* an elevated egg count was suggested in spring and an elevated sperm count in autumn, indicative that peak fecundity may be bimodal in southern populations. Bimodal peak spawning was further supported by temporal distribution of early stage larvae at *Dun*, where despite high larval abundance, early stage larvae were absent in late-summer, but recorded both previously and subsequently, indicative of at least 2 larval cohorts. Consequently, it is suggested that, even within a small geographic area, different spawning strategies occur, with prolonged trickle spawning overlaid by short boom-bust spawning in summer, and potentially spring and autumn.

5.5.2. Parental contribution to larval dispersal and success

Marine invertebrates exhibit trade-offs, whereby they either produce many small eggs with high mortality or fewer, larger eggs that develop quickly, experience reduced planktonic mortality and are fertilised at a higher rate (Levitan, 1996). This trade-off pattern has been clearly demonstrated for *S. alveolata* populations as egg sizes decreased from spring to summer at all three sites, with a subsequent increase suggested to autumn. Larger eggs were recorded before and after the peak egg count, indicative that investment into individual eggs was lower in summer. What initiates change in gamete trade-off requires further analysis, and could include a variety of hydrodynamic and biological interactions (Levitan, 1996; Levin, 2006).

The differences in egg sizes and gamete concentrations between the three study sites also provides an insight to temporal and spatial larval dispersal and supply mechanisms as large eggs are associated with limited dispersal, potentially increasing the probability of self-recruitment (Levin, 2006). Consequently, self-recruitment was promoted at all sites in colder months, whilst larvae were dispersed further afield in warmer summer months. Near the north of the range (e.g. at *Llan*), an excessive investment in gamete quantity and quality was observed in summer as peak gamete concentrations occurred prior to minimum egg size. This may facilitate self-recruitment, essential for the long-term persistence of a relatively isolated population. Summer egg size was predominantly greater in the southern population, where egg counts were relatively suppressed in comparison with northern sites, again potentially facilitating self-recruitment. Recent research has shown larval retention is more frequent in natural habitats than previously thought (Swearer et al., 2002; Sponaugle et al., 2002; Levin, 2006).

5.5.3. Larval behaviour

Settlement success is known to be highly variable year on year (Ayata et al., 2009, Bush & Davies, Chapter 4), and larval behaviour may contribute to dispersal and thus settlement success (McCarthy et al., 2002; Abdul Wahab et al., 2014). Although no phototactic response was demonstrated in early stage *S. alveolata* larvae (i.e. those without eyespots), latter stage larvae were negatively phototactic. The ability of larvae to develop alternative responses to light has been observed in other Sabellariids. For example, *Phragmatopoma lapidosa* larvae develop photonegative response with age (McCarthy et al., 2002). Within this study *S. alveolata* larvae were observed to actively move against natural forces (e.g. gravity) for light evasion. Swimming speed also increased significantly with developmental stage, and thus the ability of larvae to avoid light. An elevated concentration of many species of polychaete larvae with depth has been reported (Lagadeuc, 1992; Theibaut et al., 1992), with some physically separated by developmental stage (Lagadeuc, 1992; Carlotti, 1996), and it is theorised that latter stage *S. alveolata* larvae will descend in the water column during daylight hours, physically migrating away from light. Such negative phototaxis has been reported to reduce the risk of predation to larvae and damage by UV (McCarthy et al., 2002), increase the probability of encounter with a suitable substrata (Thorson, 1964), and potentially increase larval retention near natal site (Thiebaut et al., 1998; Garland et al., 2002; Knights, 2006; Dubois et al., 2007).

Dubois et al. (2007) also reported vertical migration of *S. alveolata* larvae in a 24 hour observation *in situ*, but in response to tide, and specified that there was no difference in vertical distribution between day and night samples, rather larvae migrate towards the surface on the flood tide, aggregate close to the surface at high tide, and then migrate down in the water column on the ebb tide, and aggregate at depth at low tide. Differences between the concentrations of latter stage larvae with depth in field observations were generally inconclusive, although an increase was demonstrated at *Aber* in Aug, and suggested elsewhere. Final stage larvae (i.e. erpochetes) were observed to settle out of the water column *in vivo* and actively search for suitable settlement, and thus may have been so closely associated with the bottom *in situ* that they were not sampled (Crimaldi et al., 2002). However, light may not be as influential in the highly turbid natural environment as it is under laboratory conditions, and the existence and extent of a vertical migration, and the dominant drivers of this change, must be investigated further.

5.5.4. Predicted dispersal of *Sabellaria alveolata* larvae

Simulated passive *S. alveolata* larvae do not travel far from their natal sites, with larval cohorts remaining within 150 km of their source after 60 days. Consequently, each larval cohort has the potential to settle at either their natal reef (larval retention) or at a close-by neighbouring reef (connectivity), whilst far-field and across-shelf connectivity is unlikely. The relatively low dispersal distances (compared with similar studies; e.g. Coscia et al., 2013; Robins et al., 2013) are partially due to natal reefs being located in more sheltered regions of coasts, rather than headlands exposed to stronger tidal currents and frontal circulation. Predicted larval dispersal (LODD and distance from source reef) demonstrated variation between sites, and within sites through time, with LODD varying by an order of magnitude between sites, and both LODD and distance from source site predicted to have been less in May than in Jun – Aug 2014 at some sites (e.g. all monitored sites), but greater at others (e.g. Limeslade Bay). Larval cohorts were generally predicted to remain in relatively close proximity to each other, or to split bimodally with some retained near source in weak coastal currents and some dispersed further afield in oceanic currents.

In most cases, there is some retention at natal reef after 60 days, and thus some self-recruitment (with the exception of within Morecambe Bay for passive particles). Generally less than 10 % of the larvae released were predicted to be retained with the exceptions of both Dunraven and Swansea Bay in South Wales, and Dubmill Point in northwest England, where at least 30 % of larvae released were predicted to be retained, due to the oscillatory nature of local tidal currents. It is suggested that several neighbouring *S. alveolata* reef populations may function as a sub-population, with larvae from one source reef settling at any other reef within the sub-population. For example, within Devon and Cornwall, larvae released from any known reef site may settle out at any other; within Mid Wales, larvae from Barmouth Bay to Criccieth may settle out at any known reef population within the region; whilst in the central Irish Sea, larvae from reef sites within Cumbria may settle out as far south as North Wales. Isolation of distinct sub-populations is partially due to relatively large geographic separation, barriers in advection (e.g. residual currents), or geographic barriers (e.g. the Llŷn Peninsula).

Knights et al. (2006) highlighted the importance of characterising larval behavioural traits (e.g. vertical migration in response to light), and noted that where such traits occur, the passive behaviour assumption may result in only a partial prediction of actual population distribution. Within the Irish Sea region, Robins et al. (2013) reported that behavioural traits were equally as influential on larval transport patterns as hydrodynamics, however incorporation of active larval vertical migration, as observed in the laboratory, decreased predicted LODD, and increased larval retention but had little impact on connectivity. By the onset of negative phototaxis (i.e. day 15), larvae were already entrained in either oceanic or coastal currents, and the inclusion of vertical migration to depth had no substantial effect beyond highlighting the existence of distinct sub-populations of *S. alveolata* on the west coast of the British Isles.

Within each sub-population, *S. alveolata* populations may act as larval source sites for several others, potentially buffering local-scale impacts, however this buffering capacity is predominantly from north to south. Following the extremely cold winter of 1962, mass mortality of many British *S. alveolata* populations was reported (Crisp, 1964, Cunningham et al., 1984), with extirpations reported throughout north Wales and the Wirral. Recolonisations within the region were not reported until the early 2000s, when Abundant reef was reported from Hilbre Island (Frost et al., 2004), followed by *Llan* in the late 2000s (Firth et al., 2015). The slow recolonisation of this area is predicted to be the result of low larval connectivity with other sites within this sub-population. It is theorised that larvae originating from persistent populations within Cumbria were responsible for the recolonisation of Hilbre. The stepwise progression of colonisation from north to south to west suggests that, despite the prediction that larvae from Cumbria can reach *Llan* (under certain hydrodynamics and meteorological conditions), larvae from Hilbre were predominantly responsible for the colonisation of *Llan*. The westward spread of larvae from Hilbre is also predicted to sustain encrusting populations that have been more recently reported in north Wales, predominantly on sea defence structures (Firth et al., 2015). It is predicted that *Llan* can act as a source site for transient low abundance populations further west in mainland north Wales and Anglesey, dependent of the timing of larval release in relation to hydrodynamics and weather conditions. Following (re)colonisation, larval recruitment to both *Llan* and Hilbre is predicted to be predominantly through larval retention.

5.5.5. Model assumptions

There are several significant assumptions to the biophysical modelling methodology, which must be considered. Larval dispersal from 26 known *S. alveolata* populations within the eastern Irish Sea was simulated. However, populations that may exist elsewhere were not considered. It is possible that larvae from further afield (e.g. Ireland, the English Channel or France) could contribute to the Irish Sea metapopulation. However, modelling results of this study suggest that outlying populations would only connect with eastern Irish Sea populations if PLD were longer than the 60 days simulated, or when meteorological conditions are atypical to those modelled. The impact of additional, potentially persistent, populations of low abundance has not been considered, thus connectivity may be greater than predicted.

The spawning season and patterns of *S. alveolata* larvae appear to vary considerably. There are reports of spawning from spring (e.g. Gruet and Lassus 1983) through summer (e.g. Wilson. 1971) to autumn (e.g. Dubois et al., 2007). Spawning has been reported in batches, or semi-continuously (Dubois et al., 2007). However, this study only considered batch-spawning during the most common spawning period, as was observed in the larval monitoring surveys. With this in mind, future studies may wish to simulate *S. alveolata* larval dispersal throughout the year, and inter-annually, to fully appreciate the potential inter-seasonal and inter-annual variability in dispersal and connectivity. Indeed, several observational studies note high inter-annual variability in recruitment success (Wilson 1971; Gruet 1986).

A 60-day PLD was simulated here, as *S. alveolata* were observed to develop to settlement stage within one month in the laboratory but are known to have the ability to delay metamorphosis to benthic juveniles if suitable settlement condition are unavailable (Wilson, 1968 b). Whist Dubois et al. (2007) reported settlement within 1 – 2.5 months in summer months, Cazaux (1970) observed PLDs of up to 3 months in winter. In circumstances of delayed metamorphosis, this study would underestimate potential dispersal distances and levels of connectivity. In contrast, this study did not consider all sources of larval mortality, with the only source considered a lack of settlement at reef habitats. Larval mortality is reportedly high in another tube building polychaete, *Pectinaria koreni* (Ellien et al., 2004). *Mytilus edulis* are capable of significantly preying upon polychaete larvae (Davenport et al., 2000; Lehane & Davenport, 2006; Dubois et al., 2007) and are often found in association with *S. alveolata* reefs (Cunningham et al., 1984; Bush et al., Chapter 3), thus it is reasonable to assume larval mortality will be high in *S. alveolata* larvae. This is a common modelling approach (e.g. North et al., 2008; Ayata et al., 2010; Sundelöf & Jonsson, 2012) and allows us to examine how dispersion alone can lead to connectivity, rather than other factors such as predation and food limitation. However, as larval behavioural characteristics, PLD of *S. alveolata* and *in situ* mortality become more understood, it is important that these are incorporated into particle tracking algorithms.

5.6. Conclusions

By incorporating traditional approaches such as long-term monitoring of both the adult and larval populations *in situ*, and laboratory experiments with passive and active larval dispersal modelling, this study has facilitated an increased understanding of the ecology, dispersal and connectivity of an intertidal reef-forming species. On the west cost of the British Isles, semi-continuous spawning of *S. alveolata* was observed, overlaid with summer peaks in both gamete and larval concentration at all sites, and a secondary autumn peak in southern populations. The timing and duration of summer peaks was not consistent between sites (or, in the case of gametes, between sexes within sites) indicative that spawning is poorly seasonally synchronised. Gamete counts were suppressed in adults from southern populations where egg size was elevated relative to northern populations providing further evidence that different reproductive strategies occur within a relatively small geographic region.

Within the laboratory *S. alveolata* larvae develop a negative phototactic response with age, in addition to increased swimming speeds, potentially resulting in diel vertical migration in latter stage larvae. An alternative vertical migration driven by tide has also been suggested (Dubois et al., 2007). However, the existence of a vertical migration was not consistently confirmed or disproved at any site. Behaviours observed in the laboratory, or at a single location may not be consistent in all natural populations, and additional holistic studies are required in the future to establish if a vertical migration indeed exists in the highly turbid natural environment and the extent to which this is driven by light and tide.

The long-term persistence and resilience of a marine species is partially dependent on successful larval recruitment (either by retention at the natal population or connectivity with another population). Larval dispersal modelling of both passive and active larvae suggested that distinct sub-populations of intertidal species (particularly those of sheltered coats) exist within the Irish Sea, separated by geographic and advection barriers (e.g. Scotland to north Wales, mid Wales, and south Wales to southwest England). Strong inter-connectivity within these sub-populations was predicted by pelagic larvae, dependent on hydrodynamics and seasonal variability in meteorological events. Inclusion of assumed behaviour in larval dispersal modelling can over- or under-estimate LODD, and dispersal from source (Knight et al., 2006). In the case of intertidal reef-forming populations of sheltered to moderately exposed coasts, the inclusion of diel vertical migration in latter stage larvae only, has little impact on overall population connectivity, although such behaviour is predicted to elevate larval retention, self-recruitment and thus promote population persistence through time, similar to the selective tidal transport suggested by Dubois et al (2007).

5.7. Acknowledgements

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5.8. Appendices

Appendix 5.1.1: Dates of plankton tow surveys at all three sites.

Month	**Llanddulas**	**Aberarth**	**Dunraven**
April	30/04/2014	na	na
May	19/05/2014	28/05/2014	28/05/2014
June	01/07/2014	18/06/2014	26/06/2014
July	22/07/2014	11/07/2014	10/07/2014
August	07/08/2014	14/08/2014	na
September	16/09/2014	23/09/2014	22/09/2014

Appendix 5.1.2: Dates of fecundity surveys at all three sites.

Month	**Llanddulas**	**Aberarth**	**Dunraven**
February	24/02/2014	17/02/2014	18/02/2014
March	27/03/2014	19/03/2014	20/03/2014
April	24/04/2014	22/04/2014	23/04/2014
May	12/05/2014	28/05/2014	29/05/2014
June	16/06/2014	11/06/2014	12/06/2014
July	28/07/2014	17/07/2014	15/07/2014
August	25/08/2014	27/08/2014	26/08/2014
September	13/09/2014	12/09/2014	12/09/2014

Appendix 5.2.1: Temporal change in egg size. Differences analysed with Kruskal-Wallis rank sum tests (df = 1). Significant differences (p-value < 0.05) are colour coded. Decreases in egg size through time are highlighted in blue (e.g. at *Llan*, egg size in Feb was greater than in Apr-Sept). Increases, and months where egg size at the northern site was less than the southern site are highlighted in red (e.g. Egg size at *Llan* was less in April than *Aber* or *Dun*).

Site	Month	Mar	Apr	May	Jun	Jul	Aug	Sep	Aber	Dun
Llan	Feb	H = 0.01, P= 0.92	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 3.15, P= 0.08	H = 0.88, P= 0.35
	Mar		H = 6.86, P = 0.01	H = 4.84, P = 0.03	H = 6.86, P = 0.01	H = 6.86, P = 0.01	H = 6.86, P = 0.01	H = 6.86, P = 0.01	H = 1.33, P= 0.25	H = 0.54, P= 0.46
	Apr			H = 0.54, P= 0.47	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 2.46, P= 0.12	H = 6.82, P = 0.01
	May				H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 0.88, P= 0.35
	Jun					H = 0.10, P= 0.75	H = 6.82, P = 0.01	H = 1.84, P= 0.18	H = 5.77, P= 0.02	H = 3.94, P= 0.05
	Jul						H = 3.93, P= 0.05	H = 0.88, P= 0.35	H = 1.32, P= 0.25	H = 0.01, P= 0.92
	Aug							H = 1.32, P= 0.25	H = 3.15, P= 0.08	H = 6.82, P = 0.01
	Sep								H = 2.46, P= 0.12	H = 6.82, P = 0.01
Aber	Feb	H = 6.82, P = 0.01	H = 3.15, P= 0.08	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01		H = 3.94, P = 0.05
	Mar		H = 0.10, P = 0.75	H = 0.27, P = 0.60	H = 3.94, P= 0.05	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01		H = 0.01, P= 0.92
	Apr			H = 1.84, P = 0.18	H = 3.94, P= 0.05	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 5.77, P= 0.02		H = 1.32, P= 0.25
	May				H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01		H = 1.84, P = 0.18
	Jun					H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 4.81, P= 0.03		H = 0.88, P= 0.35
	Jul						H = 0.54, P= 0.47	H = 4.81, P= 0.03		H = 1.84, P = 0.18
	Aug							H = 1.84, P= 0.18		H = 6.82, P = 0.01
	Sep									H = 3.15, P= 0.08
Dun	Feb	H = 0.27, P= 0.60	H = 0.10, P = 0.75	H = 0.54, P= 0.47	H = 4.82, P= 0.03	H = 5.77, P= 0.02	H = 6.82, P = 0.01	H = 3.15, P= 0.08		
	Mar		H = 0.01, P = 0.92	H = 0.27, P= 0.60	H = 5.77, P= 0.02	H = 5.77, P= 0.02	H = 6.82, P = 0.01	H = 5.77, P= 0.02		
	Apr			H = 0.88, P= 0.35	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 5.77, P= 0.02		
	May				H = 4.82, P= 0.03	H = 4.82, P= 0.03	H = 6.82, P = 0.01	H = 3.94, P = 0.05		
	Jun					H = 1.32, P= 0.25	H = 3.94, P = 0.05	H = 0.01, P = 0.92		
	Jul						H = 0.27, P = 0.60	H = 1.84, P= 0.18		
	Aug							H = 3.94, P = 0.05		

Appendix 5.2.2: Temporal change in egg count. Differences analysed with Kruskal-Wallis rank sum tests (df = 1). Significant differences (p-value < 0.05) are colour coded. Increases in count through time are highlighted in red (e.g. at *Llan*, egg count in Feb was less than Apr-Sept), and decreases in blue. Months where egg count at the northern site was greater than at the southern site are highlighted in blue (e.g. Egg count at *Llan* was greater in Apr than *Aber* or *Dun*), and less than southern sites in red.

Site	Month	Mar	Apr	May	Jun	Jul	Aug	Sep	Aber	Dun
Llan	Feb	H = 2.81, P = 0.09	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 0.01, P = 0.92	H= 0.27, P = 0.60	H = 0.28, P = 0.60	H = 1.58, P = 0.21
	Mar		H= 3.15, P = 0.08	H = 6.82, P = 0.01	H= 3.57, P = 0.06	H= 0.40, P = 0.53	H= 3.94, P = 0.05	H= 2.46, P = 0.12	H = 2.52, P = 0.11	H = 1.10, P = 0.29
	Apr			H = 6.82, P = 0.01	H = 2.46, P = 0.12	H = 4.81, P = 0.03	H = 6.82, P = 0.01	H = 4.81, P = 0.03	H = 5.91, P = 0.02	H = 6.86, P = 0.01
	May				H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01
	Jun					H = 4.81, P = 0.03	H = 6.82, P = 0.01	H= 5.77, P =0.02	H = 0.54, P = 0.47	H = 6.82, P = 0.01
	Jul						H= 2.81, P = 0.09	H= 1.32, P = 0.25	H = 6.82, P = 0.01	H = 0.54, P = 0.46
	Aug							H= 0.04, P = 0.83	H = 6.86, P = 0.01	H = 2.90, P = 0.09
	Sep								H = 6.90, P = 0.01	H = 1.36, P = 0.24
Aber	Feb	H = 6.90, P = 0.01	H = 0.29, P = 0.59	H = 4.84, P = 0.03	H = 6.86, P= 0.01	H = 6.86, P= 0.01	H = 6.86, P= 0.01	H = 6.94, P= 0.01		H = 1.34, P = 0.25
	Mar		H = 5.95, P= 0.02	H = 0, P= 1	H = 1.33, P= 0.25	H = 4.84, P= 0.03	H = 0.91, P= 0.34	H = 0.01, P = 0.91		H = 3.99, P = 0.05
	Apr			H = 4.93, P = 0.03	H = 6.99, P= 0.01	H = 6.988, P= 0.008	H = 7.03, P= 0.01	H = 7.08, P= 0.01		H = 0.91, P = 0.34
	May				H = 0.10, P= 0.75	H = 3.94, P = 0.05	H = 0.04, P= 0.83	H = 0.28, P = 0.60		H = 6.82, P = 0.01
	Jun					H = 1.84, P= 0.18	H = 0.27, P= 0.60	H = 2.49, P = 0.12		H = 6.82, P = 0.01
	Jul						H = 3.96, P= 0.05	H = 6.90, P= 0.01		H = 6.86, P = 0.01
	Aug							H = 0.57, P = 0.45		H = 6.94, P = 0.01
	Sep									H = 7.12, P = 0.01
Dun	Feb	H = 0.27, P= 0.60	H = 3.58, P= 0.06	H = 4.39, P= 0.04	H = 4.81, P= 0.03	H = 0.89, P= 0.35	H = 6.90, P= 0.01	H= 7.03, P = 0.01		
	Mar		H = 5.95, P= 0.02	H = 6.86, P= 0.02	H = 6.86., P= 0.01	H = 0.89, P= 0.34	H = 6.94, P= 0.01	H= 7.08, P = 0.01		
	Apr			H = 0.05, P= 0.83	H = 0, P= 1	H = 5.84, P= 0.02	H= 0.30, P = 0.59	H= 0.05, P = 0.83		
	May				H = 0.28, P= 0.60	H = 6.86, P= 0.01	H = 3.25, P= 0.07	H = 2.53, P= 0.11		
	Jun					H = 6.86, P= 0.01	H = 1.66, P= 0.20	H = 0.43, P= 0.51		
	Jul						H= 6.94, P = 0.01	H= 7.08, P = 0.01		
	Aug							H= 1.56, P = 0.21		

Appendix 5.2.3: Temporal change in egg count normalised by weight. Differences analysed with Kruskal-Wallis rank sum tests (df = 1). Significant differences (p-value < 0.05) are colour coded. Site specific decreases in egg count through time are highlighted in red (e.g. at *Llan*, egg count in Feb was less than in May-Jun), and increases in blue. Months where egg count at the northern sites was less than at the southern site are highlighted in red (e.g. Egg size at *Aber* was less in Feb than *Dun*), and greater than southern sites in blue.

Site	Month	Mar	Apr	May	Jun	Jul	Aug	Sep	Aber	Dun
Llan	Feb	H = 2.46, P= 0.12	H = 2.81, P= 0.09	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 3.15, P= 0.08	H = 0.10, P = 0.75	H = 0.10, P = 0.75	H = 1.32, P= 0.25	H = 1.58, P= 0.21
	Mar		H = 0.044, P= 0.834	H = 5.771, P= 0.016	H = 6.82, P = 0.01	H = 0.54, P= 0.47	H = 2.15, P= 0.14	H = 0.88, P= 0.35	H = 0.10, P= 0.75	H = 0.27, P= 0.60
	Apr			H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 0.88, P= 0.35	H = 2.81, P= 0.09	H = 0.88, P= 0.35	H = 0.10, P= 0.75	H = 1.84, P= 0.18
	May				H = 0.88, P= 0.35	H = 5.77, P= 0.02	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 2.46, P= 0.12	H = 6.82, P = 0.01
	Jun					H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 0.10, P= 0.75	H = 6.82, P = 0.01
	Jul						H = 3.15, P= 0.08	H = 3.15, P= 0.08	H = 6.82, P = 0.01	H = 0.27, P= 0.60
	Aug							H = 0.01, P= 0.92	H = 6.86, P= 0.01	H = 0.71, P= 0.40
	Sep								H = 5.77, P= 0.02	H = 0.28, P= 0.60
Aber	Feb	H = 5.81, P= 0.02	H = 4.81, P= 0.03	H = 2.45, P= 0.12	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 6.86, P= 0.01	H = 6.82, P = 0.01		H = 4.39, P= 0.04
	Mar		H = 0.27, P= 0.60	H = 0.54, P= 0.46	H = 5.81, P= 0.02	H = 6.86, P= 0.01	H = 4.87, P= 0.03	H = 4.81, P= 0.03		H = 0.27, P= 0.60
	Apr			H = 3.96, P= 0.05	H = 6.82, P = 0.01	H = 6.82, P = 0.01	H = 4.81, P= 0.03	H = 4.81, P= 0.03		H = 0.88, P= 0.35
	May				H = 3.94, P= 0.05	H = 6.82, P = 0.01	H = 2.47, P= 0.12	H = 1.32, P= 0.25		H = 1.85, P= 0.18
	Jun					H = 4.81, P= 0.03	H = 0.27, P= 0.60	H = 1.32, P= 0.25		H = 6.82, P = 0.01
	Jul						H = 3.17, P= 0.07	H = 4.81, P= 0.03		H = 6.82, P = 0.01
	Aug							H = 0.28, P = 0.60		H = 6.90, P= 0.01
	Sep									H = 6.82, P = 0.01
Dun	Feb	H = 0.27, P= 0.60	H = 0.40, P= 0.53	H = 1.84, P= 0.18	H = 5.31, P= 0.02	H = 0.54, P= 0.47	H = 6.86, P= 0.01	H = 6.32, P= 0.01		
	Mar		H = 1.10, P= 0.30	H = 2.81, P= 0.09	H = 6.82, P = 0.01	H = 0.54, P= 0.47	H = 6.86, P= 0.01	H = 6.82, P = 0.01		
	Apr			H = 0.40, P= 0.53	H = 2.15, P= 0.14	H = 2.46, P= 0.12	H = 1.89, P= 0.17	H = 2.46, P= 0.12		
	May				H = 0.88, P= 0.35	H = 3.15, P= 0.08	H = 1.35, P= 0.25	H = 2.46, P= 0.12		
	Jun					H = 5.77, P= 0.02	H = 0.04, P= 0.83	H = 0.18, P= 0.68		
	Jul						H = 6.86, P= 0.01	H = 6.82, P = 0.01		
	Aug							H = 0.71, P= 0.40		

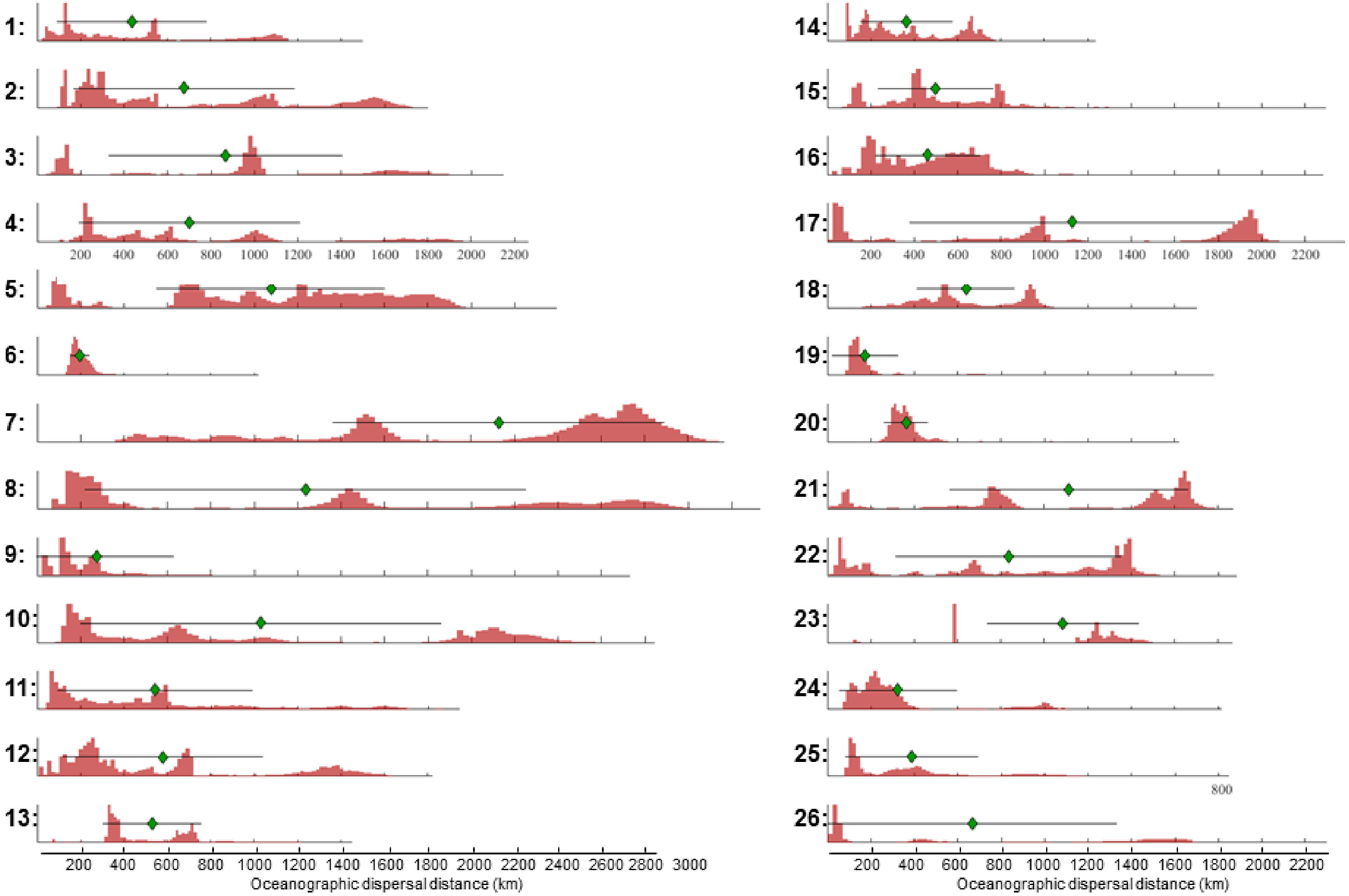
Appendix 5.2.4: Temporal change in sperm count. Differences analysed with Kruskal-Wallis rank sum tests (df = 1). Significant differences (p-value < 0.05) are colour coded. Site specific increases in sperm count through time are highlighted in red (e.g. at *Llan*, sperm count in Feb was less than in Mar-Jul), and decreases in blue. Months where sperm at the northern sites was less than at the southern site are highlighted in red (e.g. Egg size at *Aber* was less in Sept than *Dun*), and greater in blue.

Site	Month	Mar	Apr	May	Jun	Jul	Aug	Sep	Aber	Dun
Llan	Feb	🟥 H = 6.82, P = 0.01	🟥 H = 6.82, P = 0.01	🟥 H = 6.82, P = 0.01	🟥 H = 6.82, P = 0.01	🟥 H = 6.82, P = 0.01	H = 0.88, P= 0.35	H = 0.54, P= 0.47	H = 2.46, P= 0.12	H = 0.27, P= 0.60
	Mar	▨	H = 3.15, P= 0.08	🟥 H = 4.811, P = 0.028	🟥 H = 6.82, P = 0.01	🟥 H = 6.82, P = 0.01	H = 0.88, P= 0.35	🟦 H = 6.82, P = 0.01	H = 1.32, P= 0.25	H = 0.88, P= 0.35
	Apr	▨	▨	H = 3.15, P= 0.08	🟥 H = 6.82, P = 0.01	🟥 H = 4.811, P= 0.028	H = 1.32, P= 0.25	🟦 H = 6.82, P = 0.01	H = 3.15, P= 0.08	H = 1.32, P= 0.25
	May	▨	▨	▨	H = 0.54, P= 0.47	H = 2.46, P= 0.12	🟦 H = 5.77, P= 0.02	🟦 H = 6.82, P = 0.01	H = 0.10, P= 0.75	H = 2.46, P= 0.12
	Jun	▨	▨	▨	▨	H = 1.84, P= 0.18	🟦 H = 5.77, P= 0.02	🟦 H = 6.82, P = 0.01	H = 1.84, P= 0.18	🟦 H = 6.82, P = 0.01
	Jul	▨	▨	▨	▨	▨	🟦 H = 3.94, P= 0.05	🟦 H = 3.15, P= 0.08	H = 3.15, P= 0.08	🟦 H = 4.81, P= 0.03
	Aug	▨	▨	▨	▨	▨	▨	H = 0.54, P= 0.47	H = 0.10, P= 0.75	H = 0.01, P= 0.92
	Sep	▨	▨	▨	▨	▨	▨	▨	🟦 H = 6.82, P = 0.01	H = 2.46, P= 0.12
Aber	Feb	H = 0.10, P= 0.75	H = 2.46, P= 0.12	🟥 H = 6.82, P = 0.01	H = 0.27, P= 0.60	H = 0.54, P= 0.47	H = 2.46, P= 0.12	🟦 H = 6.82, P = 0.01	▨	H = 1.32, P= 0.25
	Mar	▨	H = 3.15, P= 0.08	🟥 H = 6.82, P = 0.01	H = 2.46, P= 0.12	H = 0.88, P= 0.35	🟦 H = 3.94, P= 0.05	🟦 H = 6.82, P = 0.01	▨	H = 0.54, P= 0.47
	Apr	▨	▨	🟥 H = 6.82, P = 0.01	🟥 H = 6.82, P = 0.01	H = 0.54, P= 0.47	H = 0.10, P= 0.75	🟦 H = 6.82, P = 0.01	▨	H = 0.88, P= 0.35
	May	▨	▨	▨	H = 3.15, P= 0.08	🟦 H = 6.82, P = 0.01	🟦 H = 6.82, P = 0.01	🟦 H = 6.82, P = 0.01	▨	H = 3.15, P= 0.08
	Jun	▨	▨	▨	▨	H = 3.15, P= 0.08	🟦 H = 6.82, P = 0.01	🟦 H = 6.82, P = 0.01	▨	🟦 H = 6.82, P = 0.01
	Jul	▨	▨	▨	▨	▨	H = 0.10, P= 0.75	🟦 H = 6.82, P = 0.01	▨	H = 0.27, P= 0.60
	Aug	▨	▨	▨	▨	▨	▨	🟦 H = 6.82, P = 0.01	▨	H = 0.10, P= 0.75
	Sep	▨	▨	▨	▨	▨	▨	▨	▨	🟥 H = 6.82, P = 0.01
Dun	Feb	H = 1.84, P= 0.18	H = 0.27, P= 0.60	🟥 H = 5.77, P= 0.02	H = 0.88, P= 0.35	H = 0.54, P= 0.47	H = 0.01, P= 0.92	H = 0.88, P= 0.35	▨	▨
	Mar	▨	H = 0.10, P= 0.75	🟥 H =6.82, P = 0.01	🟦 H =6.82, P = 0.01	H = 0.54, P= 0.47	H = 1.84, P= 0.18	H = 0.10, P= 0.75	▨	▨
	Apr	▨	▨	🟥 H =6.82, P = 0.01	🟦 H = 4.81, P= 0.03	H = 0.04, P= 0.83	H = 0.54, P= 0.47	H = 0.27, P= 0.60	▨	▨
	May	▨	▨	▨	🟦 H =6.82, P = 0.01	🟦 H =6.82, P = 0.01	🟦 H =6.82, P = 0.01	H = 1.32, P= 0.25	▨	▨
	Jun	▨	▨	▨	▨	🟥 H =6.82, P = 0.01	H = 2.46, P= 0.12	H = 2.46, P= 0.12	▨	▨
	Jul	▨	▨	▨	▨	▨	H = 1.84, P= 0.18	H = 0.88, P= 0.35	▨	▨
	Aug	▨	▨	▨	▨	▨	▨	H = 1.32, P= 0.25	▨	▨

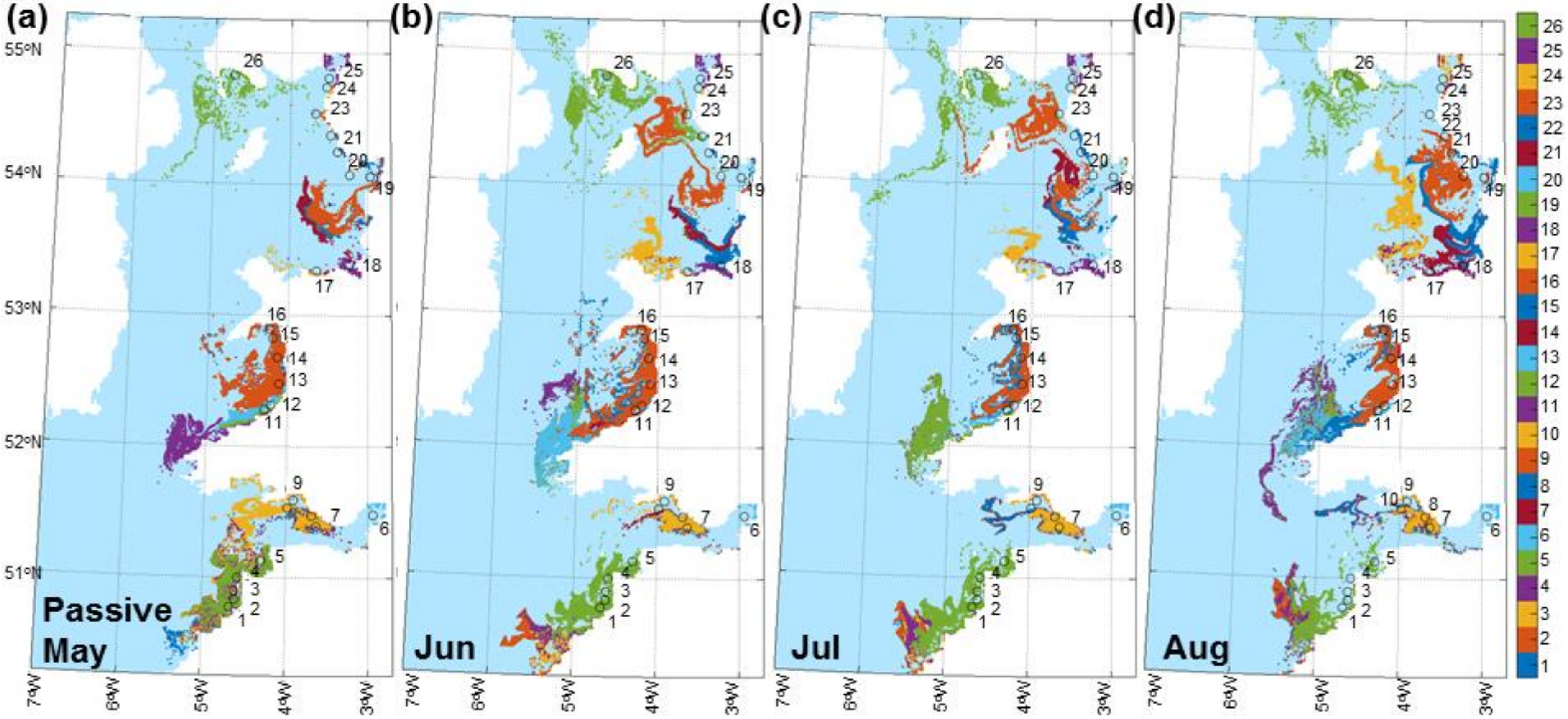
Appendix 5.2.5: Temporal change in sperm count normalised by weight. Differences analysed with Kruskal-Wallis rank sum test (df = 1). Significant differences (p-value < 0.05) are colour coded. Site specific decreases in sperm count through time are highlighted in blue (e.g. at *Llan*, sperm count in Mar was greater than in Apr). Months where egg size at the northern sites was less than at the southern site are highlighted in red (e.g. Egg size at *Llan* was less in Feb than *Dun*), and greater in blue.

Site	Month	Mar	Apr	May	Jun	Jul	Aug	Sep	Aber	Dun
Llan	Feb	🟥 H = 5.77, P = 0.02	H = 0.54, P = 0.47	🟥 H = 6.82, P = 0.01	🟥 H = 6.82, P = 0.01	🟥 H = 6.82, P = 0.01	H = 1.84, P = 0.18	H = 0.01, P = 0.92	H = 2.46, P = 0.12	🟥 H = 4.81, P = 0.03
	Mar	▨	🟦 H = 6.82, P = 0.01	H = 3.15, P = 0.08	🟥 H = 6.82, P = 0.01	🟥 H = 6.82, P = 0.01	H = 0.54, P = 0.47	🟦 H = 6.82, P = 0.01	H =0.88, P = 0.35	H = 0.01, P = 0.92
	Apr	▨	▨	🟥 H = 6.82, P = 0.01	🟥 H = 6.82, P = 0.01	🟥 H = 6.82, P = 0.01	H = 0.27, P = 0.60	🟦 H = 3.94, P = 0.05	H = 1.32, P = 0.25	🟥 H = 4.81, P = 0.03
	May	▨	▨	▨	H = 0.27, P = 0.60	H =0.88, P = 0.35	🟦 H = 3.94, P = 0.05	🟦 H = 6.82, P = 0.01	H = 0.27, P = 0.60	H = 1.84, P = 0.18
	Jun	▨	▨	▨	▨	H =0.88, P = 0.35	🟦 H = 5.77, P = 0.02	🟦 H = 6.82, P = 0.01	H = 0.01, P = 0.92	🟦 H = 6.82, P = 0.01
	Jul	▨	▨	▨	▨	▨	🟦 H = 4.811, P = 0.028	🟦 H = 6.82, P = 0.01	H = 2.46, P = 0.12	🟦 H = 6.82, P = 0.01
	Aug	▨	▨	▨	▨	▨	▨	H =0.88, P = 0.35	H = 0.01, P = 0.92	H = 0.01, P = 0.92
	Sep	▨	▨	▨	▨	▨	▨	▨	🟦 H = 3.94, P = 0.05	H = 2.46, P = 0.12
Aber	Feb	H = 1.32, P = 0.25	H = 0.10, P = 0.76	🟥 H = 4.81, P = 0.03	🟥 H = 6.82, P = 0.01	H = 0.01, P = 0.92	H = 0.01, P = 0.92	🟦 H = 3.94, P = 0.05	▨	H =0.88, P = 0.35
	Mar	▨	H = 0.01, P = 0.92	🟥 H = 6.82, P = 0.01	🟥 H = 6.82, P = 0.01	H = 0.01, P = 0.92	H = 0.01, P = 0.92	🟦 H = 6.82, P = 0.01	▨	H = 0.27, P = 0.60
	Apr	▨	▨	🟥 H = 6.82, P = 0.01	🟥 H = 6.82, P = 0.01	H = 0.01, P = 0.92	H = 0.01, P = 0.92	🟦 H = 5.77, P = 0.02	▨	H = 0.01, P = 0.92
H = 6.82, P = 0.01	May	▨	▨	▨	H = 0.10, P = 0.76	🟦 H = 4.81, P = 0.03	🟦 H = 6.82, P = 0.01	🟦 H = 6.82, P = 0.01	▨	H = 3.15, P = 0.08
	Jun	▨	▨	▨	▨	🟦 H = 6.82, P = 0.01	🟦 H = 6.82, P = 0.01	🟦 H = 6.82, P = 0.01	▨	🟦 H = 6.82, P = 0.01
	Jul	▨	▨	▨	▨	▨	H = 0.01, P = 0.92	🟦 H = 5.77, P = 0.02	▨	H = 0.10, P = 0.76
	Aug	▨	▨	▨	▨	▨	▨	🟦 H = 5.77, P = 0.02	▨	H = 0.10, P = 0.76
	Sep	▨	▨	▨	▨	▨	▨	▨	▨	🟥 H = 3.94, P = 0.05
Dun	Feb	H = 0.01, P = 0.92	H = 0.10, P = 0.75	🟥 H = 3.94, P = 0.05	🟦 H = 3.94, P = 0.05	H = 0.10, P = 0.75	H = 0.27, P = 0.60	H = 1.32, P = 0.25	▨	▨
	Mar	▨	H = 0.10, P = 0.75	🟥 H = 4.81, P = 0.03	🟦 H = 6.82, P = 0.01	H = 0.01, P = 0.92	H = 1.32, P = 0.2506	H = 0.54, P = 0.47	▨	▨
	Apr	▨	▨	🟥 H = 4.81, P = 0.03	🟦 H = 6.82, P = 0.01	H = 0.01, P = 0.92	H = 0.88, P = 0.35	H = 0.54, P = 0.47	▨	▨
	May	▨	▨	▨	🟦 H = 6.82, P = 0.01	🟦 H = 3.94, P = 0.05	🟦 H = 6.82, P = 0.01	H = 0.88, P = 0.35	▨	▨
	Jun	▨	▨	▨	▨	🟥 H = 6.82, P = 0.01	H = 3.15, P = 0.08	H = 2.46, P = 0.12	▨	▨
	Jul	▨	▨	▨	▨	▨	H = 0.54, P = 0.47	H = 1.32, P = 0.25	▨	▨
	Aug	▨	▨	▨	▨	▨	▨	H = 0.88, P = 0.35	▨	▨

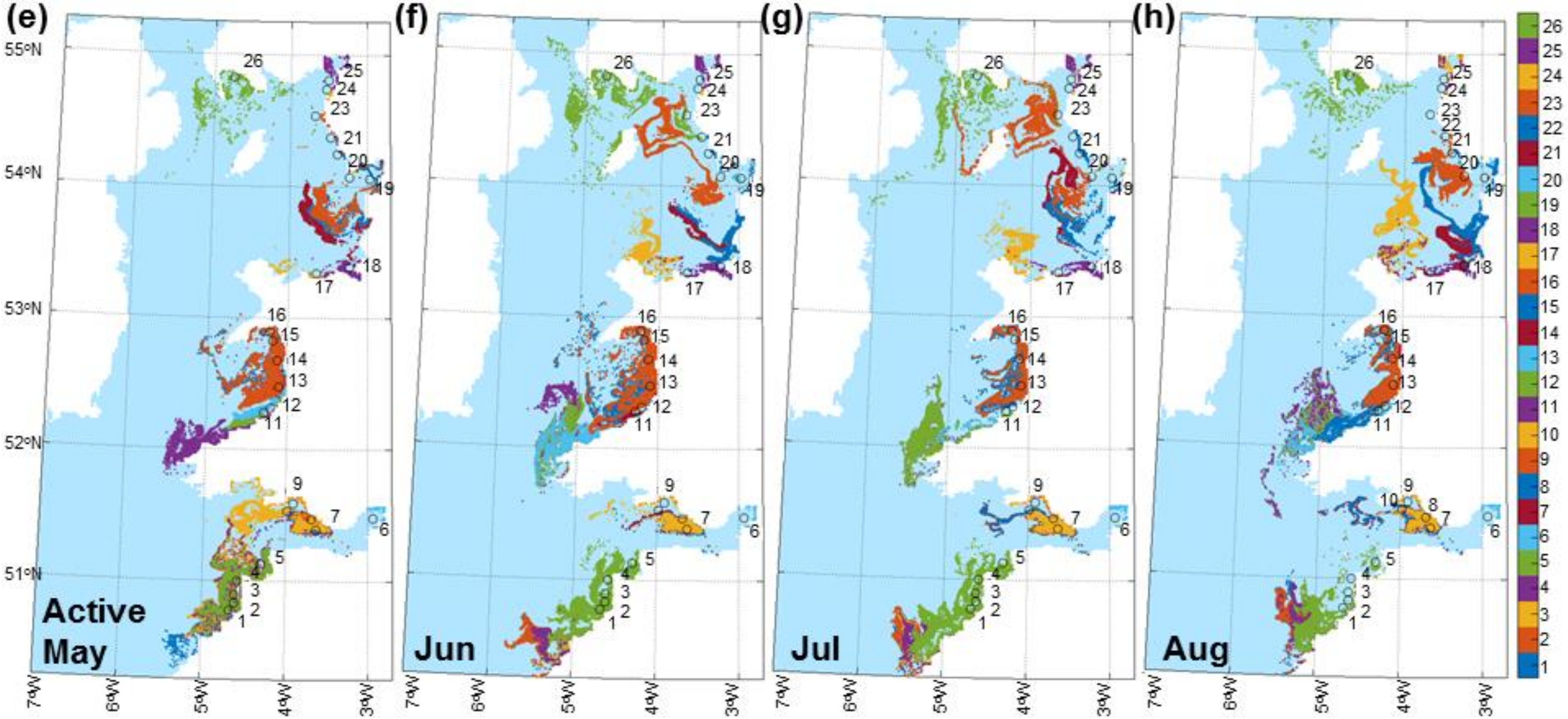
Appendix 5.3: Histograms plots of oceanographic larval dispersal distance, for all active particles released for all release dates. Each histogram depicts the normalised distribution of oceanographic dispersal for 40,000 particles released from the numbered site. The patch-mean (green diamond) and standard deviation (black line) are also plotted.



Appendix 5.4 (part 1): Particle Tracking Model (PTM) simulations of larval dispersal for *Sabellaria alveolata*, representing the potential dispersal of cohorts of larvae released (‘spawned’) from 26 selected reefs around the eastern Irish Sea. Each cohort of 10,000 particles is colour-coded to numbered release reef locations (□). Site 17 is Llanddulas (yellow), Site 11 is Aberarth (purple) and Site 7 is Dunraven (maroon). Each map depicts dispersal after a typical 60-day pelagic larval duration, for (a-d) passive particles, and (e-h) active particles. Monthly particle releases on: (a, e) 01 May, (b, f) 01 June, (c, g) 01 July, and (d, h) 01 August.



Appendix 5.4 (part 2): Particle Tracking Model (PTM) simulations of larval dispersal for *Sabellaria alveolata*, representing the potential dispersal of cohorts of larvae released (‘spawned’) from 26 selected reefs around the eastern Irish Sea. Each cohort of 10,000 particles is colour-coded to numbered release reef locations (□). Site 17 is Llanddulas (yellow), Site 11 is Aberarth (purple) and Site 7 is Dunraven (maroon). Each map depicts dispersal after a typical 60-day pelagic larval duration, for (a-d) passive particles, and (e-h) active particles. Monthly particle releases on: (a, e) 01 May, (b, f) 01 June, (c, g) 01 July, and (d, h) 01 August.



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6. General Synopsis

Investigations attempting to tease climate driven factors of change apart from natural variation require long-term datasets (Mieszkowska et al., 2014), and despite a general scarcity of such datasets, records of the abundance and distribution of this enigmatic polychaete within Britain have been prolific. A broad-scale investigation of *S. alveolata* abundance and distribution within the British Isles was completed by Cunningham et al. (1984) who collated existing data records from grey literature, in addition to collecting field data from numerous sites, providing a species-specific baseline dataset. Subsequently numerous records of presence and abundance have been collected and stored in a variety of formats from notebooks, through grey literature to published papers, some of which have been collated and stored in local and national databases. Access to reported information is difficult due to the varied data sources. Consequently, an aim of this thesis was to collate all available data, to collect contemporary data and to investigate change in both the abundance and distribution of *S. alveolata* within Britain on different spatial scales with relation to environmental parameters (e.g. temperature and wave exposure).

The coexistence of *S. alveolata* and *Mytilus edulis* has been widely reported (e.g. Cunningham et al., 1984; Allen et al., 1999; 2002; Dubois et al., 2006; Desroy et al., 2011). The resultant habitat of both species is protected under the EU Habitats Directive. However Cunningham et al., (1984) suggested a natural succession from a *Sabellaria* dominated community to a *Mytilus* dominated community on British coastlines. Consequently, a secondary aim of this thesis was to investigate short-term small-scale change of *S. alveolata* reefs, particularly to establish if the recognised intertidal ecosystem engineers within Britain function as alternative stable states. Like many coastal benthic invertebrates, *S. alveolata* and *M. edulis* feature a complex life cycle, with a planktonic larval stage in addition to a benthic adult stage (Cazaux, 1970; Folmer et al., 2014).

Ultimately the distribution of any species is determined by both environmental tolerances and larval dispersal, and the results of small-scale short-term investigation demonstrated the variability and importance of settlement success in population stability and persistence. Consequently, the final aim of this thesis was to investigate both reproductive strategy and larval dispersal, to estimate population connectivity within Britain, and thus improve understanding of recruitment (e.g. the potential for secondary settlement from out with the natal site, in addition to self-recruitment).

6.1. The importance of scale in assessment of change

Through decadal comparisons from the 1980s to the 2010s, it was clear that despite a predicted increase in both range and abundance, *S. alveolata* has demonstrated national persistence in distribution, and stability in abundance, on long temporal and broad spatial scales in the north of its range. At the majority of suitable sites, *S. alveolata* has persisted through time from the 1980s to the 2010s, and despite small scale fluctuations in abundance, the maximum abundance reported in each decade was relatively consistent. Strongholds of highly abundant populations (i.e. Common to Superabundant) have existed in Cumbria (e.g. Allonby Bay), Cardigan Bay (e.g. Criccieth), in south Wales (e.g. Porthcawl) and in southwest England (e.g. Duckpool) throughout this period. However, within this long-term trend, a reduction in distribution was demonstrated from the 2000s to the 2010s, potentially in association with the cold winters of 2009-10 and 2010-11, the latter of which was the coldest winter since 1978-9 (Wethey et al., 2011). A decrease in abundance (and distribution) has been reported following previous extremely cold winters (e.g. Crisp, 1964; Gubbay, 1988). The proportion of populated sites featuring high abundance reef-forming populations was reduced in the 1990s, potentially associated with an expansion in distribution (and thus recent colonisation by populations of potentially low abundance; Bush et al., Chapter 2).

National investigations suggested that changes may be occurring on reduced spatial scales. For example, recolonisation of sites in north Wales occurred from the 1980s to the 2000s. In regional scale studies both Frost et al. (2004) and Firth et al. (2015) concluded there had been an increase in abundance and distribution in this region. To establish if region specific changes in *S. alveolata* populations had occurred, data were considered as ‘near the range edge’ (i.e. from north Wales to Scotland) and ‘within the range’ (i.e. south Wales and southwest England). Patterns of change in both regions were assessed from the 1980s to the 2010s, demonstrating that *S. alveolata* had increased in abundance near the range edge from the 1980s to the 2010s, and in distribution from the 1980s to the 2000s. In contrast within the range, long term stability and persistence was demonstrated from the 1980s to the 2010s (Bush et al., Chapter 3). Changes in *S. alveolata* populations were related to changes in environmental variables (i.e. relative wave exposure and temperature).

Whilst temperature plays an important role in determining the distribution and abundance of *S. alveolata* as predicted, particularly in range edge populations, wave exposure also has an important role, particularly in populations well within the range. Although further increases in temperature may continue to benefit range edge populations, predicted increase in wave exposure may have a detrimental impact, particularly within range (Bush et al., Chapter 3). However the precise mechanisms by which these environmental factors act are largely unknown and many other environmental and abiotic factors still remain to be considered.

6.2. Intertidal ecosystem engineers as alternative stable states

National and regional investigations suggested that changes may also be occurring on a reduced temporal scale within individual sites (Bush et al., Chapter 2; 3). A natural cycle of reef development has previously been suggested whereby individual reefs exist in a delicate balance between stages of development (e.g. growth, stagnation and destruction), with secondary settlement required for continued persistence (Gruet, 1986). Additionally, within Britain, a succession has been suggested from *S. alveolata* dominated reef to *M. edulis* dominated reef with time (Cunningham et al., 1984). Through continued observations at four sites over a period of three years, it was demonstrated that a relatively small section of persistent reef can feature several stages of development. For example, an individual reef can feature growth, stagnation and destruction phase reef within a single metre. Highly variable temporal and spatial settlement was observed, and the importance of successful secondary settlement in long-term population persistence was suggested. In addition, it was that a succession was possible from a *S. alveolata* dominated ecosystem to a *M. edulis* dominated ecosystem, with complete transformation within a year at some sites, again dependent on successful settlement of the alternative state. However, transformation from a *M. edulis* to a *S. alveolata* dominated state was also observed following physical *M. edulis* removal after extreme winds, and physical disturbance was observed to disrupt this system with the return to bare substrata at some sites (Bush & Davies; Chapter 4).

Consequently, it is proposed that *S. alveolata* and *M. edulis* can represent alternative stable states on pebble shores of Britain. It has been demonstrated that pebble scars can be dominated by either *S. alveolata* or *M. edulis* reef, or a mosaic of both, and that disturbance history, and settlement success, currently determine which of these distinct communities is dominant (Figure 6.1; Bush & Davies, Chapter 4). However, whilst this study demonstrated increases in *S. alveolata* abundance in association with increasing temperature in Britain (Bush et al., Chapter 3), decreases in *M. edulis* have been observed elsewhere in the north Atlantic (Jones et al., 2009; 2010). Consequently, it is theorised that warming temperatures will favour the *S. alveolata* state (Figure 6.1, mid), particularly in the north of the range. Following a period of extreme wind, some *M. edulis* populations were physically removed, whilst *S. alveolata* populations thrived (Bush & Davies, Chapter 4). It is widely reported that *S. alveolata* require a certain degree of wave exposure to survive, however this study has demonstrated that within the range increases in wave exposure will ultimately also prove detrimental to *S. alveolata* populations (Bush et al., Chapter 3). Consequently, it is theorised that whilst wave exposure may be beneficial to some *S. alveolata* communities, they may ultimately prove detrimental to both (Figure 6.1).

The maintenance systems within a mussel dominated stable state have been thoroughly reviewed (e.g. Petraitis & Latham, 1999; Bertness et al., 2002), with gregarious settlement combined with the ability for mussels to move laterally on a

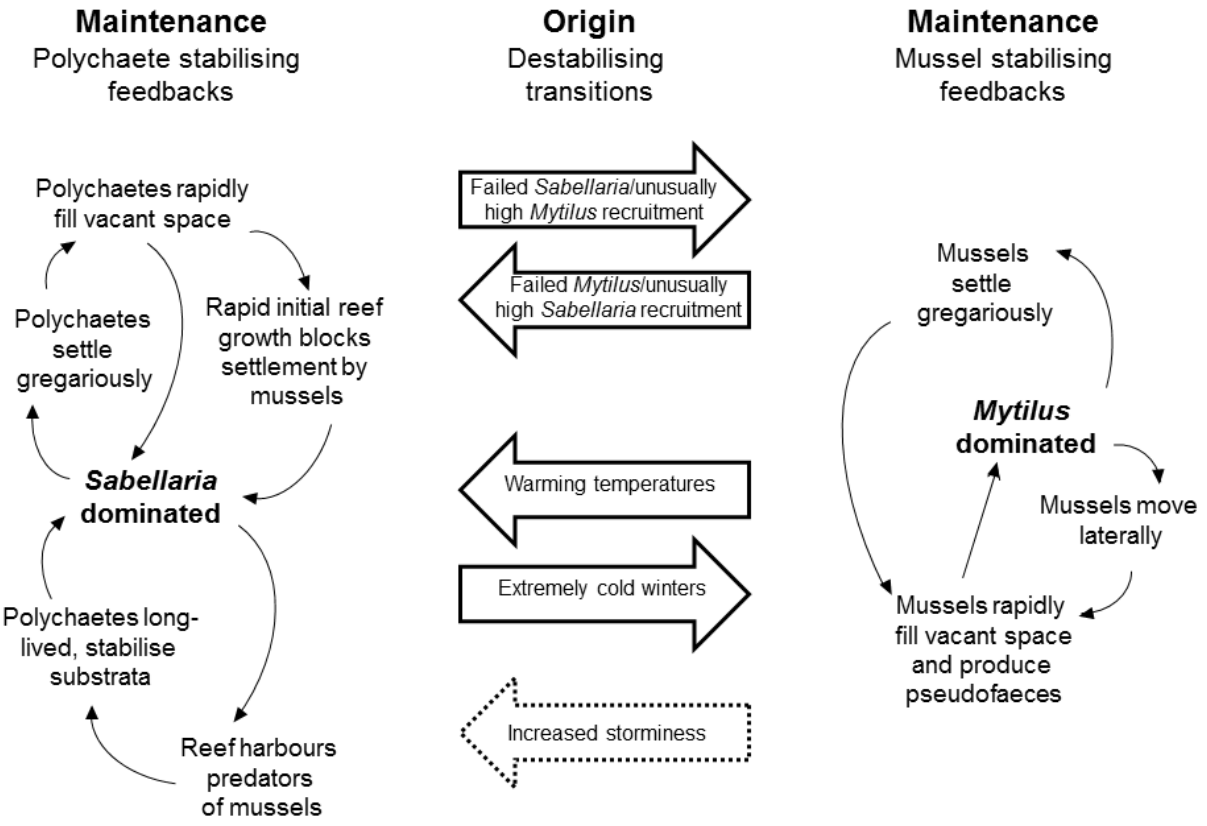

Figure 6.1: Conceptual model of the *Sabellaria alveolata* – *Mytilus edulis* reef alternative community stable state, highlighting the potential regulatory mechanisms and the influences of climate change (based on Petraitis & Latham, 1999; Bertness et al., 2002).

substrate post-settlement facilitating positive enforcement of this stable state (Figure 6.1, right). Similarly *S. alveolata* also demonstrate gregarious settlement with larvae actively attracted to reef structures and remains, in addition to rapid initial growth (Wilson, 1971; Gruet, 1986), rapidly filling bare substrata and regenerating degrading reef. Predation on *S. alveolata* reef is largely unstudied, and individuals are known to be relatively long-lived (e.g. up to 10 years, Gruet, 1986). The physical reef structure often persists beyond the lifetime of the individual *S. alveolata*, remaining attractive to secondary larval settlement, positively enforcing this stable state (Figure 6.1, left). In an example of negative feedback between states, *S. alveolata* reefs are also biodiversity hotspots that have been reported to contain elevated abundance of known *M. edulis* predators (e.g. *Asterias rubens*, *Carcinus maenus*; Elner, 1978; Dubois et al., 2002; Egerton, 2014), whilst *M. edulis* elevate the concentration of fine particulates through pseudofaeces, making the habitat potentially unsuitable for *S. alveolata* (Figure 6.1).

6.3. Larval dispersal and population connectivity

The long term persistence of a *S. alveolata* reef system is largely dependent on continued environmental suitability and settlement success (Bush et al., Chapter 2; 3; Bush & Davies, Chapter 4). Settlement success is highly variable, with Wilson (1971; 1974; 1976) reporting dense settlement in just two of 12 years at Duckpool, UK. Settlement was often spatially patchy, and temporally inconsistent. Inconsistencies have also been reported in adult fecundity (e.g. Wilson, 1971; Gruet & Lassus, 1983; Culloty et al., 2010), the length and timing of spawning (Wilson, 1971; Gruet & Lassus, 1983; Dubois et al., 2007), and planktonic larval duration (Wilson, 1968 a; b; Dubois et al., 2007). To investigate reproductive strategy within Britain, monthly monitoring of both adult fecundity and larval abundance was conducted at three sites from spring to autumn. Semi-continuous spawning was suggested as early stage larvae were detected in almost all sampled months. Overlaying this, peak fecundity, larval abundance, and thus assumed spawning were observed in summer, although the timing and magnitude of these peaks varied with site. At southern sites, a bimodal peak in adult fecundity was suggested. A bimodal peak in spawning was suggested at both southern and northern sites with a secondary occurrence of early stage larvae in autumn (Bush et al., Chapter 5).

Within the laboratory, larvae were observed to reach settlement stage within one month. Although Wilson (1968a; b) reported the ability for larvae to delay metamorphosis in the absence of suitable settlement, temperature is thought to be a determining factor in the rate of larval development (e.g. Reitzel et al., 2004) and in natural conditions, Dubois et al., (2007) reported settlement within 1-2.5 months in summer to autumn, whilst Cazaux (1970) reported planktonic larval durations of less than three months in winter. As larvae were predominantly detected in summer months within Britain (Bush et al., Chapter 5), larval dispersal was simulated from known abundant reef sites with a planktonic larval duration of 2 months (i.e. 60 days). A negatively phototaxis vertical migration was observed in latter stage larvae within the laboratory. Consequently, dispersal was modelled as both passive and active particles with monthly release from May to August. Although the incorporation of latter stage diel vertical migration reduced larval dispersal distance, and increased self-recruitment, it had little impact on population connectivity and in all simulations at least three distinct subpopulations were detected: (i) southwest Scotland to North Wales; (ii) Mid Wales; and (iii) south Wales to southwest England (Figure 6.2).

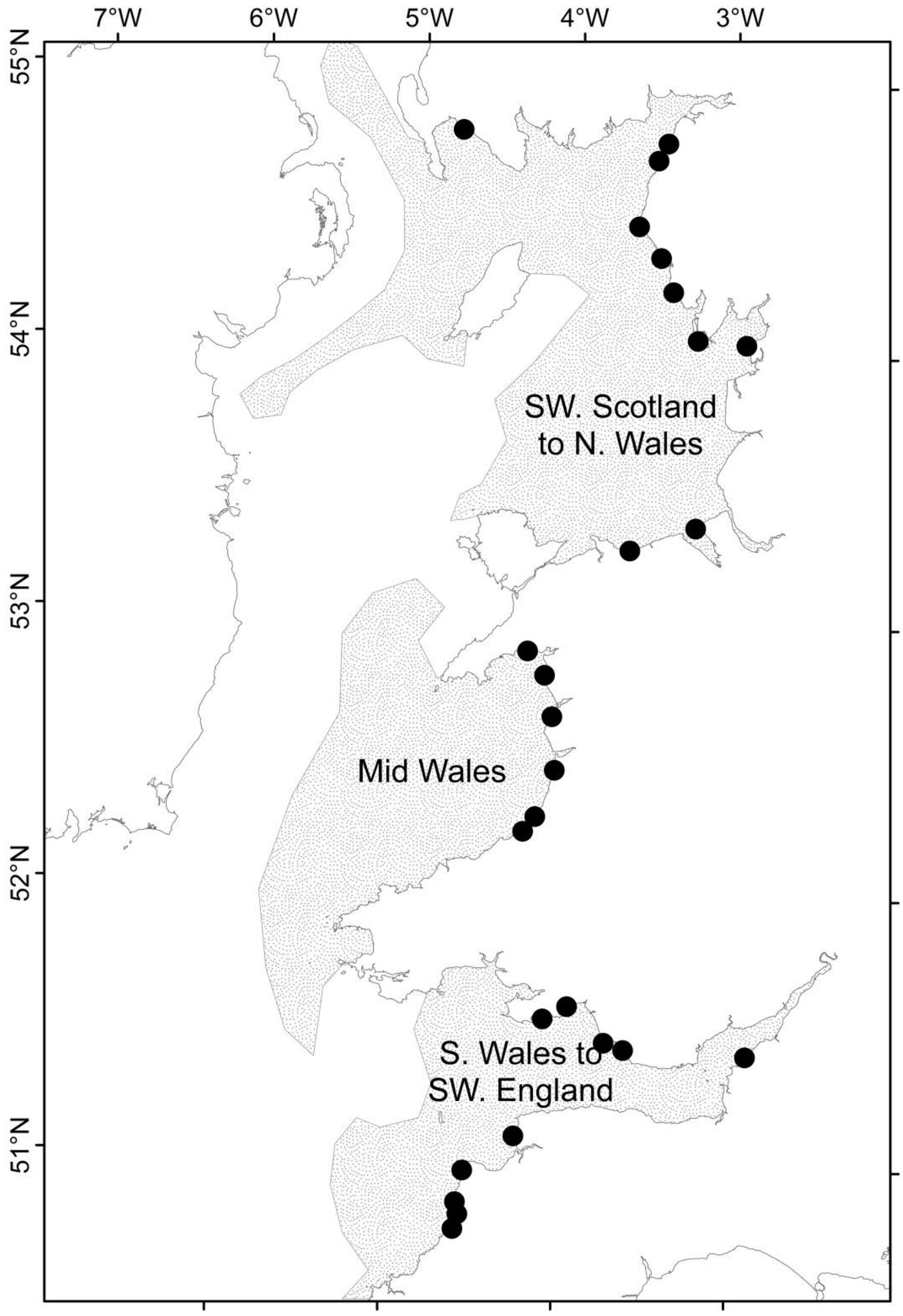

Figure 6.2: Suggested subpopulations of *Sabellaria alveolata* as predicted by simulated larval dispersal of both passive and active larvae from known reef-forming populations (●) after a 60-day planktonic larval duration. Approximate areas into which larvae dispersed if released from May to August 2014 are highlighted in grey. (i) Southwest Scotland to North Wales, (i) Mid Wales and (iii) South Wales to Southwest England).

6.4. The importance of absence records – A case study

Whilst awareness of the requirement for long-term broad-spatial scale datasets for studies investigating the impacts of climate change has been raised in recent years (e.g. Southward et al., 2005; Mieszkowska et al., 2014), the importance of absence data in these datasets is often overlooked. For example, visual comparisons of *Sabellaria alveolata* presence records suggest a westward progression of populations along the north coast of the Solway Firth (Figure 6.3). In the 1960s, a

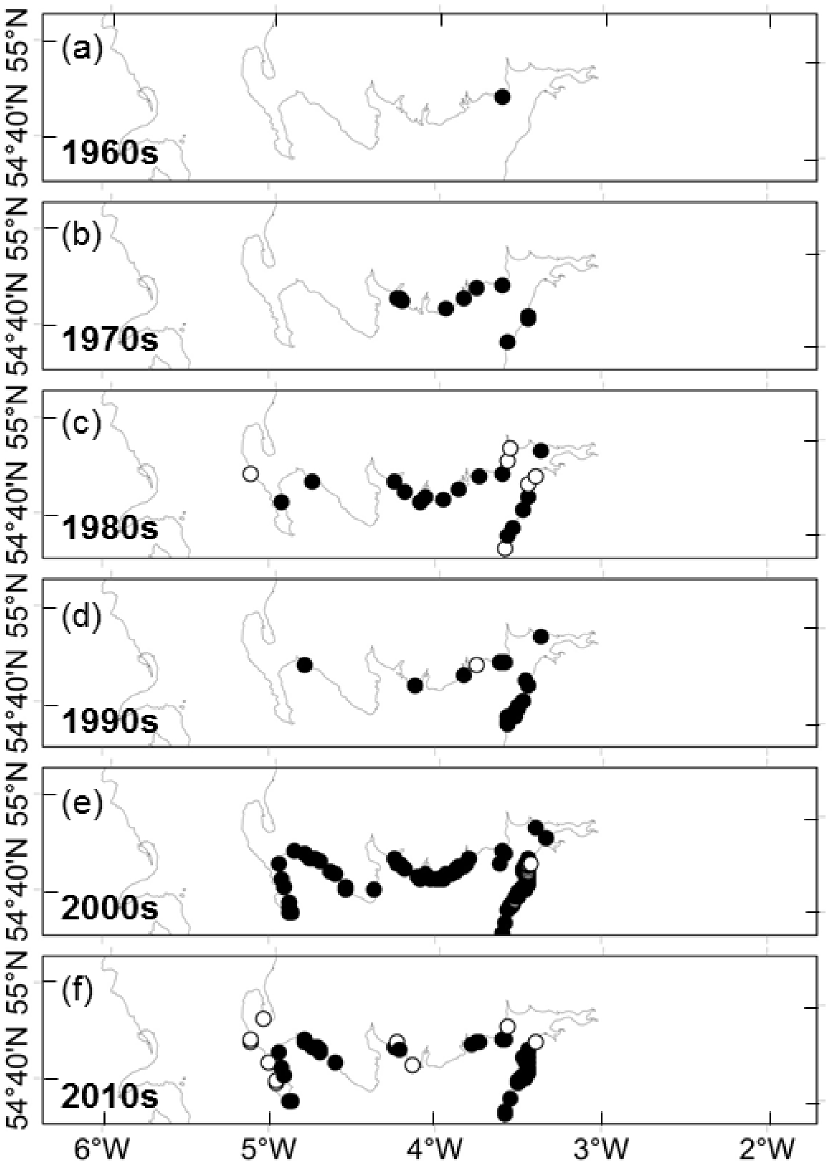

Figure 6.3: Decadal comparisons of collated and collected *Sabellaria alveolata* presence and records near the northern range edge. (a) 1960s. (b) 1970s. (c) 1980s. (d) 1990s. (e) 2000s. (f) 2010s.

solitary population was reported from Southerness Point (Figure 6.3 a). The following decade, additional populations were observed to the west of this (Figure 6.3 b). Similarly during the 1980s, populations were observed further west (Figure 6.3 c). From the 1980s to the 2010s populations were consistently reported within Luce Bay at the westernmost extreme of the Solway coast (Figures 6.3 c – f). The first absence sighting of this species reported to the west of the presence sightings was reported from Portpatrick in the 1980s (Figure 6.3 c). To the best of the authors knowledge, this site was not resurveyed until the 2010s when *S. alveolata* remained absent at this site. Consequently, despite a clear visual trend, the existence of a range extension from the 1960s to the 2010s cannot be confirmed. The author visited potentially suitable sites (i.e. areas of hard substrata adjacent to sandy shores) over the summer of 2013, revisiting several sites at which *S. alveolata* had been previously reported as absent in this region, and the data are presented in Figure 6.4 facilitating future studies of potential range extensions in this species.

6.5. Relevance to management

The biogenic habitat created by *S. alveolata* is protected internationally (e.g. under OSPAR as a threatened or declining habitat type; and under national interpretation of the EU Habitats Directive), and nationally (listed as a Priority Habitat under the UK Biodiversity Action Plan (1994); designated as a unique biotope in the Marine Nature Conservation Review (Connor et al., 2004); and a “Habitat of Principal Importance” under the UK Natural Environment and Rural Communities Act (2006)). On coastlines of the British Isles, such habitat is present in many Marine Protected Areas (e.g. Cardigan Bay, Pen Llŷn a’r Sarnau, Liverpool Bay, Morecambe Bay, the Solway Firth and Luce Bay and Sands Special Areas of Conservation). Despite the conservational interest in the resultant habitat, monitoring and management strategies for *S. alveolata* have not been established.

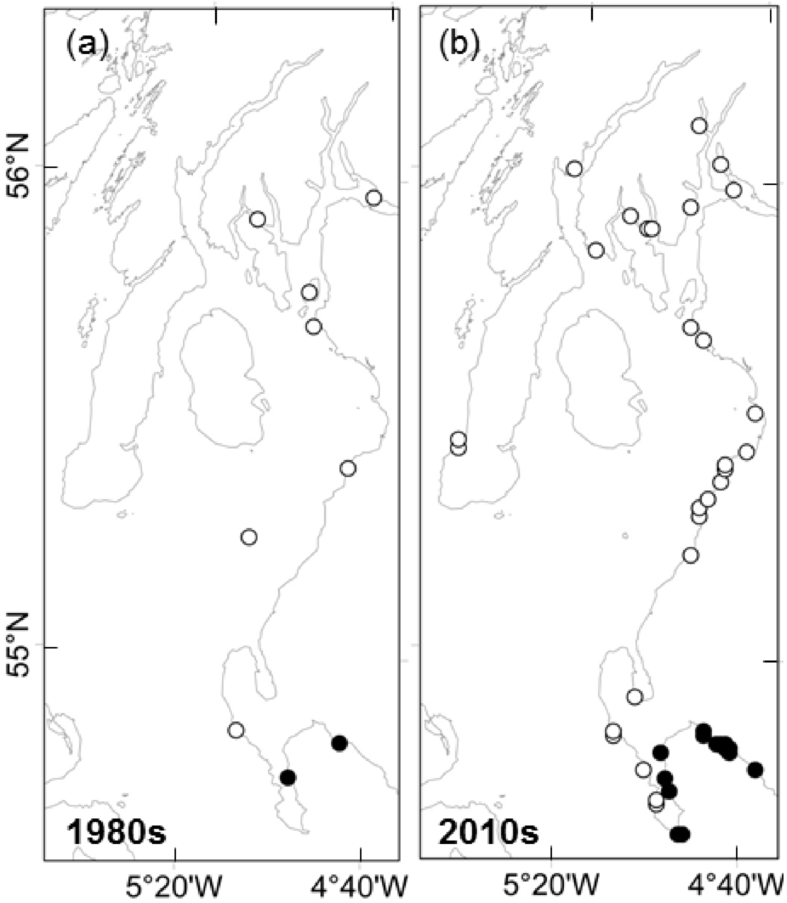

Figure 6.4: Collated and collected *S. alveolata* presence and absence records near the northern range edge. (a) 1980s. (b) 2010s

6.5.1 Importance of scale in monitoring strategy

A key finding of this thesis is the importance of spatial and temporal scale in environmental monitoring. From comparisons between contemporary and historical data, it is clear that within the British Isles, *S. alveolata* has demonstrated little change in abundance or distribution at the majority of suitable sites on long temporal scales (Bush et al., Chapter 2). When considered on a national scale, *S. alveolata* populations have demonstrated little change in either distribution or abundance on British coastlines since the 1980s. Overlaying this trend of national stability, increases in both abundance and the occupancy of known suitable sites have occurred near the northern range edge from the 1980s to the 2010s, in association with warming temperatures. Some decreases were suggested from the 2000s to the

2010s, potentially as a result of the extremely cold winters of 2009-10 and 2010-11. Some decreases have also occurred well within the range, over the same time scales, in association with increasing wave exposure (Bush et al., Chapter 3). This thesis additionally highlighted the high natural variability of *S. alveolata* on small spatial and short temporal scales, with rapid transition from settlement to a reef forming population, and additionally to reef removal (Bush & Davies, Chapter 4).

When considered on a small spatial scale, it is theorised that within a well-developed persistent reef-forming population, many growth phases can be observed as the natural cycle of reef development occurs at small spatial scales offset in time. The initiation of growth phase reef is dependent on primary or secondary settlement, whilst partial or complete reef destruction can occur in association with physical disturbance or biotic interactions (e.g. competition with *M. edulis*). Consequently, whilst an individual reef may exhibit degradation, an adjacent reef may demonstrate growth phase (Bush & Davies, Chapter 4). Monitoring on too high a spatial scale (e.g. of an individual reef), or on an infrequent or short temporal scale will not allow the assessor to separate normal variability from aberrant change in distribution or abundance. Current semi-quantitative approaches are not sufficient: the SACFOR monitoring approach does not consider the overall health of the reef, although the “Type” scale used by environmental agencies considers reef health to a certain extent. The findings of this thesis suggest that in order to fully understand the overall changes in a *S. alveolata* population, it is important to consider: (i) the maximum abundance within the entire area of suitable habitat; (ii) the developmental phase of specific areas of the reef; (iii) the frequency and success of secondary recruitment; and (iv) the abundance and recruitment of *M. edulis*, the alternative stable state.

6.5.2. Sub-population level management

Another key finding of this thesis is the indication of distinct sub-populations of reef within the Irish Sea: (i) along the coast of southern England, the Bristol Channel, and south Wales; (ii) within mid Wales (Cardigan Bay); and (iii) within north Wales, northern England and southern Scotland (Figure 6.2); with further divisions suggested, dependent on environmental conditions (Bush et al., Chapter 5). Considering the geographic and advection barriers between these physical regions, isolation between biological sub-populations was predicted, however, transient stepping stones populations and abnormal meteorological events may facilitate partial connectivity. Strong interconnectivity within these sub-populations was found to be evident due to wide reaching larval dispersal, but was dependent on hydrodynamics and seasonal variability in meteorological events (Bush et al., Chapter 5). Environmental management may be facilitated by high interconnectivity as protecting one source site will be beneficial to all sink populations, in addition to high self-recruitment as this will increase site resilience, and facilitate the persistence of the sub-population as a whole.

(i) Southwest Scotland to north Wales

In southwest Scotland, on the north coast of the Solway Firth, Auchenmalg Bay is the only persistent Abundant *S. alveolata* site, despite the presence of numerous transient or lower abundance sites. The only larvae simulated to settle at this reef are through self-recruitment, although larvae are widely dispersed from Auchenmalg Bay. Should *S. alveolata* ever breach the biogeographical barrier of the Rhins of Galloway, this thesis suggests it will be from this northernmost Abundant site which has persisted since at least the 1980s (Cunningham et al., 1984). Additionally, being at the northern range limit, this site is predicted to be susceptible to extremely cold winters. Consequently, continued monitoring of Luce Bay *S. alveolata* populations, including Auchenmalg Bay, is recommended.

In northwest England, interconnectivity was simulated between all persistent reef forming sites throughout central Cumbria (Morecambe Bay to Saint Bees, with larvae dispersed predominantly from north to south), and within the Solway Firth (Maryport to Dubmill Point, where larvae were dispersed predominantly northwest). Little connectivity occurred between these regions, dependent on environmental conditions, and separate management may be required. Greatest self-recruitment was simulated at Annaside Bank, Drigg and Dubmill Point.

Llanddulas in North Wales is predominantly a self-recruiting site, with limited connectivity with other persistent source sites within the sub-population (i.e. Hilbre Island and Annaside Bank) dependent on variability in hydrodynamics and meteorological events. Additionally Llanddulas is a source site to all transient populations further west on this coastline, increasing the conservational value of this site further.

(ii) Mid Wales

In Mid Wales, interconnectivity was again simulated between all persistent reef sites, with sites from Barmouth Bay to Criccieth functioning as source sites to all other persistent reef forming sites further south within the region. Self-recruitment was greatest from Barmouth Bay to Borth.

(iii) South Wales to southwest England

Within south Wales, interconnectivity was simulated between all persistent reef forming sites, and both Dunraven and Porthcawl demonstrated strong self-recruitment. However, Limeslade Bay functions as a source site for transient populations along the Gower, and continued monitoring and protection is recommended.

Within southwest England, interconnectivity was again simulated between all persistent reef forming sites on open coast, with the majority of larval dispersal south from Croyde towards Millook. Self-recruitment was greatest at Millook. Additionally, larvae were dispersed further south over transient or low abundance populations increasing the conservational value of this site.

No interconnectivity was demonstrated with the only known persistent site within the Severn Estuary. Additionally several extirpations have occurred on the south coast of the Severn and Bristol Channel since the 1980s. Consequently, it is recommended that populations within this region are monitored further. However, the health of *S. alveolata* at Hinkley Point Power Station (a previously Abundant and persistent population; Cunningham et al., 1984; Bamber & Irvine, 1993; 1997) could not be confirmed within this thesis due to logistical reasons, and thus it was excluded from PTMs, particularly as a decrease in both distribution and abundance of intertidal sites was observed within this region from the 1980s to the 1990s (Bush et al., Chapter 2; 3). The continued existence of this site would likely facilitate connectivity with sites in southwest England, in addition to southwest Wales. Additionally, some low abundance or transient populations have been reported on connecting coastlines (i.e. between Clevedon and Croyde; Cunningham et al., 1984), and Mettam et al. (1994) reported subtidal populations of *S. alveolata* within the Bristol Channel and Severn Estuary that were not considered within this study, both of which may facilitate population connectivity.

6.6. Future work

This thesis provides a collated long-term broad-spatial scale dataset of both distribution and abundance of an ecosystem engineer near the north of its range. Climate change is ongoing, and whilst relatively little change in the distribution of *S. alveolata* has been demonstrated at the range edge since the 1980s (Bush et al., Chapter 2), this may change and continued monitoring is worthwhile, particularly as an increase in abundance in this region has occurred (Bush et al., Chapter 3), and a range extension is suggested (Figure 6.3). Larval simulations suggest that minimal larvae enter the waters of western Scotland within a 60-day planktonic larval duration. However the ability of larvae to delay metamorphosis has been previously documented (Wilson, 1968a, b), and given a longer planktonic larval duration and different environmental conditions, settlement stage larvae may be successful in this area in the near future, particularly as temperatures continue to warm.

This study has highlighted the importance of both temperature (average and extreme), and wave exposure in driving the distribution and abundance of *S. alveolata*, and suggested that since the 1980s, these drivers have acted antagonistically, both increasing on the southwest coast of Britain in recent decades (Bush et al., Chapter 3). Continued increases in both are predicted, the impact of which should be investigated further, with consideration of site-specifics such as coastline complexity and aspect. The impact of wave exposure in particular is likely to be site-specific, resulting in a redistribution of populations as sheltered sites become more exposed (and thus suitable for *S. alveolata* occupation) whilst currently suitable sites may become too exposed (with potential extirpations). A certain degree of wave exposure is required to suspend particulates for tube growth and food supply (Frost et al., 2004), and a greater degree of wave exposure is known to inflict physical damage (e.g. Denny, 1995; Wilson, 1971), however the transition point from beneficial to destructive is unknown.

Whilst this study has demonstrated that *S. alveolata* and *M. edulis* exist as alternative stable states with changes in state observed over tens of metres within a single year, largely determined by settlement success, I have only been able to speculate on additional mechanisms controlling these states in this system (Bush & Davies, Chapter 4). This should be further investigated experimentally (e.g. addition and removal experiments, infaunal monitoring, settlement manipulation), and physical disturbance monitored. The impact of population age and developmental stage of the reef should be considered further as Cunningham et al. (1984) observed a succession on degrading reef only, whereas this study observed a complete transition from *S. alveolata* to *M. edulis* dominated in both actively growing and destruction phase reef. The spatial scale of impacts must be considered further as opposing patterns of change were observed in relatively close populations, with high small-scale short-term variation. Additionally, whilst evidence is provided that regional scale sub-populations exist within the British Isles with high within region connectivity but limited between region connectivity, this requires genetic confirmation.

Whilst this study has provided further insights into reproductive strategy of *S. alveolata* within Britain, the observed discrepancies in fecundity, larval abundance (Bush et al., Chapter 5) and settlement (Bush & Davies, Chapter 4) in time and space suggest that more work is required to understand natural variation. Similarly, whilst this study has provided evidence of a negative phototactic response by latter stage larvae in the laboratory, the existence and extent of this should be investigated further in the natural environment. Greater knowledge of both reproductive strategy and larval behaviour would increase the value of the model predictions.

6.7. Conclusions

Sabellaria alveolata is a highly persistent species within the British Isles (Bush et al., Chapter 2; 3), that demonstrates large short-term spatial variability (Bush & Davies, Chapter 4). At suitable sites, populations have been reported consistently for several decades (Bush et al., Chapter 2). Despite this, increases in abundance and distribution (i.e. colonisations) have occurred near the range edge in recent decades (i.e. from the 1980s to the 2010s). Increases near the range edge have largely occurred in association with increases in temperature (i.e. increased average temperature, decreased minimum temperature, and a decrease in the duration and magnitude of cold spells). Some decreases occurred near the range edge over this period, in association with opposing temperature parameters. In contrast, within the range, increases in *S. alveolata* were predominantly associated with decreases in wave exposure, and decreases with increases in wave exposure (Bush et al., Chapter 3). Whilst an increase in the distribution and abundance of a southern species near its range edge under warming temperatures was expected, the role of wave exposure in limiting *S. alveolata* populations has not previously been highlighted. When considered on a small spatial scale (i.e. tens of metres) high natural morphological variation was observed (e.g. height, abundance, developmental stage). High variability on a small spatial scale is partially explain by settlement success, which is itself highly spatially and temporally variable (Bush & Davies, Chapter 4).

Sabellaria alveolata and *Mytilus edulis* are alternative stable states on pebble shores within Britain, with a switch between stable states largely dependent on the settlement success of each species. For example, following failed *S. alveolata* settlement and successful *M. edulis* settlement, *M. edulis* can become dominant within a year. Settlement success in both species was highly variable in time and space, with populations in relatively close proximity (i.e. within 1 km^2) demonstrating opposing patterns of change. It is theorised that the ability of both species to rapidly fill space provides positive feedback maintaining the dominant state (e.g. both feature gregarious settlement, *S. alveolata* features rapid initial growth, *M. edulis* juveniles can actively move into bare substrata).

Sabellaria alveolata populations demonstrated semi-continuous spawning throughout the sampling period (i.e. from May to September) within Britain. Spawning is poorly seasonally synchronised, with a bimodal peak suggested in summer and autumn, particularly in southern sites. This study provides the first evidence of a negative phototactic response in latter stage larvae, however, field observations provided no clear confirmation of this in the natural environment. Modelling of both passive and active larval dispersal suggested that distinct sub-populations of *S. alveolata* exist within Britain, separated by geographic and advection barriers (i.e. southwest Scotland to north Wales, mid Wales, and south Wales to southwest England). Strong inter-connectivity within these sub-populations was predicted, dependent on hydrodynamics and seasonal variability in meteorological events. Some self-recruitment was simulated at the majority of sites in both models, however the inclusion of diel vertical behaviour increased population self-recruitment, and consequently, promoted population persistence through time.

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