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## Threats and knowledge gaps for ecosystem services provided by kelp beds: a northeast Atlantic perspective

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## Abstract:

Kelp beds along temperate and polar coastlines represent some of most diverse and productive habitats on Earth. Here, we synthesize information from >60 years of research on the structure and functioning of kelp bed habitats in European waters, with particular emphasis on the coasts of UK and Ireland. We also draw on knowledge gained from other systems, in both the wider NE Atlantic and further afield, to provide the broader context for this regional research. We collated existing data on kelp distribution and abundance and reanalysed this data to describe the structure of kelp beds along a latitudinal gradient spanning more than 10° of latitude. Ecological goods and services provided by kelp beds are examined, and we discuss current and future threats posed to kelp beds and identify key knowledge gaps. Kelp-dominated habitats along much of the NE Atlantic coastline have been chronically under-studied over recent decades in comparison with other regions such as Australasia and North America. The paucity of field-based research currently impedes our ability to conserve and manage these important systems. Targeted observational and experimental research conducted over large spatial and temporal scales is urgently needed to address these knowledge gaps.

## Key words:

Laminariales, kelp forests, marine biodiversity, subtidal benthic habitats, temperate reefs

## 1. Introduction

Rapid environmental change is a threat to the functioning of marine ecosystems. Increased temperature, storminess and changes in the frequency and magnitude of extreme climatic events will influence the distribution of species, community structure and ecosystem functioning (Brierley and Kingsford, 2009; Harley et al., 2006). These changes are likely to degrade the ecological services that natural systems provide (Hoegh-Guldberg and Bruno, 2010; Sunday et al., 2012). The upper layers of the global ocean have warmed at a rate of 0.1°C per decade since the mid-20th Century, albeit with pronounced regional and seasonal variability (Solomon et al., 2007). The NE Atlantic region represents a hotspot of warming, as temperatures have risen at rates of ~0.3°C to ~0.8°C per decade (Hughes et al., 2010; Lima and Wetthey, 2012). Seawater temperatures off the west coast of the UK and Ireland are predicted to warm by a further ~2°C by 2090 (relative to 1990, see Philippart et al., 2011), with major implications for marine ecosystems. Other human-derived stressors interact with regional-scale climate change in unpredictable and non-linear ways to impact marine ecosystem structure and functioning (Wernberg et al., 2011). In developed regions, such as the NE Atlantic, fishing and exploitation of other living marine resources including seaweeds, plus coastal land use have impacted nearshore ecosystems for centuries. Over the last 150 years diffuse (e.g. eutrophication) and point source chronic pollution increased, although recent control measures and de-industrialisation in the last few decades have led to improvements. Therefore, the current ecosystem 'baseline' is far from pristine and is to some degree a product of humankind's role as the dominant ecosystem engineer and keystone predator (sensu sliding baselines, Dayton et al., 1998). Intensifying anthropogenic impacts over recent decades, which will continue into the future (Halpern et al., 2008), dictate that comprehensive understanding of ecosystem functioning and resilience is of growing importance. This knowledge is needed to enhance sustainability in the use of ecological goods and services that coastal zones provide.

Kelps (large seaweeds of the order Laminariales) dominate rocky reefs throughout the world's temperate seas (Steneck et al., 2002), where they provide ecosystem services to humans worth billions of pounds (Beaumont et al., 2008). Kelp forests support high primary productivity, magnified secondary productivity, and a three-dimensional habitat structure for a diverse array of marine organisms, many of which are commercially important. Dominant kelp genera vary across the world's temperate bioregions, from *Laminaria* in the North Atlantic to *Ecklonia* in the Indian Ocean through to *Macrocystis* in the Pacific and South Atlantic. Despite differences in the dominant species, kelp forests the world over share some commonality in their structure and functioning. For example, dominant canopy-forming kelps influence their environment and other organisms, thereby functioning as 'ecosystem engineers' (sensu Jones). By altering light levels (Clark et al., 2004), water flow (Rosman et al., 2007), physical disturbance (Connell, 2003) and sedimentation rates (Eckman et al., 1989), kelps modify the local environment for other

organisms. Moreover, through direct provision of food and structural habitat, kelp forests support higher levels of biodiversity and biomass than simple, unstructured habitats (Dayton, 1985; Steneck et al., 2002) and, in general, kelp forests are hugely important as fuels for marine food webs through the capture and export of carbon (Dayton, 1985; Krumhansl and Scheibling, 2012).

Kelp forests can be highly dynamic systems that exhibit pronounced spatiotemporal variability. Kelps are susceptible to physical, chemical and biological changes in the marine environment so that significant reduction in kelp habitat over tens to hundreds of kilometres can occur within a year (Dayton et al., 1992; Edwards, 2004; Wernberg et al., 2013). Kelp forests within systems influenced by upwellings or variable oceanic boundary currents may be particularly dynamic, compared with those in more stable systems. Key factors include light, which is in turn influenced by latitude, water clarity, epiphytes and weather, as well as temperature, nutrient levels, the frequency and intensity of storms, and outbreaks of herbivores. Crucially, recovery from perturbations can progress once environmental conditions become favourable; most kelp species reach maturity within 1-6 years (Kain, 1975b; Parke, 1948) and entire kelp-associated communities can recover within 7-10 years (Christie et al., 1998). Indeed, the recovery of kelp canopies and their associated assemblages following physical disturbance can be very rapid, occurring within 3 years (Hawkins and Harkin, 1985). However, the resilience of kelp forests to perturbation is being eroded through multiple, concurrent chronic and acute stressors. In many regions, herbivory (usually by sea urchins) has increased as a result of trophic cascade effects associated with the removal of large predators (Estes and Duggins, 1995; Steneck, 1998). Increased herbivore pressure can cause phase-shifts from structurally and biologically diverse kelp beds to simple, depauperate barrens (Breen and Mann, 1976; Hagen, 1983; Norderhaug and Christie, 2009). In Tasmania, the impacts of a climate-mediated range expansion of a sea urchin have been compounded by overfishing of large lobsters, which would otherwise have kept the urchin population boom in check and limited grazing pressure (Ling et al., 2009). Other kelp systems have been degraded following increased nutrient and sediment input from ever-expanding coastal cities (Connell et al., 2008), or following establishment of non-indigenous species (Irigoyen et al., 2011; Krumhansl et al., 2011). Moreover, changing climatic variables, including storm frequency (Byrnes et al., 2011), the magnitude of extreme thermal events (Wernberg et al., 2013), and increased seawater temperature (Serisawa et al., 2004) have recently been attributed to ecologically-significant alterations in kelp bed structure and functioning.

This review is not intended to duplicate existing syntheses on the biology and ecology of kelp species (Dayton, 1985; Kain, 1979), the resilience of kelp beds to perturbation (Steneck et al., 2002), kelps as drivers of detrital food webs (Krumhansl and Scheibling, 2012) or the likely responses of kelp and other macroalgae to global environmental change (Harley et al., 2012). The aims of the review are threefold: (i) to synthesise existing knowledge on the structure and

functioning of kelp beds, and the ecosystem services they provide, in the NE Atlantic with specific focus on the UK and Ireland, (ii) to identify current threats to kelp beds and to assess the likely responses of kelp species and their associated biodiversity to key environmental change stressors; and (iii) to highlight pressing knowledge gaps and research priorities that will lead to improved understanding of the current and future role of kelp dominated habitats within the wider ecosystem. This information will ultimately support decision-making processes and feed into adaptive management approaches, which are needed to ensure the sustainability and continued productivity of natural ecosystems faced with rapid environmental change.

## **2. A brief history**

Quantitative research on UK kelp beds began over 60 years ago, following a demand from the Ministry of Supply to produce camouflage textiles and other goods from kelp-derived alginates during and after the Second World War (Parke, 1948; Woodward, 1951). In the early 1950s, attempts were made to quantify the total standing stock of kelp as a potential exploitable resource. The total biomass of subtidal kelp around Scotland (mostly *Laminaria hyperborea*) was estimated as 10 million tons over an area of 8000 km<sup>2</sup> (Walker, 1953). This figure was a map-based estimate derived from detailed surveys of the coastline (Walker and Richardson, 1955) over the period 1946-1955, which included aerial photography and quadrat sampling over an area of 270 km<sup>2</sup> (Walker and Richardson, 1956). Interestingly, the resultant time series depicted high inter-annual variability in kelp biomass in Scotland which, at the time, was attributed to an 11-year cycle in sunspot activity (Walker, 1956). However, re-examination of the data suggests that the highest annual biomass estimates were recorded in years following North Atlantic Oscillation (NAO)-positive summers (Folland et al., 2009). As such, it could be that calm, sunny weather led to increased biomass, suggesting that decadal and shorter-term NAO variation may be linked to kelp productivity.

Technological advances in scuba diving in the 1960s and 1970s facilitated step-wise progress in our understanding of the distribution and ecology of kelp beds in the UK. Perhaps most notable were the seminal body of work by Joanna Kain on the ecology of *Laminaria* on the Isle of Man (see Kain, 1979, for overview), and P.G. Moore's work on faunal assemblages within kelp holdfasts in NE England (Moore, 1971, 1973). Moreover, between 1970 and 2000 substantial survey work was conducted by the Nature Conservancy Council (NCC) and various successor bodies including the Marine Nature Conservation Review (MNCR). During this time, scuba divers conducted semi-quantitative surveys along the majority of the subtidal rocky coastline of the UK, to benchmark patterns of marine biodiversity. This dataset is freely available through the National Biodiversity Network gateway and remains the only large-scale, systematic assessment of subtidal rocky reef assemblages in the UK.

From the 1980s onwards, 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 beds in UK waters. Subtidal kelp beds persist along >12,000 miles of 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 (Fig. 1). For example, an ISI listed search of 'kelp' papers showed that researchers in Australia and the USA published >100 papers on the ecophysiology or ecology of kelps in the last decade, whereas just 7 papers originated from the UK (Fig. 1). Indeed, in the period 2002-2011, more kelp ecology papers originated from sub-Antarctic regions than from the UK. Similarly, a search of marine ecology papers focussing on major habitat types in the UK over the same timeframe shows that, compared with work on subtidal rocky reefs, 10 times as much research was conducted on intertidal rocky shores, 7 times as much on subtidal soft sediments, and twice as much on intertidal soft sediments (Fig. 1). With the notable exception of Norwegian research, kelp ecosystems in the wider NE Atlantic have been relatively understudied in recent years (Fig. 1). As the structure of, and current threats to, kelp beds off Norway are dissimilar to those further south, generalising ecological patterns, processes and predictions to the wider NE Atlantic is problematic. Clearly, the lack of focussed process-based research over recent years has resulted in significant knowledge gaps concerning the responses of kelp dominated habitats to environmental change, the contribution of kelps and their associated biodiversity to marine food webs, and the resilience of kelp communities to perturbation.

### **3. Kelp bed structure**

In the NE Atlantic, kelps occupy subtidal rocky reefs in all but the most sheltered or turbid locations. Dense kelp beds are found from the lower shore to depths >30 m, from northern Norway and Iceland through to Portugal and Morocco. Compared with other systems worldwide, kelp species diversity in European waters is relatively high, most likely because of the pattern of tectonic activities and the development of oceanic circulation patterns over the last 15 million years. Kelp species representative of both North Atlantic and North Pacific genera, of warm water origin, of cool water origin and of Arctic water origin, are found in the NE Atlantic. Dominant canopy formers are generally members of the family Laminariaceae (e.g. *Laminaria hyperborea*, *Laminaria digitata*, *Laminaria ochroleuca*), which exhibit an alternation of dissimilar generations; an asexual diploid phase (the sporophyte) that is usually of considerable size and a haploid dioecious phase (the gametophyte) that is microscopic (Kain, 1979). Sporophytes of members of the Laminariaceae comprise a holdfast, a stipe and a blade, which may comprise many digitate fronds as in *L. hyperborea* or a single undivided frond as in *S. latissima*. The sporophyte produces vast numbers of meiotic haploid zoospores from 'sori' on the blade which, when released, may disperse metres to kilometres from the parent. The zoospores develop into microscopic gametophytes which generally become fertile within a matter of days under

favourable conditions. Male gametophytes release motile sperm that fertilize eggs of proximal female gametophytes and the resultant zygote develops into the new sporophyte (in unfavourable conditions, however, the gametophyte may develop vegetatively). The young sporophyte then develops into a mature kelp over the next few years, which may reach up to 4 m in length and, in the case of *L. hyperborea*, live for ~20 years. For further information on the life history and biology of Laminariaceae, the reader is referred to comprehensive accounts by Kain (1979) and Lüning (1990).

In the UK and Ireland, suitable rocky reef habitat is found along much of the undulating coastline, particularly along the wave-exposed south, west and north coasts. As such, kelps occupy rocky reefs and artificial hard structures from the low water mark to, in extreme cases, depths in excess of 40 m (e.g. *Alaria esculenta* off Rockall, Scotland) along most of the coastline of UK and Ireland (Fig. 2). Kelp beds in UK waters are complex, as 7 different kelp species co-exist, of which 4 are long-lived climax canopy-forming species (Table 1), and their relative abundance is influenced by a range of abiotic (e.g. temperature, latitude, wave exposure, light levels, disturbance) and biotic (e.g. competition, grazing) factors. Even so, the dominant canopy-former on most subtidal reefs is *Laminaria hyperborea*, which is a 'stipitate' kelp species with a rigid stipe (1-3 m long) that holds the fronds above the substratum. *L. hyperborea* is distributed from the Arctic south to northern Portugal, and in the UK it persists on all but the most wave-exposed or turbid rocky reefs. The sporophyte becomes fertile after 2-6 years and may live for 5-18 years in the UK (Kain, 1979). *L. hyperborea* influences its environment and other organisms by providing food and habitat, and by altering light, water motion, sediment deposition and physical disturbance through thallus scour. It is, in the truest sense, an ecosystem engineer and functions as the assemblage dominant by outcompeting other large macroalgae under most conditions (Hawkins and Harkin, 1985).

Other members of the genus found in UK waters are *Laminaria digitata* and *Laminaria ochroleuca*. *L. digitata* is distributed from Arctic waters to its southern range edge in Brittany, France. It is perennial, reaching maturity after 1-2 years and persisting for up to 6 years, and is smaller than *L. hyperborea*, reaching a maximum total length of 3 m. *L. digitata* tends to dominate the low intertidal and immediate subtidal zones, but is outcompeted by *L. hyperborea* at depths of a few metres (Hawkins and Harkin, 1985; Kain, 1975a). In contrast to *L. hyperborea* its stipe is very flexible so that fronds scour the immediate substratum, which facilitates attachment in the wave-exposed shallow subtidal zone. *L. ochroleuca* is a warm-temperate Lusitanian species, which is distributed from the south of England to Morocco, and occurs in both the Straits of Messina and the Azores. It is very similar in morphology to *L. hyperborea* and is thought to share similar life history traits, although little is known about its biology in UK waters. *L. ochroleuca* is thought to be expanding its range polewards, perhaps in response to ocean warming. It was first recorded in the far southwest of England and subsequently progressed along the southwest peninsula as far east as the Isle of Wight and northwards onto the north Devon coast (see Blight



and Thompson, 2008, and references therein). Long-established populations on the south coast are also thought to be increasing in abundance, perhaps at the expense of *L. hyperborea* (Keith Hiscock, pers comm).

The remaining kelp species are structurally and functionally diverse and can be locally abundant and sometimes dominant. *Saccharina latissima* (formerly *Laminaria saccharina*) has a short stipe and a single, undivided frond (up to 4 m in length) with a 'frilly' undulating margin. It is a short-lived perennial, reaching maturity at 1-2 years and living for up to 4 years. *S. latissima* is found from the Arctic to France (although some isolated populations in northern Portugal may persist) and tends to attach to semi-stable substrata (e.g. boulders) or inhabit the margins of dense *L. hyperborea* beds, particularly in sheltered to moderately exposed locations. *Alaria esculenta* has a similar distribution and, in many respects, morphology (having a short stipe and single blade with distinct midrib extending to 1-3 m in length), but is restricted to wave exposed conditions and attaches to stable substrata. It is fertile in about 1 year and lives for 4-7 years. Both species mostly function as mid-successional species and are outcompeted by members of the genus *Laminaria*, although under extremely wave-exposed conditions *A. esculenta* may dominate the assemblage (Hawkins and Harkin, 1985). Finally, two short-lived, annual kelp species are found in waters off the UK and Ireland; *Saccorhiza polyschides* and the non-native *Undaria pinnatifida* ('Wakame'). *S. polyschides* is found from Norway to Morocco, and can be the dominant canopy-former in warmer waters where *Laminaria digitata* and *Laminaria hyperborea* are absent (Hawkins and Harkin, 1985). It is particularly abundant off the southwest coast of Ireland and common throughout much of the UK (Norton, 1978). It is a fast-growing opportunistic species that can tolerate very calm through to very turbulent conditions, attaches to a range of substratum types, and is often found at the margins of dense *Laminaria* beds (Norton, 1969). There has been some evidence to suggest that the relative abundance of *S. polyschides* has increased along the south coast of England (Birchenough and Bremner, 2010, Hawkins pers obs), but reliable data are lacking. There is little doubt, however, that the abundance and distribution of the global invader *Undaria pinnatifida* has increased in UK waters in recent decades; having first been recorded on the south coast of England in 1994 (Fletcher and Manfredi, 1995) it has now become established at a number of locations in the UK (Farrell and Fletcher, 2006). As it can penetrate low salinity waters, *U. pinnatifida* has become common in some marinas and estuaries. Although *U. pinnatifida* is still restricted to artificial substrates, it is anticipated that this species will shortly colonise natural intertidal and subtidal habitats.

The structure of entire kelp beds - in terms of the identity and abundance of kelp species and their associated biodiversity - varies considerably in space and time as a function of wave exposure (and storm frequency and magnitude), light levels (influenced by depth and turbidity), sedimentation and temperature. As a general rule, in moderately exposed conditions dense stands of *Laminaria digitata* will persist from the low water mark to a few metres depth, with the

upper limit of *Laminaria digitata* set by physical stress and competition with *Fucus serratus* (Hawkins and Harkin, 1985) and the lower limit set by competition with *Laminaria hyperborea* which is mediated by wave exposure. *Saccharina latissima* and *Sacchorhiza polyschides* generally inhabit the immediate subtidal, fringes of rocky reefs or boulders. As the substratum extends into deeper water and light becomes limiting, the density of kelps decreases and isolated (often large) individuals of *Laminaria hyperborea* and *Sacchorhiza polyschides* form 'park land'. In some locations, such as off the Isle of Man and in Lough Ine, grazing by sea urchins may control the lower depth limit of kelp beds (Jones and Kain, 1967; Kain, 1975a; Kitching and Ebling, 1961). While many kelp-dominated systems are dynamic and exhibit pronounced spatio-temporal variability at multiple scales (see Smale et al., 2010 for Australian examples; Wernberg and Goldberg, 2008), others are relatively more stable. For example, southerly distributed European kelp beds (i.e. along the Iberian Peninsula) are more prone to short-term temporal variability arising from variations in both the strength of coastal upwelling and recruitment patterns of dominant canopy formers (e.g. *S. polyschides*). Similarly, high latitude kelp beds may exhibit considerable temporal variability over years to decades, driven by stochastic (or perhaps cyclical) periods of overgrazing by sea urchins, in particular *Strongylocentrotus droebachiensis* (Norderhaug and Christie, 2009). It could be that mid-latitude kelp beds are more stable within ecological timescales, although explicit comparisons of variability patterns along broad scale latitudinal gradients are lacking.

At regional spatial scales across the UK and Ireland, there are some general trends in kelp bed structure that are primarily driven by the abundance distribution patterns of individual kelp species. The occurrence of the cold water kelps *Laminaria hyperborea*, *Saccharina latissima* and *Alaria esculenta* generally increases with latitude from southern England to northernmost Scotland (Fig. 3), which corresponds with a geographical shift from the southern limit towards the centre of these species' distributions. Broadly speaking, optimal kelp habitat off the west and north coasts of Scotland is characterised by dense stands of *L. hyperborea* (wave exposed) or *S. latissima* (more sheltered), whereas kelp beds off the south and west coasts of the UK and Ireland are more mixed, with a greater relative abundance of *Sacchorhiza polyschides* and *L. ochroleuca*. This regional-scale shift in kelp bed structure occurs over a latitudinal temperature gradient of some 3° C, and may provide some insights into the likely effects of gradual seawater warming on kelp bed structure and function (see 'Climate change' section below).

#### **4. Ecological goods and services**

Kelps are hugely important as primary producers (both locally and via export of detritus to nearby habitats), as habitats and repositories of marine biodiversity and secondary productivity, as natural coastal defence, and as nursery grounds for exploited species (reviewed by Steneck et

al., 2002). Specific UK-based examples of these roles are illustrated in Fig. 4 and described in detail below.

### **i. Biodiversity**

Habitat forming species or 'engineers' (sensu Jones et al., 1994), such as kelps and corals, exert control over entire communities by modifying the environment and resources available to other organisms (e.g. Bertness and Callaway, 1994; Jones et al., 1997). In particular, kelps alter light, nutrients, sediments, physical scour, and water flow conditions for proximal organisms while providing structural habitat for a wide range of flora and fauna. Within the UK alone, over 1800 species have been recorded from kelp dominated habitats. As habitat-formers, kelps directly provide 3 distinct primary habitats; the holdfast, the stipe, and the lamina. In addition, epiphytes (primarily attached to the stipe) provide a secondary habitat for colonisation. Over 40 years of descriptive research on kelp-associated faunal assemblages in the NE Atlantic has unequivocally demonstrated that kelps harbour considerable biodiversity (e.g. Blight and Thompson, 2008; Christie et al., 2003; Edwards, 1980; Moore, 1971, 1973). For example, a study on *Laminaria hyperborea* in Norway by Christie et al. (2003) showed that, on average, a single kelp plant supports ~40 macroinvertebrate species represented by almost 8000 individuals. The biogenic habitat formed within the kelp holdfast generally harbours the most diverse assemblages, with species richness per holdfast typically in the region of 30-70 macrofaunal species (Blight and Thompson, 2008; Christie et al., 2003; Edwards, 1980). However, assemblage richness and structure is strongly influenced by the volume and complexity of the holdfast habitat, as well as external local and regional factors (e.g. turbidity, exposure). The secondary habitat formed by epiphytes on kelp stipes is often utilised by a highly abundant and diverse fauna (Christie et al., 2003), which varies considerably in space (i.e. with location and depth) and time (i.e. with season and year). Kelp lamina generally support lower diversity, although epiphyte growth can be very extensive under certain conditions. While diversity may be low, the abundance of several widespread epibionts of kelp lamina (e.g. the blue rayed limpet, *Patella pellucida*, Fig. 4 and the 'sea mat' bryozoan *Membranipora membranacea*) can be locally very high (Christie et al., 2003).

At spatial scales larger than that of a single kelp plant, multiple individuals form extensive beds that provide habitat for a vast array of marine organisms. Rich understory assemblages of plants and animals persist beneath kelp canopies, which ameliorate environmental stressors, and provide shelter and food. With respect to understory macroalgae, more than 40 species (principally rhodophytes) are regularly found beneath kelp canopies, although their relative abundance varies considerably between biogeographic regions and is strongly influenced by local factors such as depth, turbidity, wave exposure and siltation (Maggs, 1986). Studies in other temperate regions have indicated that diverse macroalgal canopies may support greater biodiversity in understory assemblages compared with mono-specific canopy stands (Smale,

2010), perhaps because structurally varying canopy-formers enhance habitat diversification. While this has not yet been examined in UK waters, the region represents a tractable model system due to the co-existence of several canopy-forming kelp species.

Kelp beds in the UK and Ireland also provide habitat for large invertebrates, such as gastropod molluscs, crustaceans, and echinoderms, some of which have significant ecological (e.g. sea urchins, see Jones and Kain, 1967; Kitching and Thain, 1983) or socioeconomic (e.g. the European lobster, see Johnson and Hart, 2003) importance. Kelp beds are particularly effective nurseries for juvenile invertebrates and fish (e.g. Atlantic cod and pollock), which provide shelter from predation. Moreover, kelp beds are key feeding grounds for many NE Atlantic fish species, such as *Labrus bergylta* (Ballan wrasse) and *Ctenolabrus rupestris* (Goldsinney wrasse), which prey on kelp-associated invertebrates (Norderhaug et al., 2005). In turn, elevated fish densities in kelp beds attract large piscivores, such as large fish, seals and otters. In general, subtidal rocky reefs with extensive stands of *Laminaria hyperborea* support greater species richness than reefs without high kelp coverage (Burrows, 2012). Further analysis indicates that species richness on subtidal rocky reefs around the UK generally increases with increasing relative abundances of all the major canopy-forming kelp species (Fig. 5).

The vast majority of work on kelps as habitat formers and repositories of biodiversity has focussed on *Laminaria hyperborea*. What is clear, however, is that different kelp species have different morphologies and life histories and, as such, provide structurally varying habitat. This is important within the context of environmental change, as any shifts in the relative abundance of kelp species may have knock-on effects on their associated biodiversity. For example, understory assemblages associated with *Laminaria digitata* are distinct from those beneath *L. hyperborea* because the stipe of the former is shorter and less rigid. As a result, the substrate near to *L. digitata* plants experiences greater physical abrasion by lamina such that fewer species can inhabit the understory compared with *L. hyperborea* (Kain, 1979). However, certain species such as the limpet *Patella ulyssiponensis* and the sponge *Halichondria panacea* are facilitated by 'sweeping' by *L. digitata*, as they would otherwise be outcompeted by understory algae. Similarly, subtle differences in morphology (e.g. holdfast volume and complexity, stipe roughness and susceptibility to epiphyte growth) can have a strong influence on the structure and richness of associated assemblages (e.g. Blight and Thompson, 2008). The nature of inter-specific and regional-scale variability in kelps as habitat formers within the UK and Ireland (and the wider implications for biodiversity) is poorly understood and remains an important knowledge gap within the field of kelp bed ecology.

## ii. Productivity and food webs

Kelp beds represent some of the most productive habitats on Earth (Mann, 1973, 2000; Reed et al., 2008), and are a major source of primary production in coastal zones of temperate and polar

oceans worldwide (Steneck et al., 2002). Kelp productivity is strongly correlated with nutrient availability, but is also affected by temperature, wave exposure, light and disturbance regime (see Reed et al., 2008 for detailed discussion). Extension (i.e. growth) rates of kelp vary considerably among species and between geographic regions. In southern California maximum growth rates for the giant kelp *Macrocystis pyrifera* can exceed 30 cm per day (Abbott and Hollenberg, 1976), whereas members of the genera *Laminaria* and *Saccharina* may exhibit maximum extension rates of ~1 cm per day (Parke, 1948). However, extension rates are closely related to morphology and growth strategy, and when growth rates are converted to biomass production per unit area different kelp species tend to exhibit broadly comparable productivity rates (Fairhead and Cheshire, 2004; Krumhansl and Scheibling, 2012; Mann, 1973).

In the Atlantic, kelp primary production can be in excess of  $1000 \text{ g C m}^{-2} \text{ yr}^{-1}$ , and that from *Laminaria* species has been estimated at between 110 and  $1780 \text{ g C m}^{-2} \text{ yr}^{-1}$  (Mann, 1973, 2000), while primary production from phytoplankton in coastal temperate regions is typically between 100 and  $300 \text{ g C m}^{-2} \text{ yr}^{-1}$  (Mann, 2000). Given these relative rates of production, it is possible to approximate the relative proportion of primary production derived from both phytoplankton and benthic macroalgae in UK coastal waters. Walker (1953) estimated an area of  $8000 \text{ km}^2$  of kelp habitat in Scotland alone, which may produce  $10 \text{ M t C yr}^{-1}$  at typical production rates of  $1300 \text{ g C m}^{-2} \text{ yr}^{-1}$  (Dayton, 1985). This compares with a potential phytoplankton production of  $13 \text{ M t C yr}^{-1}$  from  $133,000 \text{ km}^2$  of sea <20km from the coast within the UK exclusive economic zone (EEZ), and  $73 \text{ M t C yr}^{-1}$  from the  $770,000 \text{ km}^2$  of the entire UK EEZ (assuming a rate of production from phytoplankton of  $100 \text{ g C m}^{-2} \text{ yr}^{-1}$ ). Kelp may therefore account for ~45% of primary production in UK coastal waters, and 12% of marine production in the entire UK EEZ. This estimate for annual UK kelp production does not include the extensive shallow subtidal rocky reef habitats found off England and Wales and may therefore be an underestimate. Moreover, when primary productivity rates of intertidal macroalgae are compared with subtidal macroalgae, intertidal production is typically 10% of that from the subtidal (Mann, 2000). Although these coarse estimates should be interpreted with caution, it is clear that kelps make a substantial contribution to primary production in coastal waters off the UK and Ireland.

Some kelp biomass is consumed directly by herbivorous fish and invertebrates, such as the conspicuous blue-rayed limpet *Patella pellucida* (Fig. 4). However, >80% of kelp production enters the carbon cycle as detritus or dissolved organic matter, since little is directly grazed by herbivores (Krumhansl and Scheibling, 2012). Kelps act as 'conveyor belts' of biomass production, as the meristematic tissue is (generally) located at the junction between the stipe and the lamina so older tissue is passed distally with continued growth. At the distal end of the blade, tissue is rapidly or gradually eroded to generate detrital fragments ranging in size from small particulates to large sections of blade. As kelp blades fragment, dissolved organic matter is released, which may account for up to 35% of annual energy production (see Krumhansl and

Scheibling, 2012 and references therein). During times of high water motion (i.e. during intense storms or at highly exposed locations), whole kelps may be dislodged following detachment at the holdfast or breakage at the stipe. The proportion of kelp production that is either eroded as fragments or dislodged as whole plants varies amongst species and with morphology and age of kelp. For *Laminaria* spp. and *Saccharina* spp., however, rates of erosion generally exceed rates of dislodgement (Krumhansl and Scheibling, 2011).

Kelp detritus is either retained within the kelp bed or exported to adjacent habitats by water movement driven by currents, tides or waves. Rates of export exhibit pronounced spatiotemporal variability as they are governed by a complex, interacting suite of factors including water flow, seabed topography, substratum type, and aspects of the detritus itself (e.g. size, buoyancy, density, age). Kelp detritus may settle locally and form a food source for a wide range of benthic invertebrates (Duggins and Estes, 1989; Norderhaug et al., 2003), or be transported to adjacent (Tallis, 2009) or distant habitats (Vanderklift and Wernberg, 2008). Either way, most kelp-derived carbon is consumed by suspension feeders, detrital grazers (such as limpets and *Littorina littorea*) and general consumers of organic material in soft sediments (deposit feeders). An important, but poorly understood, process relating to kelp detritus consumption concerns the interactions between microbes and macrofauna. It is clear that microbial degradation of kelp tissue increases palatability for many grazers by reducing C:N ratios and phlorotannin content (Norderhaug et al., 2003), but the influence of microbial processes on palatability varies between species of kelps (Duggins and Eckman, 1997) and grazers (Norderhaug et al., 2003), and microbial degradation may be less important than for angiosperms such as seagrasses (Bedford and Moore, 1984).

Kelp detritus is particularly important as a spatial subsidy of energy into low-productivity habitats. The most visible example being the deposition of kelp wrack into sandy beach habitats, where it provides a principal food source for rich and abundant microbial and faunal assemblages (Ince et al., 2007). Similarly, exported kelp represents a spatial energy subsidy into seagrass meadows (Hyndes et al., 2012; Wernberg et al., 2006), soft sediments (Bedford and Moore, 1984; Vetter and Dayton, 1998), subtidal reefs (Vanderklift and Wernberg, 2008) and rocky intertidal habitats (Bustamante and Branch, 1996; Tallis, 2009). Kelp detritus may be consumed many kilometres from its source (Vanderklift and Wernberg, 2008) and, following offshore transportation, may enrich soft sediments at depths of 900 m or more (Vetter and Dayton, 1998). In the UK and Ireland, targeted research on kelps as fuels of coastal food webs has been lacking, and specific rates of kelp detritus production and export remain almost entirely unknown (but see Johnston et al., 1977 for experiment on *Saccharina latissima* in Scotland). Evidence from elsewhere would indicate that kelp biomass is a hugely important source of exported energy which influences patterns of secondary production and the distributions of marine organisms. Detritus production and export rates are likely to vary considerably between regions and seasons, and the quantity

and quality of exported material will vary between kelp species. Using evidence from data-rich systems (e.g. northwest Atlantic) will facilitate the formation of testable hypotheses that can direct field-based research needed to enhance understanding of trophic processes and, ultimately, support management decisions.

The fraction of carbon fixed by kelps that is effectively removed from the atmosphere over decadal to century timescales is as yet poorly understood. The process of incorporation into longer-term stores of carbon may depend on the export of particulate kelp detritus from coastal habitats into sediment in deeper water or the export of recalcitrant dissolved carbon into deep ocean water, but the potential for such storage (and thereby influence on the carbon budget) is not inconsiderable.

### **iii. Coastal defence**

Kelp beds, like other biogenic structures in coastal zones (e.g. salt marshes, mangroves), prevent and alleviate the damage caused by flooding and storm events. Kelps beds alter water motion and provide a buffer against storm surges through wave damping and attenuation, and by reducing the velocity of breaking waves (Lovas and Torum, 2001). In doing so, kelp beds reduce coastal erosion and the movement of sand and pebbles from adjacent beaches (Lovas and Torum, 2001; Mork, 1996). This represents a critical ecosystem service that will become more important along many coastlines as the consequences of anthropogenic climate change intensify, namely sea-level rise and an increased magnitude and frequency of storms. However, compared with other coastal habitat-formers (e.g. mangroves, corals), there is a paucity of information on the degree of storm protection offered by kelp beds. It is clear that the magnitude of wave damping is strongly influenced by the morphology and drag co-efficient of the dominant kelp species and, as such, will vary between biogeographic regions. Moreover, the degree of water flow attenuation by kelp beds is correlated with the extent, density and morphology of both the canopy-forming kelps (Gaylord et al 2007), and the understorey macroalgal assemblage (Eckman and Duggins 1989). Other studies on various submerged vegetation types have also found significant relationships between the extent of vegetation and the degree of wave damping and coastal erosion (e.g. Türker et al., 2006). Off Norway, *Laminaria hyperborea* beds may reduce wave heights by as much as 60% (Mork, 1996). As such, *Laminaria* beds in the UK and Ireland may similarly offer some degree of coastal defence and are probably locally important to some coastal settlements. Critically, the importance of kelp beds and other biogenic structures for coastal defence will be amplified by the ramifications of anthropogenic climate change.

### **iv. Goods**

Living resources derived from kelp-dominated habitats have long been exploited by humans. Indeed, the recently proposed 'kelp-highway' hypothesis suggests that kelp forests may have

facilitated the movement of maritime peoples from Asia to America some 16,000 years ago. Around this time, a deglaciated coastal migration route through the North Pacific – a linear band of highly productive kelp forests extending discontinuously from Japan to Baja California – was probably used by maritime hunter gatherers that subsisted on shelled invertebrates, fish and large mammals inhabiting kelp habitats (Erlandson et al., 2007). Extensive kelp forests would also have buffered wave energy, offered secure moorings for boats and assisted with navigation, therefore facilitated a coastal, migratory existence (Erlandson et al., 2007). To this day, the magnified secondary productivity characteristic of kelp bed habitats is exploited for human consumption. In the UK and Ireland, kelp bed habitats are vital for the European lobster, *Homarus gammarus*, where it preys on a variety of molluscs and crustaceans, and are also home to velvet swimming crabs (*Necora puber*) and seasonal spider crab migrants (*Maja brachydactyla*). The lobster fishery is worth ~£30m per year to the UK economy, while the smaller crab fisheries are important for both export and recreation (Marine Management Organisation, 2012). Kelp beds also serve as a nursery for many fish species, including Atlantic Cod (*Gadus morhua*), and attract targeted fish species such as European sea bass (*Dicentrarchus labrax*), pollack (*Pollachius pollachius*) and conger eels (*Conger conger*).

Kelp itself has myriad of uses and applications. The first use of kelps and other macroalgae to feed domestic animals may have occurred as early as the 5<sup>th</sup> millennia BC, soon after the arrival of the first domestic herds (Balasse et al., 2005). Most famously, a breed of sheep on North Ronaldsay (Orkney Islands, Scotland) feeds almost entirely on beach wrack (principally *Laminaria hyperborea*) for most of the year. Stable isotope analysis suggests that the North Ronaldsay breed has been consuming kelp since the 4<sup>th</sup> millennia BC, during which time it has adapted its rumen bacteria to facilitate the breakdown of laminarin (the storage glucan in brown algae), and adapted an unusual pattern of grazing and ruminating that follows the tidal cycle rather than the (more typical) diurnal cycle (Balasse et al., 2005). More sophisticated methods are now used to process kelp for animal feed supplements for both agriculture and aquaculture. Kelp is rich in nutrients and alginates which condition soils and, as such, has also long been collected and used as a fertiliser (a practice that is still commonplace in parts of Scotland, Ireland and the Channel Islands).

Industrial scale kelp harvesting in Scotland stems back to the 17<sup>th</sup> Century, when it was collected in great quantities and burnt in kelp kilns to produce sodium carbonate. 'Kelp ash' was used in the manufacture of glass and soap and for pottery glazing, as well as for fertiliser. Since the early 20<sup>th</sup> Century, kelps have principally been harvested for alginates, which are used in foods, textiles and pharmaceuticals. Alginates are extracted chemically and used in bulking, gelling, and stabilizing processes; about 25,000 tonnes of alginate per year are extracted world-wide (Bixler and Porse, 2011). Kelp is currently commercially harvested in the northern and western isles of Scotland,



while commercial farming of *Laminaria digitata* has recently been developed off the west coast of Ireland. However, the magnitude of kelp harvesting in the UK and Ireland is low in comparison to neighbouring France and Norway, where 50,000 tonnes of *L. digitata* and 200,000 tonnes of *Laminaria hyperborea* respectively are harvested each year (primarily for alginate production).

The current demand for clean, non-fossil fuel based energy production has thrown kelps into the limelight as potential sources of biofuels. Kelps can grow very quickly (up to 50 cm per day), are rich in polysaccharides and do not compete with land-based crops for space, fertilisers and water. Moreover, recent advances in bioengineering now allow alginate polysaccharides to be degraded, metabolised and converted to ethanol (Wargacki et al., 2012). There is, therefore, increasing interest in large-scale harvesting and culturing of kelps for biofuels, including in Scotland and Ireland. However, a recent cradle-to-grave analysis of the carbon footprint of the production of biofuels (ethanol and methane) from seaweeds indicated that other production of biofuels from other sources (e.g. corn, wheat, sugar cane) is more efficient (Fry et al., 2012). Clearly, the magnitude of kelp production for biofuels would need to be substantial to have any bearing on the energy market, which could have wide-ranging implications for coastal ecosystems that remain poorly understood (see 'threats' section, below).

Kelp itself has long been directly consumed by humans. In Asian cuisine, kelps such as *Saccharina japonica* ('Kombu') and *Undaria pinnatifida* ('Wakame') – now a global invasive pest - have been vital ingredients for many centuries. In coastal communities in the UK non-kelp seaweeds have been consumed for at least 4000 years, particularly *Palmaria palmata* ('Dulse'), *Chondus crispus* ('Carageen'), *Porphyra umbilicalis* ('Purple laver') and *Ulva lactuca* ('Green laver'). Although all kelps in the UK and Ireland are edible, *Saccharina latissima* is considered the most palatable due to its sweet taste. Kelp 'crunchies' – a cornbread snack flavoured with *Alaria esculenta* – were briefly on the market in the 1980s-90s, but failed to achieve mainstream popularity. More recently, kelps including *A. esculenta* and *S. latissima* are being marketed as 'sea vegetables' by health food companies, due to their high levels of vitamins and minerals and low levels of salt and digestible sugars (alginate has also been touted as an effective slimming agent as it reduces fat absorption). As such, some suppliers in Scotland and Ireland harvest kelps for human consumption but these operations are currently fairly small scale.

## **v. Socio-economic importance**

Coastal marine biodiversity in the UK and Ireland is of significant socio-economic importance. For example, Beaumont et al. (2008) calculated that the leisure and recreation industries directly reliant on coastal marine biodiversity contribute >£11 billion to the UK economy each year. In addition to this monetary value, engagement with marine life has considerable benefits for human health and wellbeing and has directly influenced cultural and economic activities for thousands of years. Kelps as primary producers and habitat providers play a key role in the maintenance of fish

stocks and ecosystem structure and, therefore, indirectly help to sustain regional fisheries and the coastal communities they support (see 'Goods' section above for examples). Diverse, healthy kelp-dominated habitats offer a range of recreational activities which significantly contribute to regional economies and have wider benefits from human health and wellbeing. Key recreational activities associated with kelp beds include snorkelling, scuba diving, free diving, kayaking, wildlife watching and angling.

In Lyme Bay (a medium-sized embayment off the south coast of England) recreational scuba diving – much of which is conducted on submerged kelp-dominated rocky reefs – contributes >£2.5 million per year to the local economy and supports ~10 independent dive operators (Rees et al., 2010). With regards to sea fishing, the total expenditure by anglers resident in England and Wales is estimated at £538 million per year from 12.7 million angler days (estimate for 2004, see Beaumont et al., 2008). Although this activity is not wholly focused on or near kelp beds, submerged rocky reefs are often favoured by anglers targeting demersal species and, as such, a substantial component of that valuation relies on kelp bed biodiversity. The socio-economic importance of kelp bed habitats is magnified in isolated coastal regions such as the Western Isles of Scotland and the Isles of Scilly. The vast kelp beds along the north and west coasts of Scotland support abundant wildlife, such as sea birds, seals and otters, and the value of this biodiversity to local economies through 'green' tourism has long been recognised. Similarly, tourism accounts for 85% of the economy of the Isles of Scilly, primarily through coastal based activities like sea angling, seal and bird watching and scuba diving (Beaumont et al., 2007). Much of this is based around the widespread shallow water kelp beds that extend from the islands.

Finally, there are myriad of non-monetary benefits derived from kelp bed biodiversity. There is growing appreciation for the 'feel good' or 'warm glow' benefits which are derived from marine organisms without using them (Beaumont et al., 2007). Kelp-associated species, from seaweeds to sea stars to seals, have inspired artists, facilitated educators and fascinated tourists for many generations.

## **5. Threats and knowledge gaps**

### **i. Climate change**

In Europe, marine plants and animals have undergone climate-driven shifts in their distribution, and major changes in assemblage structure and ecosystem function are projected to occur as a result (Hawkins et al., 2009; Helmuth et al., 2006). Ecological responses to recent warming in the NE Atlantic have included shifts in the distributions of plankton (Beaugrand et al., 2009; Pitois and Fox, 2006), intertidal invertebrates (Hawkins et al., 2003; Mieszkowska et al., 2006) and fish (Genner et al., 2004), as well as phenological and behavioural changes (Edwards and

Richardson, 2004; Moore et al., 2011; Sims et al., 2001). For plankton, intertidal invertebrates and fish, access to long-term historical data has facilitated robust examinations of temporal shifts in assemblage structure in response to climate. Whilst patterns of ecological change, and the processes driving them, have been well documented in both intertidal (Hawkins et al., 2009; Helmuth et al., 2006) and pelagic (Richardson and Schoeman, 2004) systems, there is currently limited information from subtidal benthic systems, especially from hard-bottom habitats that cannot be routinely trawled, dredged or cored. This was highlighted by the recent 'Marine Climate Change Impacts Knowledge Gaps' report, which stated that "*knowledge of large scale benthic species distributions within UK waters is required, to detect changes over large areas of the seabed and patterns of benthic response to climate change*". This understanding is urgently needed to maintain "*healthy and biologically diverse seas*" (MCCIP, 2012).

Kelps are cool-water species that are stressed by high temperatures (Steneck et al., 2002), so that seawater warming will affect the distribution, structure, productivity and resilience of kelp beds (Dayton et al., 1992; Harley et al., 2012; Wernberg et al., 2010). Poleward range contractions have been predicted for several more northerly-distributed kelp species (e.g. *Alaria esculenta*, *Laminaria digitata*, *Laminaria hyperborea*) in response to ocean warming in the Atlantic (Hiscock et al., 2004; Muller et al., 2009). It is evident that the relative abundance of several kelp species changes with latitude along NE Atlantic coastlines, which corresponds to a regional-scale temperature gradient, and that several habitat-forming kelps are at their range edge in the UK and Ireland (e.g. *Laminaria ochroleuca* at its northernmost limit, *A. esculenta* at its southernmost limit, Fig.3). Because of these distribution patterns, and because the distributions of some intertidal species have shifted, several authors have predicted that relatively southerly-distributed species will increase in abundance while more northerly-species will decrease in abundance and/or undergo range contractions in the UK and Ireland (Breeman, 1990; Hiscock et al., 2004). There is some evidence to suggest that more southerly-distributed kelp species (e.g. *L. ochroleuca* and *Saccorhiza polyschides*) have increased in abundance and have undergone poleward range-edge expansions while, conversely, northern species (e.g. *A. esculenta*) have decreased in abundance in response to recent warming (Birchenough and Bremner, 2010; Simkanin et al., 2005). However, the evidence base is largely based on anecdotal reports and unpublished survey data, and detailed historical examinations of distribution patterns are lacking.

In conjunction with ocean warming, observed and predicted increases in storminess (Lozano et al., 2004; Weisse et al., 2005) will impact kelp beds, as canopy-forming macroalgae may be damaged and dislodged during periods of intense wave action. Increased storminess and canopy removal will affect the structure and functioning of entire kelp habitats, by altering patch dynamics (Dayton and Tegner, 1984) and potentially driving ecological phase shifts (Dayton et al., 1999; Wernberg et al., 2011). Crucially, multiple concurrent stressors do not act in isolation but often combine synergistically in their effects, so that the total impact is far greater than the sum of

individual factor effects (Crain et al., 2008; Harvey et al., 2013). Synergism can cause 'ecological surprises', where unexpected regime shifts occur quickly because a tipping point is exceeded (Crain et al., 2008). In kelp beds, multiple stressors can cause irreversible shifts from complex, biologically diverse habitats to simple turf-dominated 'barrens' (Dayton and Tegner, 1984; Ling et al., 2009).

As changes in the identity and abundance of habitat-forming species can have wide-ranging consequences for community structure and ecosystem functioning (Jones et al., 1994), there is a pressing need to examine climate-driven distribution shifts and their wider implications. For example, if a cool water habitat-former is replaced by a warm water species that is functionally and structurally similar, it is plausible that the wider community or ecosystem will be relatively unimpacted (e.g. Terazono et al., 2012). Conversely, if a structurally or functionally dissimilar species becomes dominant, or habitat formers are lost and not replaced, then widespread changes in biodiversity patterns and ecological processes are likely to ensue (Ling, 2008). In the UK and Ireland, a range contraction of *Alaria esculenta*, the dominant species on very exposed shores and an important mid-successional species in more sheltered locations (Hawkins and Harkin, 1985), would impact community structure and functioning as there is no warm water equivalent. *A. esculenta* is particularly susceptible to climate fluctuations, having disappeared from much of the English Channel during a warm period in the 1950s, and not recovering as conditions became cooler in the 1960s. Replacement of *Laminaria hyperborea* with *Laminaria ochroleuca*, which are more similar both structurally and functionally, may have less knock-on effects, although subtle differences in kelp species traits have been shown to influence local biodiversity patterns (Blight and Thompson, 2008). Most dramatically, the predicted increase in the relative abundance of *Saccorhiza polyschides* (Birchenough and Bremner, 2010) could have major implications for kelp bed structure and functioning as it is a fast-growing, annual species with distinct morphological and ecological traits (Table 1). As kelps make a significant contribution to coastal primary production, facilitate export of carbon from high to low productivity systems, and fuel entire food webs, changes in the quality or quantity of detrital material resulting from climate-driven changes in kelp species identity, abundance or productivity could have far-reaching consequences (Krumhansl and Scheibling, 2012). In the UK and Ireland the wider implications of shifts in kelp species identity and abundance for kelp bed productivity, trophic linkages and ecosystem functioning are almost entirely unknown.

It may be possible to predict the future structure of kelp beds under continued ocean warming in the UK and Ireland by examining the current structure of kelp beds under warmer conditions further south. For example, coastal waters off northern Portugal are some ~3°C warmer than off southern England and some ~5°C warmer than northwest Scotland, which is within the projected range of NE Atlantic warming within the next 50-80 years (Philippart et al., 2011). The structure of kelp bed habitats off northern Portugal and Spain is strikingly different to those in UK waters

(Fernandez, 2011; Hawkins and Harkin, 1985; Tuya et al., 2012). Most obviously, the geographical range of *Laminaria digitata* does not extend further south than France and therefore does not form dense stands in the low intertidal and shallow subtidal zones. *Laminaria hyperborea* is present southward to north Portugal, but is generally much smaller and lower in abundance, forming 'parks' rather than dense canopies under warmer conditions. Conversely, *Laminaria ochroleuca* is more abundant and often larger, while *Sacchoriza polyschides* is generally more abundant across a wider depth range. Recent observations indicate that *Sacchoriza polyschides* and (Fernandez, 2011), probably, *Laminaria ochroleuca* (Fernandez, 2011) and *L. hyperborea* (Tuya et al., 2012) have undergone range contractions in recent decades in response to warming off the Iberian Peninsula. In contrast, Lima et al. (2007) suggest that the southern distribution limits of *L. hyperborea* and *Saccharina latissima* have not shifted in response to ocean warming over 50 years, based on historical surveys of intertidal habitats. It is very likely that kelp bed biomass and productivity will be diminished under warmer, stormier conditions (Krumhansl and Scheibling, 2012), although direct measurements of kelp bed structure, biodiversity, productivity, detritus production and export, and resistance and resilience to perturbation along a regional scale temperature gradient along the NE Atlantic coastline are lacking. Comparative experimental work along regional scale temperature gradients is a promising approach in climate change ecology and can yield critical information on the mediation of ecological processes by ocean climate (Wernberg et al., 2012; Wernberg et al., 2010). Comparative kelp research along a regional scale temperature gradient along Western Europe, spanning from Portugal (average sea temperature ~16°C) to Norway (average sea temperature ~8°C), would significantly enhance our understanding of climate change impacts on kelp bed structure and functioning.

Finally, two key knowledge gaps concerning the climate change ecology of kelp beds. First, there is a paucity of information on the capacity of local kelp populations to acclimatise or even adapt to climate mediated change. It is clear that kelp populations can maintain physiological processes under a wide range of environmental conditions through local adaptation (e.g. Delebecq et al., 2013), but the rate at which kelp species can respond to rapidly changing temperatures and other localised stressors is unclear. Second, seaweed populations are particularly susceptible to short term extreme warming events (Dayton and Tegner, 1984; Smale and Wernberg, 2013; Wernberg et al., 2013), which may increase in magnitude and frequency as a consequence of anthropogenic climate change (Feng et al., 2013; Jentsch et al., 2007). Short-term climate variability may pose greater threat to kelp populations at lower latitudes (i.e. towards range edges) than those within mid-latitude temperate regions. For example, southerly-distributed kelp beds off Spain and Portugal, which are subjected to environmental variability driven by the strength of coastal upwelling, comprise edge-of-range species with dynamic distributions (Fernandez, 2011; Tuya et al., 2012). Anomalous warming events also have the potential to

cause step-wise changes in the structure and functioning of kelp beds in mid-latitude systems, and greater understanding of the resistance and resilience of kelp populations and their associated communities to such events is of ever-growing importance.

## ii. 'Top down' processes

Overgrazing by invertebrate herbivores, particularly sea urchins, can decimate kelp forests and cause phase shifts from structurally and biologically diverse habitats to depauperate 'barrens' (reviewed by Steneck et al., 2002). Sea urchin populations are kept in check by a wide range of predators, including lobsters (Ling et al., 2009), fish and sea otters (Estes and Duggins, 1995), and by disease outbreaks (Scheibling, 1986). Conversely, sea urchin population booms have been attributed to overfishing of sea urchin predators (Jackson et al., 2001; Ling et al., 2009), climate change (Ling, 2008) and episodic recruitment events (Hereu et al., 2004; Valentine and Edgar, 2010). Following the formation of urchin barrens, a complex suite of interacting factors and feedback mechanisms affect the persistence of barrens and the likelihood of kelp bed recovery towards a pre-perturbed state (Norderhaug and Christie, 2009). In the North Atlantic, the green sea urchin *Strongylocentrotus droebachiensis* has deforested extensive areas of kelp forest in eastern Canada (Mann, 1977), Iceland (Hjorleifsson et al., 1995) and northern Norway (Leinaas and Christie, 1996), with major consequences for ecosystem structure and functioning (Steneck et al., 2002). At lower latitudes, the importance of grazing by the purple sea urchin *Paracentrotus lividus* on macroalgal assemblages has been recognised along Mediterranean and Atlantic coastlines (Bulleri et al., 1999; Hereu et al., 2004; Tuya et al., 2012).

In the UK and Ireland, the extent of deforestation by urchin grazing is generally restricted and patchy, although heavily grazed areas are more common in Scotland. Urchin grazing can certainly be important in setting local distributions of macroalgae, including kelps. Some of the earliest grazing work was conducted in the Isle of Man (Jones and Kain, 1967), which showed that the edible sea urchin *Echinus esculentus* may determine the lower depth limit of *Laminaria hyperborea* stands through intense grazing of young sporophytes. Similarly, *Paracentrotus lividus*, which is relatively common along the west coast of Ireland, influences the distribution of macroalgae within Lough Ine through grazing activity (Kitching and Thain, 1983; Norton, 1978). The green sea urchin *Strongylocentrotus droebachiensis*, which is only found in the north of Scotland, may also cause restricted patchy deforestation, but extensive barren formation has not been attributed to this species.

Unlike many other temperate regions of the world, including Nova Scotia, the Gulf of Maine, eastern Australia, Alaska and Northern Japan (reviewed by Steneck et al., 2002), there is little evidence for the formation of extensive, widespread sea urchin barrens off the UK and Ireland. Some of the most dramatic impacts of sea urchin grazing have been documented in regions where sea urchin predators, such as large lobsters (Ling et al., 2009) and sea otters (Estes and

Duggins, 1995), have recently been removed through human activity. The consequent trophic cascade effects have, in some cases, led to widespread destruction of kelp forests and diminished biodiversity. In the UK and Ireland, apex predators (especially large finfish) have been overfished for centuries, so that large predatory crabs have become the dominant predators in many coastal ecosystems. As such, the likelihood of sea urchin population explosions resulting from removal of apex predators is probably low (see Sivertsen, 2006 for Norwegian context). However, trophic interactions in kelp forests off the UK and Ireland are poorly understood and targeted research is required to address the level of threat posed by top down processes, which will be influenced by environmental change in complex and non-linear ways.

### **iii. Harvesting and cultivation**

The demand for kelp for human consumption, alginate production, aquaculture feed and (potentially) biofuel has increased in recent decades and will almost certainly continue to grow. Direct removal of kelps has major implications for kelp population structure, whole community dynamics and wider ecosystem functioning (Christie et al., 1998; Krumhansl and Scheibling, 2012; Vásquez, 2008). There is some evidence to suggest that, due to the rapid recruitment and growth of kelps and their associated species, industrial-scale wild harvesting of kelps can be achieved sustainably. For example, in both Norway and Chile some 130,000 to 200,000 tonnes are extracted annually, and have been for some time (Vásquez, 2008; Veá and Ask, 2011). However, while a limited natural harvest may be sustainable if properly managed with appropriate fallow periods, the potential for impact on the other services provided by kelp may be considerable. Although kelps recruiting into harvested areas may reach pre-perturbed densities and sizes within a few years, their associated assemblages may take considerably longer to recover (Christie et al., 1998). Kelp harvesting also negatively impacts the abundance of gadoid fishes and reduces the area of habitat preferred by foraging seabirds (Lorentsen et al., 2010), for example.

Within the UK and Ireland, the potential for kelp biomass to be used for conversion to biofuels has reignited interest in large scale kelp production. A realistic contribution to energy markets through bioethanol production may require more kelp than can be wild harvested from natural habitats, prompting efforts to develop methods of farming kelp. Mariculture of kelps is commonplace in Asia, particularly in China, where demand for seaweeds for human consumption is high. It is clear that kelp farming can impact local patterns of water movement, and may cause organic enrichment of sediments and anoxia (Krumhansl and Scheibling, 2012). However, many researchers are championing integrated aquaculture practises that utilize kelps as bio-filters within multi-trophic farming operations (Neori et al., 2004; Troell et al., 2009). Within the UK context, the Crown Estate recently commissioned an independent investigation into the wider ecological effects of proposed seaweed mariculture off the west coast of Scotland (Aldridge et al.,

2012). Using ecosystem-based modelling approaches, the authors concluded that; *“the effects of the proposed farming activity on nutrient concentrations are expected to be 'marginally significant'.....and “might become 'certainly significant'.....The observable effects of nutrient removal would be a lower nutrient concentration in the water, decreased productivity and energy fluxes through the pelagic system, decreased flux of organic material to the seabed, and subtle alteration to community structure.”* (Aldridge et al., 2012). It is beyond doubt that large scale kelp production, through both wild harvesting and mariculture, has the potential to impact kelp populations, their associated benthic communities, and wider ecosystem structure and functioning. While it is recognised that a conservative ecosystem-based management approach is a pre-requisite for achieving sustainable production, the baseline knowledge on the structure and functioning of kelp ecosystems at regional scales needed to underpin such an approach is currently lacking.

## **6. Conclusions**

Global emissions of greenhouse gases are tracking the high emission scenarios considered by the IPCC, suggesting that future climate impacts will be more severe than widely acknowledged in policy (New et al., 2011). A robust appreciation of the likely ecological consequences of climate change is therefore increasingly urgent. Moreover, coastal ecosystems, dominated by highly productive seagrass and macroalgal habitats, provide ecosystem services valued at ~US\$19,000 ha<sup>-1</sup> yr<sup>-1</sup>, making them the third most productive systems globally in terms of value per hectare (Costanza et al., 1997). In the UK alone, the estimated direct economic value of coastal marine ecosystems exceeds £15 billion per year (Beaumont et al., 2008). As such, any changes in productivity as a result of either the direct effects of anthropogenic change on ecologically important species, or through climate mediated changes in the strength and direction of ecological processes, could lead to broad scale implications for the goods and services coastal ecosystems provide. There is a paucity of large scale benthic distribution data for UK waters, especially for subtidal rocky reef habitats, which hinders our ability to detect changes in species distributions across large spatial scales. Such information, when combined with experimental studies of the effects of climate warming and predictive modelling approaches, will allow us to confidently describe and forecast responses to environmental change and human activities such as harvesting.

Pre 1980s, the marine biological community of Britain and Ireland significantly contributed to the wider understanding of kelp bed structure and function through world-leading research. However, in recent decades, following rising costs associated with scuba diving and shifts in research priorities, subtidal kelp-dominated habitats have been strikingly understudied despite their fundamental role in coastal food webs and ecosystems. In contrast, research on *Macrocystis* forests in California has yielded critical information on the relative importance of ‘top down’ versus



'bottom up' factors in structuring marine benthic communities (Byrnes et al., 2011; Foster et al., 2006; Guenther et al., 2012; Halpern et al., 2006), shed light on regional-scale variability in environmental drivers (Edwards, 2004; Reed et al., 2011), and informed management actions such as the implementation of MPAs (see White et al., 2011 and references therein). Similarly, intense field-based research on *Eckonia* beds in Australia has yielded novel insights into scale-dependency in species interactions (Irving and Connell, 2006) and biodiversity patterns (Smale et al., 2010), the connectivity of populations (Coleman et al., 2011) and habitats (Wernberg et al., 2006), as well as the resilience of kelp beds to perturbations including increased herbivory (Ling, 2008; Ling et al., 2009), short-term climate variability (Wernberg et al., 2013), and physical disturbance (Wernberg et al., 2010). In the UK, there is considerable scope for cutting-edge research on ecological resilience, functional ecology and range-edge dynamics because (i) a number of habitat-forming kelp species co-exist, (ii) some kelp species are found at the edge of their range, and (iii) the northwest Atlantic region has warmed at rates above the global average. However, the current state of knowledge is poor and even basic information on species distributions, kelp bed biodiversity, and species interactions is lacking (but see Burrows 2012). The current evidence-base is largely anecdotal and entirely inappropriate for informing management decisions, while process-based knowledge acquired from realistic field-based observations and experiments is completely absent. We strongly urge that (i) funding agencies and marine management organisations acknowledge these knowledge gaps and provide the resources needed to begin to fill them, (ii) researchers and institutions adopt the collaborative approach needed to share the financial and logistical burden of conducting field-based research in UK waters, and (iii) researchers develop close alliances with kelp ecologists in knowledge-rich regions (e.g. Australasia and North America) in order to adopt contemporary, cross-disciplinary approaches to kelp bed research in UK waters, which will expedite progress and facilitate comparative work across contrasting systems. In this manner, significant progress can be made in understanding the resilience of kelp beds to rapid environmental change, which will ultimately improve our ability to manage and conserve these important habitats.

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Table 1. Kelp species in UK waters. The geographical range and approximate depth range, mature sporophyte length and lifespan of kelps in UK waters are shown. Also indicated is the predicted change in abundance and/or range of each species in response to continued environmental change. <sup>a</sup>The lifespan of *L. ochroleuca* in UK waters is unknown and is estimated based on its close affinity with *L. hyperborea*.

Species	Distribution	Depth range	Length	Lifespan	Change(?)
<i>Laminaria hyperborea</i>	Arctic-Portugal	0-30 m	2-4 m	5-18 yrs	decrease
<i>Laminaria digitata</i>	Arctic-France	0-15 m	2-3 m	4-6 yrs	decrease
<i>Laminaria ochroleuca</i>	UK-Morocco	0-30 m	2-4 m	5-18 yrs <sup>a</sup>	increase
<i>Saccharina latissima</i>	Arctic-France	0-30 m	1-4 m	2-4 yrs	decrease
<i>Alaria esculenta</i>	Arctic-France	0-35 m	1-3 m	4-7 yrs	decrease
<i>Saccorhiza polyschides</i>	Norway-Morocco	0-35 m	2-4 m	1 yr	increase
<i>Undaria pinnatifida</i>	Global NIS	0-15 m	1-3 m	1 yr	increase

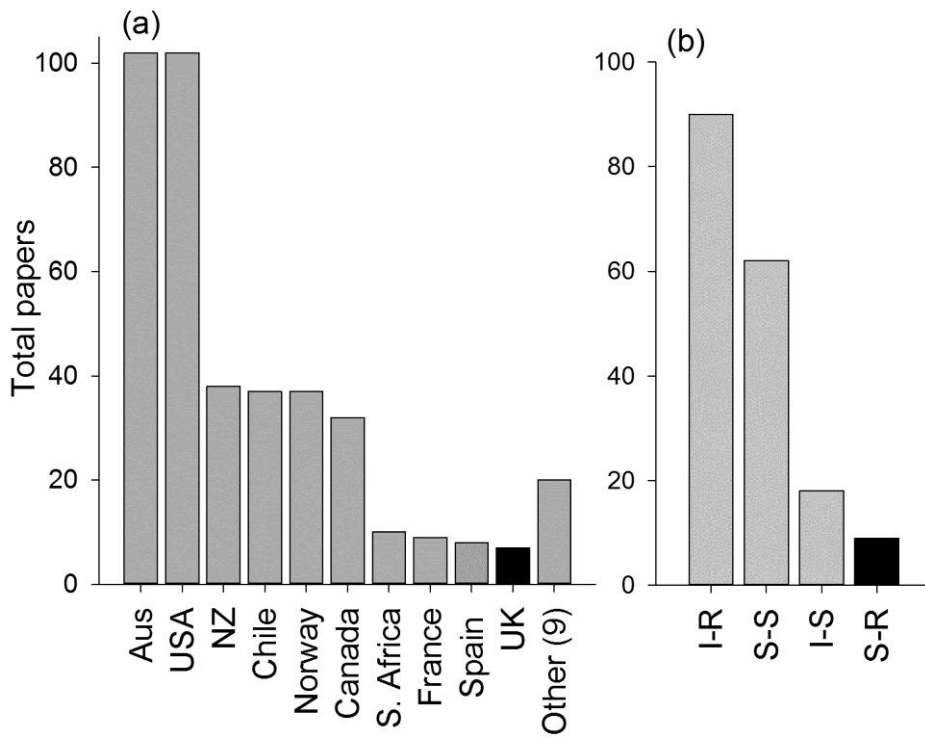


Fig. 1: (a) Number of kelp ecology papers by nation (ISI Web of Science search on 'kelp', 2002-2011,  $n = 402$  ecology papers). (b) Number of ecology papers focussed on each major benthic marine habitat type in the UK (2002-2011,  $n = 187$  papers); I-R = Intertidal rocky, S-S = subtidal soft, I-S = intertidal soft, S-R = subtidal rocky.

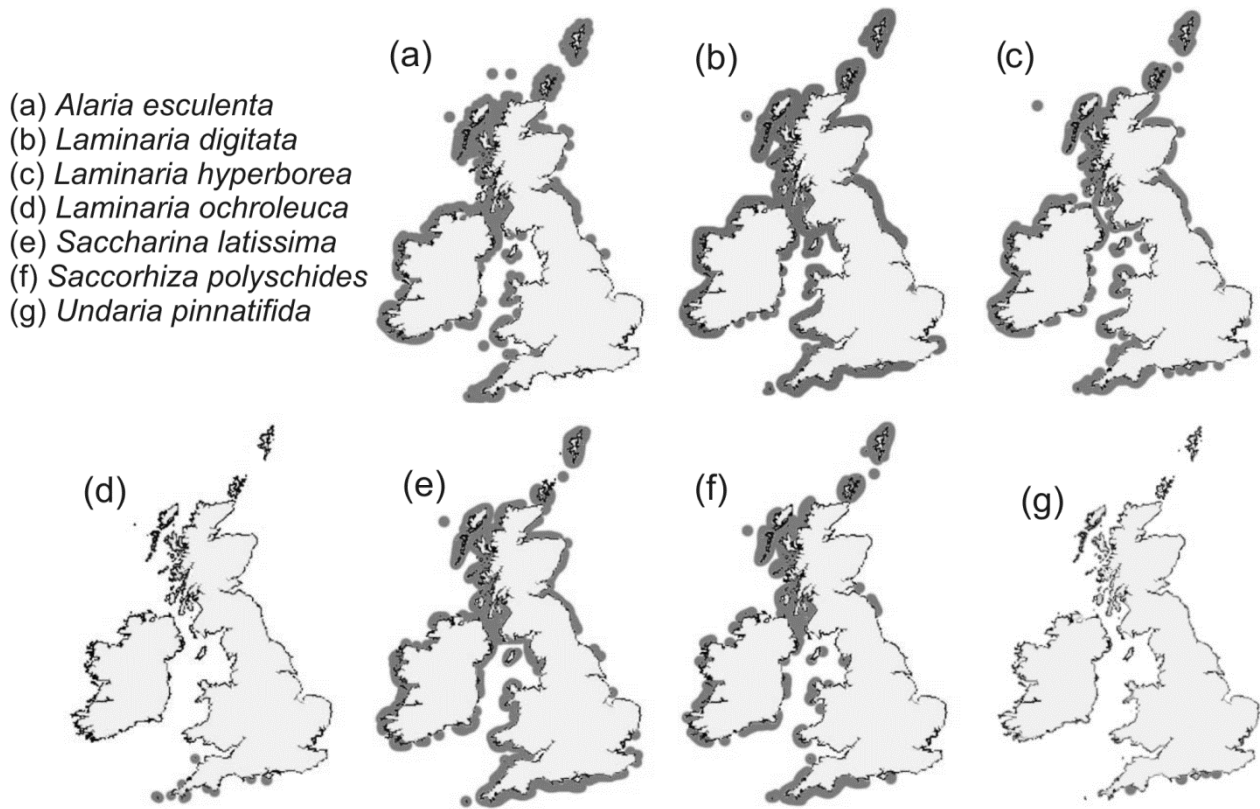


Fig. 2: Dark grey hatching indicates the recorded distributions of kelp species in the UK and Ireland (data reproduced from MarLIN, with permission).

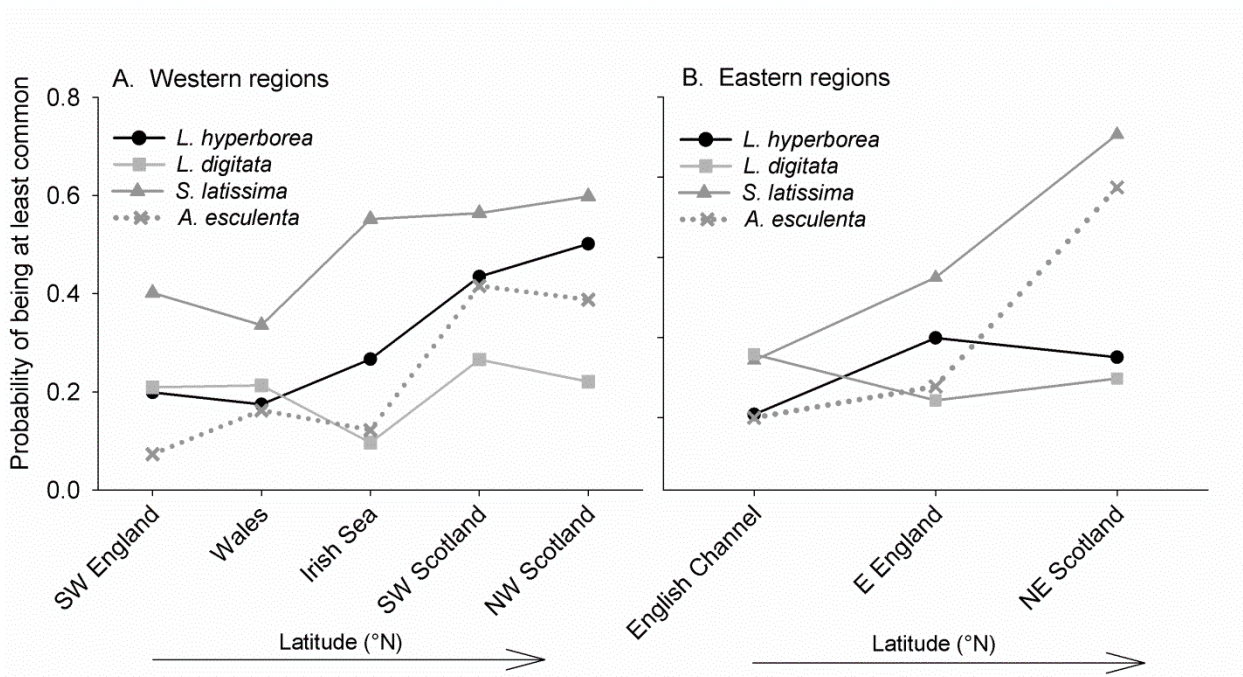


Fig. 3. Habitat-specific probability of occurrence for dominant kelp species in UK waters, for both western regions (A) and eastern regions (B), along a latitudinal gradient (~49-59°N). Probabilities derived from subtidal habitat surveys conducted at 0-10 m depth (data from Marine Nature Conservation Review, 1977-2000, see Burrows 2012 for more methodological details and geographical limits of regions), which used ACFOR values (a semi-quantitative abundance scale) to quantify benthic organisms. The number of independent surveys per region (i.e.  $n$ ), ranged from 300 to 734.

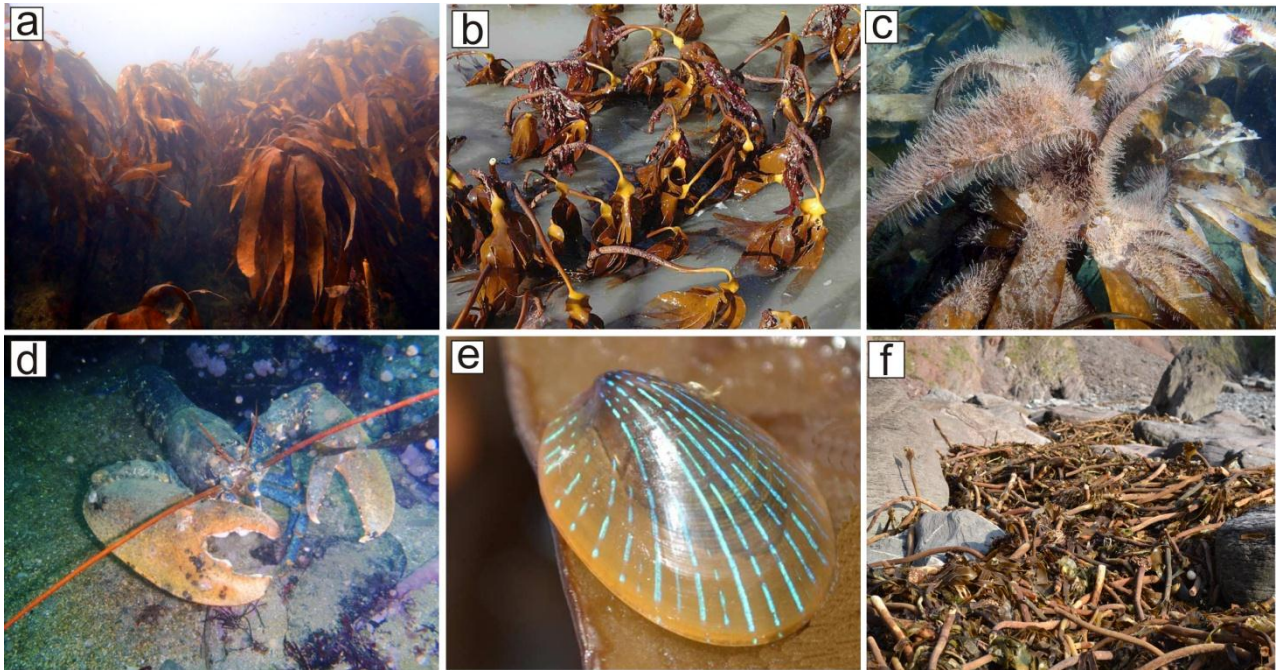


Fig 4. The kelp *Laminaria hyperborea* is a dominant canopy-former on both subtidal (a) and intertidal (b) rocky reefs around the UK and the wider NE Atlantic. Kelp forests provide habitat for a wide range of flora and fauna, including the hydroid *Obelia geniculata* (c) and the commercially important European Lobster *Homarus gammarus* (d). Although kelps and their epiphytes are grazed directly, by the blue-rayed limpet *Patella pellucida* for example (e), the majority of kelp production is consumed as detritus (f).

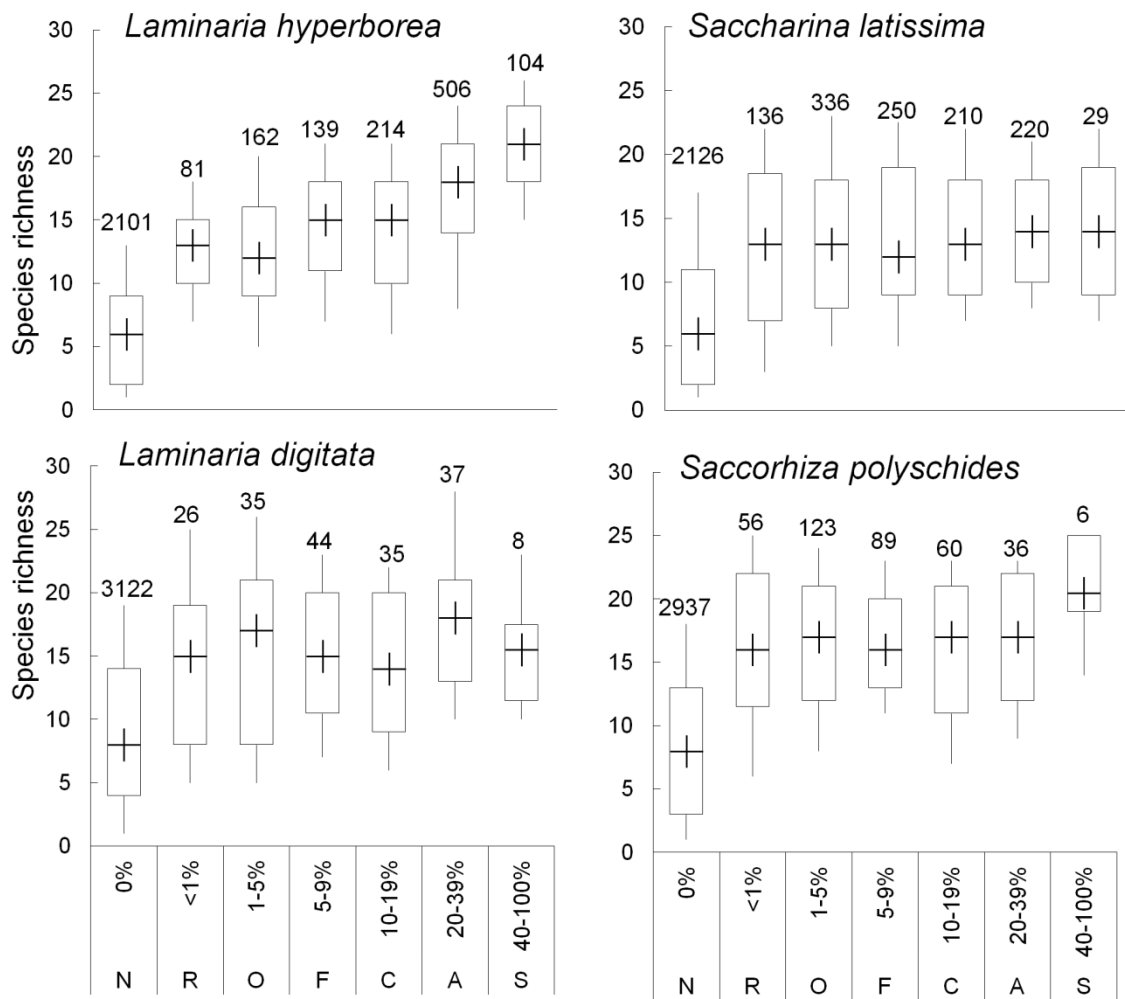


Fig. 5. Kelp species abundance and local species richness. Box plots show 10<sup>th</sup>, 25<sup>th</sup>, 50<sup>th</sup>, 75<sup>th</sup> and 90<sup>th</sup> percentiles of species richness data for each modified SACFOR category of kelp species abundance. For each SACFOR category, *n*, which is the number of independent surveys conducted during the Marine Nature Conservation Review (1977-2000), is given.