



Variability in kelp forest structure along a latitudinal gradient in ocean temperature



Dan A. Smale^{a,b,*}, Pippa J. Moore^{c,d}

^a Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK

^b School and Plant Biology and Oceans Institute, University of Western Australia, Crawley WA 6009, Western Australia, Australia

^c Institute of Biological, Environmental and Rural Sciences, Aberystwyth University, Aberystwyth SY23 3DA, UK

^d Centre for Marine Ecosystems Research, School of Natural Sciences, Edith Cowan University, Joondalup 6027, Western Australia, Australia

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ABSTRACT

Subtidal forests comprised of kelps and other canopy-forming macroalgae represent critically important marine habitats. Kelp forests exhibit high rates of primary productivity, magnified secondary productivity, support high levels of biodiversity and provide various ecosystem services. Compared with many other regions, kelp forests around the UK have been largely understudied despite their recognised importance and the possible impacts of environmental change factors. We conducted surveys at 12 kelp-dominated open-coast sites within four regions in the UK, spanning $\sim 9^\circ$ in latitude and $\sim 3^\circ\text{C}$ in mean sea temperature. We used a combination of quadrat-scale abundance and percent cover data as well as transect-scale canopy cover estimates to quantify ecological structure at multiple spatial scales. Kelp forest structure varied significantly between sites (nested within region) and also between regions. Regional-scale differences were principally driven by a higher abundance/cover of *Alaria esculenta* at the colder northern regions (i.e. north and west Scotland), and the presence of the Lusitanian kelp *Laminaria ochroleuca* at some sites in the southernmost region (i.e. southwest England) but nowhere else. The kelp *Laminaria hyperborea* dominated all sites and varied significantly between sites but not regions. All assemblage-level and population-level response variables were highly variable between sites within regions, suggesting that environmental factors varying at corresponding spatial scales (e.g. wave exposure, turbidity, sedimentation) are important drivers of pattern. The detection of regional-scale variability suggests that predicted changes in ocean climate, particularly increased sea temperature, may lead to changes in kelp forest structure in the future, with poleward range contractions (for *A. esculenta*) and expansions (for *L. ochroleuca*) likely. However, as the distribution-abundance patterns of the assemblage dominant *L. hyperborea* did not vary predictably with ocean temperature at this spatial scale, the fundamental structure of these habitats may be more influenced by localised factors, at least in the short-term. The relative importance of multiple, concurrent environmental change factors in structuring UK kelp forests remains largely unknown.

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1. Introduction

Kelp species (order Laminariales) dominate shallow rocky habitats in temperate and subpolar regions around the world (Steneck et al., 2002; Teagle et al., in press). Kelps function as foundation species by supporting high levels of primary productivity (Mann, 2000; Steneck et al., 2002) and promote and maintain diversity by providing food and habitat for a wealth of associated flora and fauna (Christie et al., 2003; Norderhaug et al., 2005; Teagle et al., in press). While some kelp derived material is consumed directly and transferred to higher trophic

levels in situ (Norderhaug and Christie, 2009; Sjøtun et al., 2006), most is exported as kelp detritus which may be processed through the microbial loop, exported to adjacent habitats or consumed by a wide range of detritivores (Krumhansl and Scheibling, 2012). Kelps therefore play an important role in the capture and export of energy in coastal marine food webs (Dayton, 1985; Krumhansl and Scheibling, 2012). Kelps also provide a suite of other ecosystem services including biogenic storm protection, nutrient cycling, natural resources and nursery grounds and habitat for commercially important fish, mollusc and crustacean species (Beaumont et al., 2008; Bertocci et al., 2015; Steneck et al., 2002).

The structure and extent of kelp forest habitat is influenced by a variety of physical variables, including temperature (Tuya et al., 2012; Wernberg et al., 2016), light availability (Desmond et al., 2015; Lüning, 1979), nutrient levels (Dayton et al., 1999; Kain, 1989) and wave disturbance (Dayton and Tegner, 1984; Filbee-Dexter and

* Corresponding author at: Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK.
E-mail address: dansma@mba.ac.uk (D.A. Smale).

Scheibling, 2012). Ecological processes such as overgrazing (Hart and Scheibling, 1988; Leinaas and Christie, 1996), competition (Arkema et al., 2009; Hawkins and Harkin, 1985) and facilitation (Arkema et al., 2009; Bennett and Wernberg, 2014) can also affect kelp forest structure and functioning. In addition, kelp forest ecosystems are currently threatened by a range of anthropogenic stressors (Mineur et al., 2015; Smale et al., 2013), including overfishing (Ling et al., 2009) increased temperature (Filbee-Dexter et al., 2016; Wernberg et al., 2016) and storminess (Byrnes et al., 2011; Smale and Vance, 2015), the spread of invasive species (Arnold et al., 2016; Saunders and Metaxas, 2008) and elevated nutrient and sediment inputs (Gorgula and Connell, 2004; Moy and Christie, 2012). As such, a range of concurrent, interacting processes operate at multiple spatial and temporal scales to exert control on kelp-dominated communities and ecosystems (Wernberg et al., 2011a).

As kelps and other brown canopy-forming macroalgae (i.e. fucoids) are generally cold-water adapted species, their geographical distributions, particularly the equatorial range edge, are strongly controlled by temperature (Lüning, 1984), although other factors such as light and nutrient levels are important in determining species distributions (Desmond et al., 2015; Gorman et al., 2013; Smale et al., 2016). The thermal ranges and optima of macroalgae differ between populations and species (Müller et al., 2009; Pang et al., 2007) and, as such, the structure and extent of kelp forests and macroalgal beds have been shown to change along natural gradients of temperature. For example, recent observational studies in Western Australia (Smale et al., 2010; Wernberg et al., 2011b) and Portugal (Tuya et al., 2012) have shown that the structure of macroalgae-dominated communities shift predictably with changes in temperature along latitudinal gradients. Within the context of climate change, increased sea temperatures have been linked to loss of marginal populations, range contractions and significant reductions in kelp forest extent (Raybaud et al., 2013; Tuya et al., 2012; Voerman et al., 2013; Wernberg et al., 2016). On the other hand, oceanic warming has also been linked with range expansions at the poleward edge for some warmer water species, such as *Laminaria ochroleuca* (Smale et al., 2015). Interestingly, in temperate regions that have undergone ocean cooling in recent decades, such as South Africa, cold water kelp species have extended their ranges, again highlighting the important role of ocean temperature in setting geographical distributions (Bolton et al., 2012). It is evident that recent changes in ocean climate have influenced the structure and extent of kelp forests in many regions, and further changes are predicted to occur (Brodie et al., 2014; Müller et al., 2009).

In the UK, suitable rocky reef habitat for kelp populations is found along much of the extensive and complex coastline, particularly along the wave-exposed south, west and north coasts (Yesson et al., 2015). Kelps are found on rocky reefs and artificial hard structures from the low intertidal (<1 m above chart datum) to depths in excess of 40 m (e.g. *Alaria esculenta* off Rockall, Scotland). Eight kelp and pseudo-kelp species co-exist in UK waters (Smale et al., 2013), of which five are long-lived perennial species (*Laminaria hyperborea*, *L. digitata*, *L. ochroleuca*, *Saccharina latissima*, *Alaria esculenta*) and three are annual or pseudo-annual (*Saccorhiza polyschides*, *Chorda filum*, *Undaria pinnatifida*). The dominant canopy-former on most moderately-exposed to exposed sublittoral reefs is *L. hyperborea*, which is a stipitate canopy-forming kelp species with a rigid stipe (1–3 m long) that holds the fronds above the substratum.

Technological advances in scuba diving in the 1960s and 1970s facilitated step-wise progress in our understanding of the distribution and ecology of kelp forests in the UK, particularly through an estimable body of work conducted by Joanna Kain on the ecology of *Laminaria* (see Kain, 1979, for an overview) and P.G. Moore's work on faunal assemblages within kelp holdfasts (Moore, 1971, 1973). From the 1980s onwards, however, changes in attitudes and regulations concerning scientific scuba diving, coupled with shifts in research priorities and relatively little commercial interest in kelps, have led to a dearth of

primary research on kelp forests in UK waters (Smale et al., 2013). Sub-littoral kelp beds persist along >12,000 miles of the UK coastline yet the volume of directed research in recent years pales in significance when compared with kelp studies conducted in other research intensive nations (Smale et al., 2013). This lack of targeted research has led to significant knowledge gaps that currently hinder management and conservation of these habitats, such as a scarcity of robust baseline data against which to detect ecological change driven by contemporary stressors. Here, we conducted large-scale kelp forest surveys across 9° of latitude in order to generate a robust baseline of ecological pattern at relevant spatial scales. The study regions encompassed a gradient in sea temperature of ~3 °C and survey sites ranged from moderately to fully wave-exposed. As such, we predicted that kelp forest structure would (1) vary at regional spatial scales due to changes in ocean climate (e.g. temperature) and (2) vary at smaller spatial scales (i.e. between sites) due to variability in localised factors (e.g. wave exposure, sedimentation, turbidity).

2. Material and methods

2.1. Study area

Surveys were conducted at 12 sites within four regions in the UK, which spanned ~9° in latitude (~50°N to ~59°N) and were situated on the exposed western coastline of mainland UK (Fig. 1) where kelp forest habitat is abundant (Smale et al., 2013; Yesson et al., 2015). Adjacent regions were between ~180 and 500 km apart (Fig. 1). Within each region candidate study sites were selected based on the following criteria: (i) sites should support extensive sublittoral rocky reef habitat at ~3–5 m depth (below chart datum); (ii) sites should be representative of the wider region (in terms of coastal geomorphology) and not obviously influenced by localised anthropogenic activities (e.g. sewage outfalls, fish farms); and (iii) sites should be 'open coast' and moderately to fully exposed to wave action to ensure a dominance of *L. hyperborea* (rather than *Saccharina latissima* which dominates sheltered coastlines typical of Scottish sea lochs, for example). Data on light intensity and nutrient levels from most sites are presented in Smale et al. (2016) and were not suggestive of any point-source anthropogenic impacts. Three sites were randomly selected from a larger pool; sites were situated between ~1 and ~13 km apart within each region (Fig. 2). At one site within each region, sea temperature within the kelp forest was monitored for 1 annual cycle (July 2014–July 2015) by deploying a 'HOBO Tidbit' logger on the reef's surface, which measured temperature every 30 min. Information on environmental factors of known importance to kelp population structure were collated for each survey site. Satellite-derived SSTs were obtained (from the NASA Giovanni Data Portal, using 9-km resolution data from the Pathfinder AVHRR satellite) and used to generate monthly means for February and August (i.e. monthly minima and maxima), averaged from 2000 to 2006. Land masks were used to remove any influence of coastal pixels and site values were averaged across all pixels within a 30 km radius. Remotely-sensed estimates of chlorophyll a concentrations (collected by the MODIS Aqua satellite at an estimated 9-km resolution) were extracted and averaged over the period 2002–2012 as a proxy for water turbidity (see Burrows, 2012 for similar approach). Wave exposure was quantified using fetch values presented in Burrows et al. (2008) and Burrows (2012). Finally, average summer day length (mean value for all days in June and July) was used as a proxy for maximum photoperiod for each region. Grazing by sea urchins is not considered to be a major driver of kelp forest structure within the study region (Smale et al., 2013) and densities of sea urchins (predominantly *Echinus esculentus*) are low at these sites (Smale et al., 2016). In general, benthic communities within these kelp forest sites are characterised by a high coverage of understory algae (predominantly Rhodophytes), patchy cover of sessile invertebrates (e.g. sponges, ascidians, bryozoans) and extensive and dense kelp canopies.

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