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The role of kelp species as biogenic habitat formers in coastal marine ecosystems

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ABSTRACT

Kelps are ecologically important primary producers and ecosystem engineers, and play a central role in structuring nearshore temperate habitats. They play an important role in nutrient cycling, energy capture and transfer, and provide biogenic coastal defence. Kelps also provide extensive substrata for colonising organisms, ameliorate conditions for understorey assemblages, and provide three-dimensional habitat structure for a vast array of marine plants and animals, including a number of commercially important species. Here, we review and synthesise existing knowledge on the functioning of kelp species as biogenic habitat providers. We examine biodiversity patterns associated with kelp holdfasts, stipes and blades, as well as the wider understorey habitat, and search for generality between kelp species and biogeographic regions. Environmental factors influencing biogenic habitat provision and the structure of associated assemblages are considered, as are current threats to kelp-dominated ecosystems. Despite considerable variability between species and regions, kelps are key habitat-forming species that support elevated levels of biodiversity, diverse and abundant assemblages and facilitate trophic linkages. Enhanced appreciation and better management of kelp forests are vital for ensuring sustainability of ecological goods and services derived from temperate marine ecosystems.

Keywords: benthic communities, epifauna, epiphyte, facilitation, macroalgae, temperate reefs

1. Introduction

Kelps dominate rocky reefs in lower intertidal and shallow subtidal zones throughout temperate and subpolar regions of the world (Fig. 1, Steneck et al., 2002). Kelp forests represent some of the most productive and diverse habitats on Earth (Brady-Campbell et al., 1984; Mann, 1973; Reed et al., 2008) and provide humans with ecosystem services worth billions of dollars annually (Beaumont et al., 2008). Kelps are a major source of primary production in coastal zones (Krumhansl and Scheibling, 2012; Mann, 1973). They promote secondary productivity through provision of three-dimensional habitat structure, which supports a vast array of marine life, including species of commercial and conservation importance (Smale et al., 2013; Steneck et al., 2002). The biogenic habitat structure provided by large canopy-forming seaweeds has been shown to offer protection to several commercial fish species (Bologna and Steneck, 1993), and kelp forests in particular serve as important nursery grounds (Holbrook et al., 1990; Tegner and Dayton, 2000). Kelps are ecosystem engineers (Jones et al., 1994) in the truest sense; they alter the environment and resources available to other organisms, playing a crucial role in the functioning of ecosystems. Specifically, kelp canopies alter light (Connell, 2003a), sedimentation (Connell, 2003b), physical abrasion (Irving and Connell, 2006), flow dynamics (Eckman et al., 1989), substratum availability and condition (Christie et al., 2007) and food quantity and quality (Krumhansl and Scheibling, 2012).

Strictly speaking, 'kelp' is a taxonomic distinction that refers to members of the Order Laminariales, although several species of large canopy-forming brown algae that perform similar functions are often referred to as kelp in ecological studies (and will be considered here). While the phylogeny of the Laminariales is complex and still uncertain (Bolton, 2010), significant progress has been made towards unravelling evolutionary pathways and relationships. There are currently 9 accepted families of Laminariales, represented by 59 genera and 147 species (Guiry and Guiry 2015). At present, 84% of all described species are found within the 3 most speciose families (Alariaceae, Laminariaceae, Lessoniaceae) and 63% of all kelp species are found within just 5 genera (*Alaria*, *Laminaria*, *Saccharina*, *Ecklonia*, *Lessonia*). Members of these genera are widely distributed across the temperate regions of their respective hemispheres where they serve as foundation species within rocky reef ecosystems (Fig. 1). Other widespread and ecologically important genera include *Macrocystis*, *Nereocystis* and *Undaria* (Fig. 1).

Akin to other benthic foundation species, such as hard corals, seagrasses and massive sponges, kelps support elevated biodiversity by increasing habitat volume, heterogeneity and complexity, and through direct provision of food and shelter (Bruno and Bertness, 2001). A great deal of research globally has unequivocally demonstrated that kelps harbour significant biodiversity, even at the scale of an individual. For example, Christie et al. (2003) found, on average, ~130 species and 8,000 individuals on individual *Laminaria hyperborea* sporophytes in Norway. As habitat formers, mature thalli directly provide three distinct micro-habitats: the holdfast, the stipe and the lamina/blade (hereafter referred to as blade, see Fig 2). These biogenic habitats differ considerably in structure (Fig. 2) and, as a result, the diversity and composition of their associated assemblages is also highly variable. In addition to variability within individuals, the structure and quantity of biogenic habitat provided by kelps may vary markedly between populations and species, so that the abundance or identity of kelp species within macroalgal canopies influences the structure and diversity of the entire community (Arnold et al., 2016).

As well as direct provision of primary habitat, dense stands of epiphytes may develop on some kelp species, such as on *Laminaria* stipes, to provide a secondary habitat which may be utilised by a rich and abundant invertebrate assemblage (Christie et al., 2003). These invertebrate assemblages comprise highly mobile species and prey species for fish and crustacean predators, thereby providing a direct link between lower and higher trophic levels (Norderhaug et al., 2005). The extent of kelp forest habitat is positively related to the abundance of fisheries resources, perhaps due to an increased abundance of prey items and the protection offered to targeted species, especially juveniles, within the kelp canopy (Bertocci et al., 2015). Previous studies on kelp forest biodiversity and utilisation of kelp-derived habitat by marine flora and fauna have tended to focus on a single species and/or region. Here we synthesize existing knowledge of the ecological functioning of kelps (and kelp-like canopy-forming brown algae) as biogenic habitat providers and examine consistency and variability in patterns of associated biodiversity across species and biogeographic regions. We also present novel information on spatial patterns of diversity in kelp forests, estimate the quantity of biogenic habitat provided by kelps in typical coastal ecosystems, identify threats to habitat provision by kelps and highlight knowledge gaps and priority research areas.

2. Direct provision of biogenic habitat

2.1. Holdfast assemblages

The holdfast structure, which anchors the thallus to the substratum, is the most complex microhabitat offered by kelps (e.g. Arnold et al., 2016). The vast majority of true kelps share a common 'laminarian' holdfast structure, formed by the growth of individual haptera from the diffuse meristematic tissue at the base of the stipe (Novaczek, 1981; Smith et al., 1996). As the plant ages, additional haptera are laid down in layers, growing outwards and downwards, to form a dense mass, in a broadly conical shape (Smith et al., 1996). The upper and outer portions of the holdfast tend to be formed by large, moderately spaced haptera; while towards the base haptera intertwine to form a complex of fine branches and smaller interstitial spaces (Smith et al., 1996). The holdfast changes little over the life span of the kelp. For large perennial species like *Laminaria hyperborea* this is typically ~10 years (Kain, 1979) and may be considerably longer under optimal conditions (up to 20 years old; Sjøtun et al., 1995). Although holdfasts of the majority of kelp species are formed in this way, there is considerable interspecific variation in the size, structure, complexity, openness and longevity of the holdfast habitat (Fig. 3).

Within the true kelps the volume of the holdfast habitat provided by mature plants may range from <100 cm^3 for smaller species such as *Ecklonia radiata* (Smith et al., 1996) and *Undaria pinnatifida*

(Raffo et al., 2009) to >3500 cm^3 for *Macrocystis pyrifera* (Rios et al., 2007). The morphology of the structure is also highly variable, being dependent on the density, thickness, complexity and arrangement of the haptera (Fig. 3). For example, *Macrocystis* and *Nereocystis* tend to form intricate holdfast structures, with many fine intertwining haptera, whereas *Laminaria* tend to grow fewer but thicker haptera, with larger interstitial spaces (Fig. 3). *Lessonia* holdfasts are highly atypical, exhibiting poorly defined haptera and a flattened, massive basal holdfast structure. With regards to important 'false-kelps', the holdfast structure of *Saccorhiza polyschides* (Fig. 3) differs much from the laminarian holdfast structure. It characteristically forms a large, hollow, bulbous structure up to 30cm in diameter, of which the upper surface is covered in small protuberances, while the lower surface attaches to the substratum through small, claw-like haptera (Norton, 1969). The bull kelp *Durvillaea antarctica*, being a fucoid, forms a solid, robust structure with little morphological differentiation. With regards to intraspecific variation, holdfast structure can vary markedly between populations subjected to different environmental conditions, particularly in response to gradients in wave exposure or current flow (Sjøtun and Fredriksen, 1995). For example, the biomass and internal volume of holdfasts of mature *Laminaria* plants can more than double along a wave exposure gradient (Smale, Teagle, unpublished data). Thus the majority of studies include some measure of habitat volume (i.e. the volume of space available for colonization by fauna between haptera; hereafter called 'habitable space', as opposed to the total space of the holdfast; hereafter 'holdfast volume'); using either a mathematical approach (Jones, 1971), or displacement (Sheppard et al., 1980). Recent work by Walls et al. (2016) suggests that these methods provide similar results, and can, therefore, be compared across studies using these different techniques.

The biogenic habitat provided by kelp holdfasts is generally highly complex, extensive (certainly at the scale of kelp forest, see below) and, for many species, temporally stable. The interstitial space between the hard substratum and the haptera represents favourable habitat for colonising fauna, as the holdfast structure offers protection from predators and adverse environmental conditions, accumulates food sources and increases the area of substrata and volume of habitable space available for colonisation (Ojeda and Santelices, 1984). For some species, such as *L. hyperborea,* the holdfast offers a capacious internal habitable space, relative to the overall size of the structure. Within the context of single kelp plants, the holdfast generally supports the greatest diversity of the three primary habitats, with species richness per holdfast typically reaching 30-70 macrofaunal species, but in some cases reaching up to 90 species (Christie et al., 2003; Jones, 1972; Moore, 1972a; Thiel and Vásquez, 2000). Invertebrate abundance can exceed 10,000 individuals per holdfast (Christie et al., 2003; Schaal et al., 2012). Reported values for the richness and abundance of holdfast assemblages vary greatly between species and regions (Table 1). Even so, holdfast structures consistently support high levels of biodiversity (Table 1) and the vast majority of studies conclude that invertebrate richness and abundance is elevated within these structures. For example, work on *Ecklonia radiata* in Australia has yielded study-wide total richness values in excess of 350 taxa inhabiting holdfasts (Anderson et al., 2005; Smith et al., 1996). Although variability between kelp species is high, generally those that form large, laminarian type holdfasts (e.g. *Laminaria hyperborea*, *Ecklonia radiata*) support greatest biodiversity (Table 1).

Holdfast assemblages are typically dominated by mobile invertebrates taxa including copepods, polychaetes, gastropods and amphipods, and by sessile fauna such as bryozoans, bivalves and sponges (Anderson et al., 2005; Arroyo et al., 2004; Blight and Thompson, 2008; Christie et al., 2003; Christie et al., 2009; Moore, 1972a; Norderhaug et al., 2002; Ojeda and Santelices, 1984; Rios et al., 2007; Schaal et al., 2012). Amphipods and polychaetes are typically numerically dominant, often representing >75% of total faunal abundance (Smith et al., 1996), although the relative abundance of taxonomic groups is strongly influenced by environmental conditions (Moore, 1973a; Sheppard et al., 1980; Smith and Simpson, 1992). A significant proportion of the holdfast fauna is highly mobile and can quickly colonise new available habitat; exchanges between kelp plants and also from kelp to surrounding habitat are thought to occur frequently (Norderhaug et al., 2002; Waage-Nielsen et al., 2003). The composition of the sessile fauna is largely dependent on the availability of dispersal stages in the overlying water column (Marzinelli, 2012), which influences recruitment rates onto holdfasts, as well as local turbidity and sedimentation rates, as many suspension feeding species are susceptible to smothering (Moore, 1973a). Food supply, principally from detrital kelp and other macroalgae and deposited phytoplankton, is rarely thought to be limiting in most kelp forest habitats (Schaal et al., 2012). Kelp holdfasts (particularly laminarian holdfasts) efficiently trap and accumulate sediment (Arroyo et al., 2004; Moore, 1972b), limiting detritus export in highly hydrodynamic areas (Schaal et al., 2012). Species recorded in holdfasts are generally found elsewhere in the surrounding wider habitat, such as amongst epilithic understorey algae, rather than being obligate holdfast inhabitants (Christie et al., 2003; Smith et al., 1996). Perhaps the most remarkable exception to this observation is the terrestrial spider (*Desis marina*), which inhabits bull kelp (*Durvillaea antarctica*) holdfasts found on the extreme low shores of New Zealand (McQueen and McLay, 1983). The specific microhabitat provided by the holdfast structure allows the spider to survive submergence for at least 19 days (McQueen and McLay, 1983).

A range of trophic guilds are represented within holdfasts, including deposit feeders, filter feeders, grazers, scavengers and predators (McKenzie and Moore, 1981), although organisms that feed on detrital organic matter (i.e. deposit feeders and filter feeders) tend to dominate (Schaal et al., 2012). Larger predators, such as the edible crab *Cancer pagurus* (McKenzie and Moore, 1981) and the spiny lobster *Panulirus interruptus* (Mai and Hovel, 2007), commonly shelter in kelp holdfasts. Recent stable isotope analysis has shed light on kelp holdfasts as micro-scale ecosystems, given that the food web within a holdfast may attain 3.5 trophic levels and involve many complex trophic pathways (Schaal et al., 2012). The overall composition of holdfast assemblages in terms of the relative abundance of higher taxa or trophic groups is, to some extent, predictable and consistent across seasons and biogeographic regions where habitats are relatively unimpacted by human activities (Anderson et al., 2005; Christie et al., 2003; Smith et al., 1996). Assemblage composition is, however, sensitive to local environmental factors and predictable shifts in holdfast assemblages (especially at coarser taxonomic levels) occur in response to increased turbidity (Sheppard et al., 1980), pollution from oil spills (Smith and Simpson, 1998), and sewage outfall effluent (Smith and

Simpson, 1992). This has led to feasibility studies on the utility of kelp holdfasts as self-contained units for environmental monitoring (Anderson et al., 2005; Sheppard et al., 1980; Smith and Simpson, 1992).

The structural complexity and the size (volume) of the holdfast have been shown to impact the diversity and abundance of associated assemblages (Norderhaug et al., 2007). Habitat complexity has been shown to influence assemblage structure in a number of macrophyte groups (Christie et al., 2009); this trend holds true for kelp holdfasts. Indeed, by experimentally altering the complexity of artificial holdfast mimics, Hauser et al. (2006) found significantly higher abundance and diversity on high complexity mimics in comparison to those of a lower complexity. The increase in the complexity potentially providing greater niche space and increased microhabitat availability to inhabiting fauna (Kovalenko et al., 2012).

The size of the holdfast habitat (whether quantified by total volume, biomass or internal habitable space) has long been recognised as an important driver of faunal richness and abundance (Moore, 1978; Sheppard et al., 1980). However, the reported relationships between habitat volume and faunal richness and abundance are not consistent, and appear to vary between kelp species, regions and locations (e.g. Walls et al., 2016). While all studies report that the total abundance of holdfast fauna increases with habitat size, some studies have found this relationship only holds for smaller, younger holdfasts and abundance is independent of habitat size in older plants (Anderson et al., 2005; Ojeda and Santelices, 1984). Others have reported a consistent positive relationship between faunal abundance and habitat size throughout the entire size range of the kelp holdfast (Christie et al., 2003; Smith et al., 1996; Tuya et al., 2011). Even so, space availability is clearly an important determinant of faunal density. Patterns of faunal richness are also inconsistent, with some studies reporting positive relationships between richness and habitat size (Smith et al., 1996), some reporting asymptotic trends (Anderson et al., 2005; Ojeda and Santelices, 1984) and others reporting no clear trend at all (Christie et al., 2003). Richness patterns are likely to be dependent on the regional/local species pool, the time available for colonisation, and the complexity of the habitat. Several studies have suggested that successional processes within kelp holdfasts do not involve species replacement but rather an additive progression; this is because species recorded in small holdfasts are also recorded in older, larger ones and are not necessarily replaced by competitively superior species (Ojeda and Santelices, 1984; Smith et al., 1996). This may be related to the fact that the habitat is dynamic and grows throughout succession or that the complexity of the holdfast promotes and maintains niche separation. A major impediment in the search for generality in holdfast assemblage structure and functioning is that the methods used to quantify assemblages have been inconsistent, with many studies considering only mobile or sessile fauna (e.g. Christie et al., 2003; Tuya et al., 2011) and other studies focussing on specific taxonomic groups (e.g. peracarid crustaceans; Thiel and Vásquez, 2000), which makes overarching inferences and generalisations difficult.

Several studies have examined interspecific variability in holdfast assemblage structure to determine whether different kelps support different levels of biodiversity. McKenzie and Moore (1981) compared holdfast assemblages associated with *Saccorhiza polyschides* with those of *Laminaria hyperborea* in the UK and noted marked differences in faunal composition, richness and abundance. *L. hyperborea* supported far greater diversity and abundance, which was attributed to greater complexity and longevity of the holdfast structure; but *S. polyschides* housed larger animals, including several predatory fish and crustaceans that were typically absent from *L. hyperborea*. Some years later, Tuya et al. (2011) repeated the comparison in northern Portugal, where *L. hyperborea* is found at its southern range edge and sporophytes are much smaller, and found no differences in faunal composition or abundance between the two host species despite marked differences in holdfast morphology. As such, biogeographic context – in terms of both the structure of the kelps themselves and the regional/local species pool comprising holdfast assemblages – is clearly important. Recent studies have examined whether, outside its native range, the invasive kelp *Undaria* pinnatifida supports impoverished assemblages compared with native habitat-forming macroalgae (Arnold et al., 2016; Raffo et al., 2009). In Argentina, the larger holdfasts offered by *M. pyrifera* support higher faunal richness and abundance than *U. pinnatifida* (Raffo et al., 2009). In the UK the longer-lived holdfasts offered by native perennial kelps support greater richness and biomass of sessile fauna (Arnold et al., 2016). Both studies stated, however, that native kelp species may not be negatively impacted by non-native *U. pinnatifida*, which may occupy a different niche both spatially and temporally, and community-wide responses to invasion are likely to be complex and context-specific. With further reference to intraspecific variability, studies on *Macrocystis pyrifera in* Chile have revealed high levels of variation in holdfast assemblage structure and diversity between kelp populations (Ojeda and Santelices, 1984; Rios et al., 2007). Spatial differences in physical disturbance regimes driven by wave exposure and storm intensity were suggested as the most likely driver of associated biodiversity patterns (see below).

2.2. Stipe assemblages

In contrast to the holdfast, the stipe is relatively simple in structure but also exhibits significant variability between species and populations. The majority of kelps have a defined stipe; a single rigid structure arising from the apex of the holdfast and supporting the blade in the water column. The structure of the stipe itself, in terms of rugosity, rigidity, tensile strength and whether it is branching, terete, solid or hollow, varies considerably between species. The length of the stipe, and therefore the total area of biogenic habitat available for colonisation, also varies considerably between populations and species. For example, the average stipe length of mature *Laminaria hyperborea* plants may more than double along a steep wave exposure gradient (Smale et al., 2016), although smaller differences in water motion between moderately exposed and sheltered habitats may have minimal effect on the rate of stipe elongation (Kregting et al., 2013). Interspecific variation is considerable, with some kelp species exhibiting stipe lengths in excess of 15 (*Ecklonia maxima*) or even 30 m (*Nereocystis luetkeana*). Several species (e.g. *Nereocystis* spp., *Macrocystis pyrifera*) have evolved gas-filled bladders to assist with flotation and some species (e.g. *M. pyrifera*) develop mid-water fronds to facilitate photosynthesis (Graham et al., 2007). Several ecologically-important species, including *Undaria pinnatifida* and *Saccorhiza polyschides* have flattened stipes (Castric-Fey et al., 1999; Norton, 1969; Norton and Burrows, 1969). Although most kelps produce a single stipe, some species (including *Lessonia nigrescens* and *M. pyrifera*) grow multiple stipes from the same holdfast structure. As such, the physical structure and properties of kelp stipes are likely to have a major influence on the structure and diversity of the associated assemblage.

Studies on the invertebrate assemblages associated with the surface of kelp stipes are scarce, with most focus on the assemblage associated with secondary epiphytic algae. However, there is emerging evidence to suggest that some species (e.g. *L. hyperborea*) can support rich and abundant assemblages of sessile invertebrates attached directly to the stipe (Leclerc et al., 2015). Within a kelp forest, the total biomass of filter feeders, particularly demosponges, attached to stipes can be substantial, and represents an important link between trophic levels. With regards to flora, epiphytic algae are common on marine macroalgae (Bartsch et al., 2008). Some are obligate epiphytes (e.g. on *Ecklonia maxima* in South Africa; Anderson et al., 2006), while the majority are facultative, simply occupying free space on the surface of larger macroalgae, as well as being found attached to abiotic substrata (Bartsch et al., 2008). Experimental removals of kelp canopies have resulted in early settlement of common epiphytic species in cleared areas, perhaps suggesting that competition for light with canopy algae limits these facultative species to an epiphytic strategy (Hawkins and Harkin, 1985). Studies utilising artificial macrophyte mimics have shown that epiphytes readily grow on abiotic structures, supporting the assertion that the biotic nature of the macrophyte involved is often insignificant (Cattaneo and Klaff, 1979; Harlin, 1973).

The diversity and abundance of epiphytic algae colonising kelp is highly variable. Nearly 80 species of epiphytes (red, green and brown algae) have been recorded on *Laminaria* species in the Sea of Japan (Sukhoveeva, 1975), whereas in the North Sea, 7 and 8 species of epiphytes (predominantly red algae) were recorded on *Laminaria digitata* and *L. hyperborea* respectively (Schultze et al., 1990). *L. hyperborea* stipes in Norway support a diverse, red algae dominated, epiphytic community of up to 40 species (Christie et al., 1998; Sørlie, 1994). Whittick (1983), however, found that 95% of epiphyte biomass found on samples of *L. hyperborea* in southeast Scotland comprised just 4 species. The diversity and abundance of epiphytes can also be extremely variable between host species, with significant differences observed between closely related and morphologically similar species. For instance, *L. hyperborea* has been shown to support up to 86 times more epiphytes (by weight) than *Laminaria ochroleuca*, in areas where both species co-exist in mixed stands (Smale et al., 2015). In this case, differences were most likely related to variability in surface texture and, perhaps, production of chemical antifoulants (see Jennings and Steinberg, 1997 for *Ecklonia* example; Smale et al., 2015). The composition of epiphytes often changes vertically along the stipe (Whittick, 1983), and also exhibits pronounced differentiation along abiotic gradients (Bartsch et al., 2008). Epiphyte biomass decreases with depth, due to light attenuation in the water column, often by a factor of ten or more (Allen and Griffiths, 1981; Marshall, 1960; Whittick, 1983). Depth (and associated changes in light levels) also plays a part in structuring epiphyte assemblages, with distinct zonation of different epiphytic algal species along depth gradients (e.g. *Palmaria palmata* and *Phycodrys rubens* on *L. hyperborea*; Whittick, 1983). Under certain conditions, specifically where light levels, water motion (particularly tidally-driven currents) and kelp densities are very high, the kelp sporophytes themselves may be epiphytic on older kelp plants (Velimirov et al., 1977), thereby initiating a complex facilitation cascade (Thomsen et al., 2010).

The often extensive secondary habitat provided by epiphytic algae on kelp stipes, has been shown to support a diverse and extremely abundant faunal assemblage (Christie, 1995; Christie et al., 2003). While the holdfast generally supports the most diverse assemblage, the stipe/epiphyte complex usually supports the greatest densities of fauna (Table 1). Christie et al. (2003) recorded in excess of 55,000 individual mobile macrofauna per kelp on the stipe of *L. hyperborea* in Norway; but noted that the assemblage associated with the stipe was the most variable, with very low abundances observed on some specimens. These assemblages tend to be dominated by amphipods, gastropods, and other molluscs (Norderhaug et al., 2002). Habitat size is very important for stipe and epiphytic algal associated macrofauna, as it is for holdfast fauna. Larger habitats (i.e. larger biomass of epiphytic algae) have been shown to support a more abundant and diverse assemblage (Norderhaug et al., 2007). It is, once again, also important to consider the complexity of the epiphytic algal material concerned when considering the effect of habitat space, not only considering the algal surface itself, but also the interstitial volume (Christie et al., 2009; Hacker and Steneck, 1990). It has been shown that macrofaunal density on epiphytic red algae is higher on structurally complex species (e.g. *Rhodomela* spp. and *Ptilota gunneri*) than those with simple, smooth surfaces (e.g. *Palmaria palmata*; Christie et al., 2009; also see Schmidt and Scheibling, 2006). Similarly, recent work has shown that the diversity and richness of faunal assemblages is greater on large, roughened epiphytes compared with smooth, simple forms (Norderhaug et al., 2014). This assertion is supported by work with artificial mimics of differing complexity (Christie et al., 2007). It is important to note, however, that while habitat size seems to be of importance in driving the abundance of macrofauna, the patterns do not hold true for meiofauna, suggesting that other processes (e.g. predation by macrofauna) may be playing a role in controlling their abundance (Norderhaug et al., 2007), and that meiofauna may be more closely associated with holdfasts than epiphytes (Arroyo et al., 2004).

2.3. Blade assemblages

The blade, or lamina, provides a large surface area for photosynthesis and also for colonisation by a range of epibionts. Although the blade has the lowest structural complexity of the primary microhabitats, inter and intraspecific variability in morphology is still evident (Arnold et al., 2016; Włodarska-Kowalczuk et al., 2009). Blade structures vary in thickness, rigidity, surface texture, edge formations, presence of a mid-rib, and the number and arrangement of divisions; all of which can differ between species and populations and will have some influence on the settlement, growth and survivorship of epiflora and epifauna.

The blade generally supports the lowest diversity of epibionts of the primary habitats (Włodarska-Kowalczuk et al., 2009), although competitively inferior species may persist here due to intense competition for space in other areas (i.e. the stipe; Seed and Harris, 1980). The blade of healthy kelp plants typically support a low coverage of epiphytic algae, which would likely compete for light and nutrients to the detriment of the host alga. However, heavy epiphytic loading on kelps has been observed under stressful conditions, such as periods of intense warming or low light and high nutrients (Andersen et al., 2011; Moy and Christie, 2012; Smale and Wernberg, 2012), and, in perennial species, as the old blade senesces at the end of the growing season (e.g. Andersen et al., 2011). Moreover, kelps with short annual life-cycles (e.g. *Undaria pinnatifida* and *Saccorhiza polyschides*) often support dense epiphytic assemblages during the senescent period of the sporophyte stage (e.g. Norton and Burrows, 1969).

The low faunal diversity characteristic of kelp blades may be due, in part, to the inherent flexibility and instability of the substratum (Bartsch et al., 2008). However, in certain conditions, epifaunal abundance and spatial cover can be high (Saunders and Metaxas, 2008). The bryozoan *Membranipora membranacea* has been noted to be one of the few, often the only, species of sessile fauna associated with the blade of *Laminaria* species (Seed and Harris, 1980). This is probably due to the growth plan of this species, which develops non-calcified bands of zooids thought to prevent cracking of colonies on a flexible substratum (Ryland and Hayward, 1977). *M. membranacea* is now a common invasive species in the northwest Atlantic, thought to be introduced from Europe via ship ballast water (Lambert et al., 1992). Survival of native northwest Atlantic kelp has been shown to be lower in the presence of invasive *M. membranacea* (Levin et al., 2002), making plants more susceptible to defoliation during intense wave action by making the blade of affected species brittle (Dixon et al., 1981; Lambert et al., 1992; Saunders and Metaxas, 2008; Scheibling et al., 1999). It should be noted, however, that in other settings extensive growth of sessile epiphytic fauna (including *M. membranacea*) have been shown to have no negative impact on the growth of kelps (Hepburn and Hurd, 2005). There is evidence that growth rates increase in heavily colonised fronds during periods of low inorganic nitrogen concentrations in seawater, potentially due to the provision of ammonium excreted by sessile fauna (e.g. hydroids on *Macrocystis pyrifera*; Hepburn and Hurd, 2005). Recent work on four kelp species by Arnold et al. (2016) reported a maximum of just five or six sessile invertebrate species attached to kelp blades, which were predominantly bryozoans. Other work conducted at larger scales have, however, reported considerably higher richness values (Włodarska-Kowalczuk et al., 2009). Clearly, richness of blade epifauna varies considerably between host species and location (Table 1).

Larger mobile organisms can also be locally abundant on blade surfaces, some of which have a very high affinity to kelp species. For example, the blue-rayed limpet, *Patella pellucida* (previously *Helcion pellucidum*), is a common and locally abundant grazer found on *Laminaria* spp., where it feeds predominantly on the kelp tissue (Christie et al., 2003; Vahl, 1971). Similarly, the gastropod *Lacuna vincta* can colonise laminae in high densities (Johnson and Mann, 1986) and, although the direct impacts of grazing may be relatively minor and spatially restricted across the blade surface, the indirect effects of tissue weakening may promote defoliation of kelp canopies during intense storms (Krumhansl and Scheibling, 2011b). Other conspicuous and ecologically important macroinvertebrates include the sea urchin *Holopneustes* spp. found within *E. radiata* canopies (Steinberg, 1995) and the turban snails *Tegula* spp., which inhabit *M. pyrifera* fronds (Watanabe, 1984). More generally, the mid-water fronds and surface canopies of the giant kelp *M. pyrifera* can form mini-ecosystems that support high abundances of invertebrates and fish (see Graham et al., 2007 and references therein).

Crucially, many invertebrates associated with kelp thalli maintain their association with the host plant even if it becomes detached from the substratum. Detached kelp may be transported great distances from source populations and, as a result, aid the dispersal of fauna that remains affiliated and viable. Positively buoyant kelps, such as *M. pyrifera* and *Durvillaea antarctica*, form kelp rafts which can drift many hundreds of km, facilitating the dispersal of associated invertebrate assemblages (Fraser et al., 2011; Hobday, 2000; Ingólfsson, 1995). Such rafts are particularly numerous in the Southern Ocean (Smith, 2002) and may have played an important role in species dispersal and colonisation of novel habitats over both ecological and evolutionary timescales (Fraser et al., 2011). Rafting may also be an effective means of long-range dispersal for positively buoyant species of invasive algae (e.g. *Sargassum muticum*; Kraan, 2008; Rueness, 1989).

2.4. Habitat preference of kelp fauna

Although most species of kelp associated fauna are found in more than one micro-habitat (e.g. stipe and holdfast), there is some evidence of habitat 'preference' among a number of taxa. A study of *L. hyperborea* along an extensive stretch of the Norwegian coastline found no species associated solely with the blade, but that around 70 species were exclusively associated with either the holdfast or the epiphytes on the stipe (Christie et al., 2003). This pattern has also been shown in other studies of *L. hyperborea* (Norton et al., 1977; Schultze et al., 1990). It is important to note that these patterns are consistent in highly mobile groups that have the means to move throughout the entire plant (Christie et al., 2003). Dispersal beyond a single plant has, however, been documented with both holdfast and stipe epiphyte associated species (Jorgensen and Christie, 2003). Jorgensen and Christie (2003) found, using artificial substrata, that holdfast related species tended to disperse close to the seabed, but that stipe epiphyte associated fauna travelled throughout the kelp forest as a whole, and even above the canopy layer. Some of these very mobile fauna (e.g. amphipods and isopods) have been shown to actively emigrate from kelp forest systems in relatively high numbers (1 - 2% total biomass daily; Jorgensen and Christie, 2003), and kelp associated fauna represent a large source of food for adjacent systems (Bartsch et al., 2008). Thus kelp forests can be considered ecologically important near shore export centres (Bartsch et al., 2008).

While the majority of mobile kelp associated fauna can be found on other macroalage, a number of species may be considered 'kelp specialists'. For instance, the limpets *Cymbula compressa* and *Patella pellucida* are found almost exclusively on kelps (*C. compressa* on *E. radiata* in South Africa;

Anderson et al., 2006; and *P. pellucida* on laminarian kelps in the northeast Atlantic; Marques de Silva et al., 2006). Although *P. pellucida* spat settle on crustose algae and later migrate to macroalgae, including *Mastocarpus stellatus* (McGrath, 2001), those individuals found on *Laminaria spp.* have been shown to have higher growth rates than those found elsewhere (McGrath, 1992).

2.5. The quantity of biogenic habitat provided by kelps

Kelp species are widespread throughout temperate and subpolar regions, where they provide vast, complex habitat for a myriad of other organisms. Although estimating the actual standing stock of kelps is problematic and subject to some uncertainty, it is possible to use a combination of high-resolution fine scale sampling techniques and larger-scale survey approaches to generate useful approximations of kelp distribution and biomass. For example, the estimated standing biomass of *Laminaria* spp. along the northwest coastline of Europe is in excess of 20 million tonnes (wet weight, Burrows et al., 2014; Werner and Kraan, 2004). The biomass and volume of habitat provided by kelps varies considerably between species, sites and regions, and is strongly influenced by environmental factors including wave exposure, light availability and substratum characteristics (Smale et al., 2016). Even so, it is possible to use existing data on kelp populations to illustrate the quantity of biogenic habitat provided on representative kelp-dominated rocky reefs. At a relatively wave sheltered site in Plymouth Sound (Firestone Bay), subtidal rocky reefs support a mixed kelp bed comprising *Laminaria ochroleuca*, *Saccharina latissima*, *Undaria pinnatifida* and *Saccorhiza polyschides* (Arnold et al. 2016). While the total biomass, internal holdfast volume and surface area (annual means) provided varies considerably between species, the total kelp canopy generates significant biogenic habitat (Table 2). Within a typical 1 m^2 area of rocky substrata, kelps supply an average (wet weight) biomass of >2.5 kg, holdfast habitable space of ~380 ml and a surface area available for colonisation of >4 m^2 (Table 2). To contextualise, the total biomass and surface area of biogenic habitat provided by kelps exceeds maximum reported values for mature seagrass meadows

(~95 g dry weight m^2 and ~3.7 m^2 respectively; Duarte and Sand-Jensen, 1990; Larkum et al., 1984; McKenzie, 1994).

At the more wave exposed site, which is dominated by *Laminaria hyperborea* but also supports populations of *L. ochroleuca*, *S. latissima* and *S. polyschides* (Smale et al., 2015), the quantity of biogenic habitat provided by kelps is even greater, particularly with regards to total biomass and internal holdfast habitable space (Table 2). Due to the much larger holdfasts, the internal habitable space generated (>1.7 L m^{-2}) is almost 5 times that of the wave-sheltered site, and represents sizable high-quality protective habitat. For both examples, when values are scaled-up to the site level (which is prone to error but still a valuable 'best guess' approach), it is clear that kelps yield substantial biogenic habitat (Table 2) and that deforestation of such reefs (see 5. Threats to biogenic habitat provided by kelps) would result in significant loss of three-dimensional structure and habitat complexity, as has been observed in kelp forests in many regions in response to contemporary stressors (Ling et al., 2009; Moy and Christie, 2012; Wernberg et al., 2013).

3. Physical and biological regulation of habitat provision

3. 1. Physical regulation

Hydrodynamic forces (i.e. wave action and currents) have long been recognised to influence the structure of marine communities (Ballantine, 1961; Brattström, 1968; Knights et al., 2012). With regards to macroalgae-associated assemblages, wave action represents a physical disturbance, and can result in considerable loss of fauna due to dislodgement and mortality (Fenwick, 1976; Fincham, 1974). Such disturbance may, however, increase overall diversity of the community by preventing superior competitors from outcompeting other, less competitive, species and by creating a mosaic of habitats at different stages of succession (Connell, 1978). The intermediate disturbance hypothesis (Connell, 1978) would suggest that moderately exposed sites would harbour the highest diversity of flora and fauna (Dial and Roughgarden, 1998), a prediction supported by experimental work in some areas (e.g. England et al., 2008; Norderhaug et al., 2014). Hydrodynamics also influence the availability of food and rates of sedimentation, which can influence biotic assemblages by limiting access to food, or through the smothering of some filter feeding fauna (Moore, 1973a).

Wave exposure can also have an effect on the kelps themselves, and therefore a subsequent indirect effect on associated communities. A number of kelp species have been shown to exhibit changes in morphology in response to changes in wave exposure (Fowler-Walker et al., 2006; Molloy and Bolton, 1996; Wernberg and Thomsen, 2005). Adaptations to exposed environments can result in an increase in holdfast size and volume (Sjøtun and Fredriksen, 1995, Smale, Teagle, unpublished data), increased stipe length (Smale et al., 2016) and thickness (Klinger and De Wreede, 1988), and increased blade thickness (Kregting et al., 2016; Molloy and Bolton, 1996). Such strength-increasing adaptations may reduce the probability of dislodgement, or other damage caused by wave action (Wernberg and Thomsen, 2005). An increase in overall thallus size is also a common adaptation to increased wave exposure in kelps (Klinger and De Wreede, 1988; Pedersen et al., 2012; Wernberg and Thomsen, 2005; Wernberg and Vanderklift, 2010); 'going with the flow' with a long, flexible thallus reduces hydrodynamic forces (Denny et al., 1998; Denny and Hale, 2003; Friedland and Denny, 1995; Koehl, 1999). Some species, however, also exhibit an increase in overall thallus size in very sheltered conditions (e.g. *Laminaria hyperborea*; Sjøtun and Fredriksen, 1995; and *L. digitata*; Sundene, 1961). Faunal abundances generally increase with increasing habitat size (Norderhaug et al., 2007); thus a relationship exists between local hydrodynamic conditions, and the diversity of communities found in association with kelps (Anderson et al., 2005; Christie et al., 1998; Christie et al., 2003; Norderhaug and Christie, 2011; Norderhaug et al., 2012; Norderhaug et al., 2007; Norderhaug et al., 2014; Schultze et al., 1990; Walls et al., 2016). Water movement can dislodge epiphytic algae, but also increases algal growth by transporting nutrients over algal surfaces (Norderhaug et al., 2014). The abundance of kelp-associated assemblages depends on both the amount of habitat provided by the algae (Norderhaug et al., 2007) and on algal morphology (Christie et al., 2007). Christie et al. (2003) found that the volume of epiphytic algae on the stipe of *L.*

hyperborea increased by a factor of 35, and the number of algal species increased by a factor of 1.7, in response to increasing wave exposure. The abundance of associated fauna increased by a factor 100 (Christie et al., 2003). It is important to note, however, that most studies conducted along wave exposure gradients have not sampled 'extremely' exposed sites (e.g. remote offshore islands which are rarely visited due to logistical constraints) and under such conditions the morphology of kelp sporophytes and the composition and density of the kelp canopy will be distinct (e.g. Rockall, see Holland and Gardiner, 1975).

At high latitudes physical disturbance by ice-scour can limit the distribution of some species of kelp, reducing available biogenic habitat significantly. For example, *Durvillaea antarctica* is absent from severely ice-scoured areas around the Antarctic and sub-Antarctic islands (Fraser et al., 2009; Pugh and Davenport, 1997). *Macrocystis pyrifera*, however, will persist in such areas as its holdfast can anchor below the maximum keel depth of ice-bergs (Pugh and Davenport, 1997).

Increased temperature and decreased nutrients (e.g. during El Niño events) can also reduce the quality or quantity of habitat provided by kelps by increasing mortality and reducing recruitment of kelps (Edwards and Hernández-Carmona, 2005), and reducing growth rates (Dean and Jacobsen, 1986). Recent work from Norway has highlighted how increased temperature and nutrient levels may interact to influence host kelp species and their associated communities, reducing overall benthic diversity (Norderhaug et al., 2015).

Alongside temperature and nutrient availability, light defines where kelps, and in turn their associated assemblages, can develop (Steneck and Johnson, 2013). Kelps are constrained to shallow, well-illuminated coastal areas; in areas lacking herbivores or other disturbance, kelp densities and thallus size decline rapidly with depth (Steneck et al., 2002). High levels of turbidity reduce the amount of light that can penetrate the water column, thus restricting the photic zone and therefore the habitable area for kelps (Steneck et al., 2002; Vadas and Steneck, 1988). As such, levels of light (whether as a function of latitude, depth or water clarity) can control the amount of habitat provided by kelps. Singularly, turbidity can also impact on kelp associated assemblages, reducing diversity by to the increased dominance of few species in turbid waters (e.g. Moore, 1978), or through the increased provision of particulate organic matter as a food source (Moore, 1972b).

3. 2. Biological regulation

The longevity of individual kelp plants can have an effect on the faunal assemblages associated with them. Age has been shown to have significant impacts on the epiphytes growing on the stipe of *Laminaria hyperborea* (Whittick, 1983), and the diversity and abundance of epiphytes has been shown to increase with the age of the host (Christie et al., 1994); a pattern also shown in other species (e.g. *Saccharina latissima*; Russell, 1983). Epiphytes are often confined to the older, more rugose, basal parts of the stipe (Whittick, 1983), and the distal, older parts of the blade (Bartsch et al., 2008; Christie et al., 2003; Norton et al., 1977). The holdfasts of *L. hyperborea*, however, have been shown to reach maximal diversity at around six years old, despite the plant persisting for up to 15 years, potentially due to reduced habitable space within the holdfast as encrusting fauna increase in size and coverage (Anderson et al., 2005), or to the more accessible nature of larger holdfasts to predators (Christie et al., 1998). Age structure of entire kelp populations can be affected by local environmental conditions, particularly wave exposure. Studies of *Laminaria setchellii* (Klinger and De Wreede, 1988) and *L. hyperborea* (Kain, 1971, 1976) have documented a higher proportion of younger plants at more exposed sites, suggesting a higher mortality of plants in these areas. Thus the influences of wave exposure, kelp size, and kelp age are intrinsically linked and highly dependent on both the species and the local conditions involved.

A major factor limiting the abundance and diversity of the assemblages associated with kelps, particularly the blade microhabitat, is the longevity of the substrata. While the stipe (excluding the epiphytes) and holdfast structures persist for the life span of the kelp (in excess of 15 years for some species), the blade is a more ephemeral structure and in many species is replaced annually, which can limit the persistence and accumulation of species (Christie et al., 2003; Norton et al., 1977). For kelp species with blades that persist for multiple years, the age of the substratum may influence the diversity and structure of the associated epibiotic assemblage (Carlsen et al., 2007). Carlsen et al. (2007) found that the number of epifaunal species found on the blade of *Laminaria digitata* and *Saccharina latissima* in Svalbard was negatively correlated with increasing age, possibly due to a reduction of substrate (blade) surface area, increased physical stress at the distal tips, and increased tissue decay with age.

While assemblages associated with the holdfast seem to be relatively stable throughout the year, stipe epiphytes are prone to a high degree of variability between seasons (Christie et al., 2003). The biomass of epiphytic algae tends to decline in the winter, reducing available habitat (Whittick, 1983) and therefore faunal diversity and abundance (Christie et al., 2003). Christie et al. (2003), however, found no reduction in the volume of epiphytic algae growing on *Laminaria hyperborea* in winter, instead suggesting that other factors may also be responsible for the observed reduction in the abundance of faunal assemblages (e.g. reduced habitat complexity, greater predation pressure, increased exposure to winter storm events, and emigration; Christie et al., 2003; Christie and Kraufvelin, 2004). Increases in the abundance of holdfast fauna have also been observed in winter months, suggesting that stipe/epiphytic algae associated species may migrate down to the holdfast during the winter (Christie et al., 2003); holdfasts represent a year round stable habitat and a source of food (i.e. through retention of sediment; Moore, 1972b). Faunal species in epiphyte-associated assemblages generally have higher dispersal rates than those found within the holdfast (Norderhaug et al., 2002), perhaps partly in response to this annual cycle. Epibiotic assemblages associated with kelp blades also exhibit seasonality as they are strongly influenced by processes occurring in the overlying water column, such as seasonal variability in phytoplankton production and related patterns of invertebrate larvae density (Carlsen et al., 2007).

While patterns in the abundance, diversity and structure of faunal assemblages inhabiting kelps can vary at small scales, similarities can be seen at much larger spatial scales. Comparisons between studies carried out in the northeast Atlantic show that the species utilising kelps as habitat in this area are relatively consistent (Blight and Thompson, 2008; Christie et al., 2003; Jones, 1971; Moore, 1973a, b; Schultze et al., 1990). Similarly, Anderson et al. (2005) examined assemblages in *Ecklonia radiata* holdfasts in New Zealand and reported high levels of consistency in structure and diversity at large spatial scales. At coarser taxonomic levels, and global scales, Smith et al. (1996) commented that the dominant faunal groups found within *E. radiata* in Australia were comparable to those inhabiting *Laminaria hyperborea* holdfasts in the UK. Conversely, early work on *Macrocystis pyrifera* in the eastern Pacific reported pronounced large-scale variability in holdfast assemblage structure, which was attributed to biogeographic differences in faunistic composition (Ojeda and Santelices, 1984; Santelices, 1980). Similarly, holdfast assemblages in the high Arctic are impoverished and distinct from those at lower latitudes, most likely due to a smaller species pool arising from ecological and evolutionary processes (Włodarska-Kowalczuk et al., 2009).

While kelp detritus is an important source of carbon and nitrogen for both subtidal (Fielding and Davis, 1989; Mann, 1988) and intertidal consumers (Bustamante and Branch, 1996; Krumhansl and Scheibling, 2012), the majority of fauna inhabiting kelps do not directly feed on fresh kelp material, due in part to their high C:N ratios (Norderhaug et al., 2003; Schaal et al., 2010) and the presence of anti-herbivory compounds in their tissues (Bustamante and Branch, 1996; Duggins and Eckman, 1997; Norderhaug et al., 2003). There is evidence that palatability, and thus the susceptibility to grazing, of kelp differs between species, which may be related to the phlorotannin concentration of the tissue, but also to tissue toughness, the area of the kelp concerned and overall nutritive values (Dubois and Iken, 2012; Macaya et al., 2005; Norderhaug et al., 2006). Nevertheless, a number of species do feed directly on fresh kelp material. The blue-rayed limpet, *Patella pellucida*, for example, is commonly found on laminarian kelps (McGrath, 1997, 2001) and it is known for those that are to feed exclusively on kelp tissue (Vahl, 1971). Two forms of the species exist; the annual *pellucida* form is found solely on the blade, while the *laevis* form migrates downwards where it grazes the stipe, and excavates the base of the stipe within the holdfast where it can persist for 2 years (Graham and Fretter, 1947; McGrath and Foley, 2005). As such, this species may cause considerable mortality of host kelps due to the weakening of the holdfast (Kain and Svendsen, 1969). Grazing by larger invertebrate herbivores (e.g. sea urchins) can reduce the amount of biogenic habitat available to the wider community by over-grazing kelp sporophytes and in extreme instances can cause phase shifts from structurally and biologically complex and diverse habitats to depauperate “barrens” (Filbee-Dexter and Scheibling, 2014; Johnson et al., 2011; Ling et al., 2015; Steneck et al., 2002).

Competition for suitable hard substratum, light and nutrients can also influence biogenic habitat provision by kelps. Shading by neighbouring canopy-forming macroalgae and epibionts can restrict light availability, while dense epibiont assemblages can limit the exchange of nutrients and/or gases by blocking the surface of thallus cells (Wahl et al., 2015), potentially reducing growth rates, altering morphology and, in extreme cases, leading to mortality.

4. Understorey assemblages and wider biodiversity

At spatial scales greater than a single kelp, multiple individuals form extensive canopies that provide three-dimensional habitat for a vast array of larger marine organisms (Smale et al., 2013), a number of which are of ecological (e.g. sea urchins; Kitching and Thain, 1983) or economical (e.g. the European Lobster; Johnson and Hart, 2001) importance. Kelp forests have long been recognised to be important in regards to a number of fish species, which utilise them as nursery and feeding areas, and as refugia from predators (Bodkin, 1988; Norderhaug et al., 2005; Reisewitz et al., 2006). Elevated abundances of fish species consequently attracts larger piscivores, such as seabirds and sea otters, whose distribution may be closely linked to kelp forests (Estes et al., 2004; Graham, 2004; Steneck et al., 2002). Stable isotope analysis has shown that a number of species of seabird derive a high proportion of their carbon from local kelps (e.g. the great cormorant and the eider duck; Fredriksen, 2003).

The kelp canopy ameliorates conditions for the development of diverse epilithic, understorey algal assemblage (Maggs, 1986; Norton et al., 1977), which provides habitat for an array of invertebrate fauna. Understorey assemblages are generally dominated by red algae, with commonly over 40 species present (Clark et al., 2004; Flukes et al., 2014; Maggs, 1986). For example, recent biodiversity surveys within kelp forests in the UK and Australia have recorded between 40 and 108 species of understorey macroalgae with richness values generally in the order of 50-60 species (Fig. 4). Spatial variability in the richness of understorey algal assemblages is likely to be influenced by both local (e.g. wave exposure, turbidity) and regional (e.g. available species pool) processes (Fig. 4). It is clear, however, that understorey assemblages are generally species-rich (Dayton, 1985). They have been shown to be more diverse than comparable assemblages on reefs lacking a canopy (Melville and Connell, 2001; Watt and Scrosati, 2013), most likely because canopies increase habitat heterogeneity and ameliorate environmental conditions.

The influence of canopy-forming macroalgae on understorey assemblages has been examined through both monitoring natural occurrences of canopy removal or thinning (e.g. by grazing; Bulleri and Benedetti-Cecchi, 2006; Ling, 2008; storms; Thomsen et al., 2004; or localised warming events; Smale and Wernberg, 2013; Wernberg et al., 2013), and experimentally by *in situ* removal experiments (Clark et al., 2004; Flukes et al., 2014; Hawkins and Harkin, 1985; Melville and Connell, 2001; Reed and Foster, 1984; Toohey et al., 2007). The structure, abundance and diversity of understorey assemblages is regulated by shading (Arkema et al., 2009; Foster, 1982; Kennelly, 1987; Reed and Foster, 1984) and alterations to water flow caused by the canopy (Eckman, 1983), as well as physical disturbance caused by the kelps themselves (i.e. thallus scour, particularly by those species lacking an erect stipe, e.g. *Ecklonia radiata*; Irving and Connell, 2006). The majority of algal species commonly found beneath kelp canopies are tolerant of low light conditions, and often occur below the depth limits of the kelps themselves (Norton et al., 1977). Culture experiments have shown that a number of typical understorey algae grow more rapidly and successfully at lower irradiances (Boney and Corner, 1963; Norton et al., 1977), and suffer mortality at higher irradiances (see Jones and Dent, 1971 and references therein).

Changes in hydrodynamics caused by macroalgae and seagrass canopies may alter the supply and dispersal of algal propagules and invertebrate larvae, thereby affecting settlement processes (Eckman, 1983; Eckman et al., 1989). With respect to adult life stages, alterations to water flow can influence feeding activities, and therefore the growth and survival, of filter feeding invertebrates (Knights et al., 2012; Leichter and Witman, 1997) and increased sedimentation has been shown to have a negative impact on the recruitment and survival of sessile invertebrates (Airoldi, 2003; Irving and Connell, 2002). Moreover, physical disturbance caused by the scouring of the seabed by kelp thalli has been shown to have negative effects on the abundance of some morphological (i.e. erect) forms of understorey algae (Irving and Connell, 2006).

Habitat-forming kelps may also interact with habitat-forming sessile invertebrates, with spatial and temporal variability in their relative abundances influencing the wider community. An interesting example is the sea palm *Postelsia palmaeformis*, an annual kelp which occurs in patches within mussel beds (*Mytlius californianus*) along wave-exposed coastlines of the northeast Pacific (Blanchette, 1996; Dayton, 1973). *P. palmaeformis* has limited dispersal potential and is competitively inferior to *M. californianus*, but can rapidly colonise areas of reef following disturbance to mussel beds (Blanchette, 1996). Moreover, recruitment of *P. palmaeformis* sporophytes onto *M. californianus* individuals increases the probability of their dislodgement during winter storms, which subsequently frees up space on the reef for further *P. palmaeformis* colonisation (Dayton, 1973). As such, the interaction between these species and their environment (i.e. storm disturbance) shapes the wider habitat and influences community structure.

All of the governing factors are context dependent and differ between kelp species, reef topography, and local hydrodynamic conditions (e.g. Harrold et al., 1988). For instance, while all kelp canopies regulate the amount of light reaching the seabed, the degree of shading is dependent on the morphological structure of the species. The rigid stipe and relatively small blade of *Laminaria hyperborea* can reduce sub-canopy light levels to as little as 10% of surface irradiance in the summer (Norton et al., 1977; Pedersen et al., 2014). The buoyant, extensive fronds of *Macrocystis pyrifera*, however, can reduce light levels to <1% of surface levels (Reed and Foster, 1984). Indeed, within Californian *M. pyrifera* systems the abundance of understorey algae beneath the canopy may be light-limited (Foster, 1982; Rosenthal et al., 1974), so that removal of the canopy can lead to increases in both abundance and richness of understorey assemblages (Kimura and Foster, 1984; Reed and Foster, 1984). In Chile, however, similar canopy removal experiments deliver a comparatively muted ecological response (Santelices and Ojeda, 1984).

Unlike in *M. pyrifera* dominated systems, sessile invertebrates are conspicuously absent from the understorey assemblages in temperate Australia (Fowler-Walker and Connell, 2002). It appears that the negative impacts of the constant sweeping of the seabed by the dominant canopy forming kelp, *Ecklonia radiata*, outweighs the positive effects of the canopy, and act to exclude sessile invertebrates (Connell, 2003b). Thus the morphological differences between *M. pyrifera* (large, buoyant species) and *E. radiata* (small, sweeping species) act to provide conditions suitable for vastly different understorey assemblages. Within a single species of kelp, wider environmental conditions will also lead to differences in the morphology of individual kelps, and to the population structure of localised forests, and therefore to a difference in conditions experienced by understorey species. The age structure of *L. hyperborea* has been shown to be different in more exposed conditions, with generally younger individuals due to the high mortality of larger plants (Kain, 1971, 1976). Young *L. hyperborea* plants have a shorter, more flexible stipe, potentially resulting (particularly with the high degree of wave action associated with more exposed locations) more physical disturbance of the seabed, in comparison to older, larger plants (Leclerc et al., 2015). This, again, highlights the importance of context in the study of understorey assemblages (see Santelices and Ojeda, 1984).

The majority of experimental manipulations of understorey assemblages are concerned with a monospecific canopy, and studies on diverse algal canopies are comparatively scarce. Diverse macroalgae canopies may promote greater biodiversity in understorey assemblages than monospecific canopies (Smale et al., 2010) due to the enhanced habitat heterogeneity and niche diversification found under mixed canopies (Clark et al., 2004; Smale et al., 2013). The reef itself also plays a role in regulating understories, by altering the structure of the forest canopy (Toohey et al., 2007). Topographically complex reefs have a higher irradiance and greater water motion than simple, flat reefs, and are therefore less likely to impact the degree to which the seabed is shaded by the canopy (Toohey and Kendrick, 2008). Thus, such reef communities are complex, and should be taken into account both in future work on these systems, and in future management decisions (Leclerc et al., 2015).

Removal or thinning of kelp forest canopies cannot only serve to alter the structure of understorey assemblages, but such disturbances can also provide opportunity for the recruitment and growth of non-native species (Valentine and Johnson, 2003), potentially with detrimental effects on the diversity and habitat structure of these systems (Bax et al., 2001). It has been shown that disturbance to native algal assemblages is required for the colonisation of non-native species such as *Undaria pinnatifida* (Valentine and Johnson, 2003). *U. pinnatifida* has also been shown to host a less diverse and structurally distinct epibiotic assemblage when compared with native algae (Arnold et al., 2016; Raffo et al., 2009). Thus invasion of native reef assemblages by non-native species may result in impoverished kelp associated assemblages and overall lower local biodiversity (Arnold et al., 2016; Casas et al., 2004). Alternatively, invasion by *U. pinnatifida* and other macroalgae may have limited or transient effects on recipient kelp forest communities (South et al., 2015) and, as such, non-native species could enhance overall biodiversity by increasing habitat heterogeneity and/or volume.

Along urbanised coastlines globally, replacement of natural substrate with artificial structures relating to human activities is common and widespread (e.g. >50% of shores in Sydney Harbour are artificial seawalls; Chapman, 2003). Such structures differ from natural reefs in a number of ways, including their composition, complexity and orientation, and have been shown to support distinct assemblages from those found on natural substrates (Bulleri et al., 2005; Glasby, 1999). Recently there has been a focus on elevating the ecological value of such structures, including the 'gardening' of habitat-forming species (Firth et al., 2014; Perkol-Finkel et al., 2012). Habitat-forming species growing on artificial substrates, however, support different associated assemblages compared to those growing on natural substrate (Marzinelli et al., 2009; People, 2006). For example, Marzinelli (2012) showed that *Ecklonia radiata* growing on pier-pilings supported different assemblages of bryozoans than those found on natural reefs, and that the abundances of bryozoans, including the invasive *Membranipora membranacea*, were significantly greater on kelps on artificial substrates. This variability in ecological pattern was driven by both direct (through shading) and indirect factors (by altering abundances of sea urchins; Marzinelli et al., 2011). Clearly, the functioning of kelps as habitat forming species varies between natural and artificial habitats and, given the rate of coastal development and habitat modification, this represents an important area of research.

5. Threats to biogenic habitat provided by kelps

Kelp forests are under threat from a range of anthropogenic pressures, such as decreased water quality, climate change and overgrazing driven by trophic cascade effects from overfishing (Brodie et al., 2014; Smale et al., 2013; Steneck et al., 2002; Steneck and Johnson, 2013). Threats to ecosystems services provided by kelp forests have been examined in recent reviews by Smale et al. (2013) and Steneck and Johnson (2013) and will be briefly considered here in relation to biogenic habitat provision. While physical disturbance by wave action is important in maintaining diversity within kelp forests, as well as promoting turnover of nutrients and species (Kendrick et al., 2004; Smale et al., 2010; Smale and Vance, 2015), extreme wave action can cause damage to kelps and associated fauna, leading to high rates of mortality and widespread loss of habitat (Filbee-Dexter and Scheibling, 2012; Krumhansl and Scheibling, 2011a). During intense storms, wave action can cause dislodgement of entire kelp plants, and can lead to large areas of reef being cleared of canopy cover (e.g. Reed et al., 2011; Thomsen et al., 2004). As many climate models predict an increase in the frequency of extreme high-intensity storms in the future, as a consequence of anthropogenic climate change (Easterling et al., 2000; Meehl et al., 2000), increased wave action may reduce kelp forest extent and biodiversity and simplify food webs (Byrnes et al., 2011), and possibly facilitate invasion by non-native species (e.g. Edgar et al., 2004). An increase in the frequency or magnitude of storm events will probably impact the quality and quantity of biogenic habitat available for associated assemblages, as removal of material, from an individual kelp plant to large swathes of kelp forest, represents removal of a vast amount of biogenic habitat from the system. Smaller-scale removal and thinning of kelp forest canopies will also influence associated species, and alter associated structure (Clark et al., 2004; Connell, 2003b; Flukes et al., 2014; Hawkins and Harkin, 1985; Santelices and Ojeda, 1984). Furthermore, increased storminess and physical disturbance may interact with other environmental change factors, such as climate-driven range shifts of species (Smale and Vance, 2015) or the spread of non-native species (Krumhansl et al., 2011), to further drive alterations or loss of biogenic habitat.

Over-grazing of kelp forests, particularly by sea urchins, can lead to considerable loss of biogenic habitat from temperate ecosystems, in extreme cases causing phase-shifts from structurally complex habitat to depauperate “barrens” (Breen and Mann, 1976b; Filbee-Dexter and Scheibling, 2014; Hagan, 1983; Johnson et al., 2011; Ling et al., 2015; Steneck et al., 2002). The regulation of sea urchin abundances is often linked to the structure and spatial extent of kelp forests (Steneck et al., 2002). Disease (Scheibling et al., 1999), storms (Dayton, 1985) and turbulence (Choat and Schiel, 1982) can all influence sea urchin abundances, but predators are the single most important regulator of sea urchin populations (Estes and Duggins, 1995; Johnson et al., 2011; Ling et al., 2015; Sala et al., 1998; Steneck, 1998). Where key sea urchin predators (e.g. lobster; Breen and Mann, 1976a; Ling et al., 2009; and cod; Tegner and Dayton, 2000) are the focus of intensive fishing pressure, a trophic cascade may occur whereby sea urchin populations proliferate and large-scale deforestation of kelp forests ensues.

The regularity and intensity of the removal of kelp canopies, through storms or harvesting, is important with regards to the recovery of affected communities. Studies on the impacts of regular harvesting of kelp (e.g. in Norway; Christie et al., 1998) have shown that recovery rates for kelps themselves may not reflect recovery rates for the whole community. While kelp density and morphology may return to a pre-harvested state (> 1 m in height) within 2 – 3 years, associated epiphytic assemblages can take considerably longer to recover (4 - 6 years; Christie et al., 1998). Epiphytic algal communities have been shown to recover particularly slowly and, despite species richness returning to pre-disturbance levels in line with kelp recovery (2 – 3 years), the three-dimensional structure of these assemblages requires a longer period to fully recover, potentially limiting the recovery of associated faunal assemblages (Christie et al., 1998). This level of disturbance has also been shown to impact the abundance of some fish species, as well as impact on the foraging behaviour of some seabirds (Lorentsen et al., 2010). Commercial-scale kelp harvesting (for alginates, food, biofuel and other products) has the potential to severely impact provision of biogenic habitat (e.g. Anderson et al., 2006; Christie et al., 1998), and consequently biodiversity and ecosystem structure, and needs to be carefully managed and regulated into the future. Similarly, aquaculture of kelps and other seaweeds is a rapidly growing global industry (Loureiro et al., 2015) and farming practises have the potential to impact biogenic habitat provision by kelps through the spread of disease (Loureiro et al., 2015) and non-native species (James and Shears, 2016), as well as through interbreeding between wild and farmed populations (Tano et al., 2015). Kelps are cool water species and are stressed by high temperatures (Steneck et al., 2002). As such, seawater warming (in association with global climate change) will impact the distribution, productivity, resilience and structure of kelp forests (Harley et al., 2012; Wernberg et al., 2010; but see Merzouk and Johnson, 2011). Both increased frequency and severity of extreme warming events (Dayton and

Tegner, 1984; Smale and Wernberg, 2013) and longer-term gradual warming (Wernberg et al., 2011) are likely to have significant impacts on habitat structure and, particularly for those species at the equatorial range edge, may cause widespread losses of kelp populations (Fernandez, 2011; Raybaud et al., 2013; Voerman et al., 2013).

In addition to increasing temperature, changes in water quality (particularly turbidity) will influence the spatial extent (i.e. both the geographical distribution and maximum depth of populations) and the structure of kelp habitat which, in turn, will influence associated biodiversity patterns. Decreased water quality (i.e. increased nutrients, sediments and turbidity) in coastal environments has led to widespread losses of kelp populations and caused structural shifts in habitats and communities (Connell et al., 2008; Moy and Christie, 2012). As such, human activities influencing processes acting across the land-sea interface, such as coastal development, agricultural practises and catchment management, have the potential to significantly alter kelp forest structure.

Physiological stresses are likely to make kelps more susceptible to disease. Disease can cause wide-spread mortality or have sub-lethal impacts, such as reduced growth and fecundity (Wahl et al., 2015), and may induce alterations in community structure and facilitate the spread of non-native species (Gachon et al., 2010). Mass mortality of kelps in New Zealand was attributed to disease, induced by increased physiological stress (Cole and Babcock, 1996). Infected *Saccharina latissima* individuals have been shown to grow more slowly than healthy plants (Schatz, 1984), and infection can cause thallus deformity (Peters and Schaffelke, 1996), and affect depth distributions (Schaffelke et al., 1996). The virulence of many marine microbes is temperature-regulated (Eggert et al., 2010; Harvell et al., 2002). Thus, warmer temperatures may lead to stressed susceptible hosts being exposed to more abundant and virulent pathogens (Wahl et al., 2015), which will ultimately affect biogenic habitat provision. The influence of multiple concurrent stressors will impact habitat provision by kelps in complex and potentially unexpected ways. Thus, more research is required in order to predict how the diversity and abundance of kelp associated flora and fauna will respond to future conditions.

In order to alleviate the impacts of current threats and stressors, and to reduce further loss of habitat, there are a few recent examples of management and conservation measures specially targeted at kelp species. In eastern Tasmania, dramatic declines in the extent of *Macrocystis pyrifera* have been observed since the 1980s; likely caused by the southward penetration of the warm, nutrient-poor waters of the Eastern Australian Current (Johnson et al., 2011). In August 2012, as a result of these losses, the Australian giant kelp forests were listed as ‘endangered’ under the *Environmental Protection and Biodiversity Conservation Act* (see Bennett et al., 2016 and references therein). Recent evidence also shows that the Adriatic population of the Mediterranean deep-water kelp, *Laminaria rodriguezii*, has suffered a decline of >85% of its historical range, presumably from bottom trawling, and is now present only around the small off-shore island of Palagruža (Žuljević et al., 2016). This has prompted calls for the species to be classified as ‘endangered’ under the IUCN Red List in the Adriatic (Žuljević et al., 2016). In Europe ‘Reefs’ are listed under Annex I of the Habitats Directive as a marine habitat to be protected by the designation of Special Areas of Conservation (SACs). While kelp forests are not specifically targeted in the Habitats Directive, species of the genus *Laminaria* are named components of the ‘Reefs’ habitat (Airoldi and Beck, 2007). Additionally, two species of *Laminaria* from the Mediterranean (*L. rodriguezii* and *L. ochroleuca*) are listed in Annex 1 of the Bern Convention (Airoldi and Beck, 2007). At the National level, some countries have implemented legislation and policies specifically aimed at kelp populations and communities. For instance, the commercial harvesting of kelp is strictly regulated in France and Norway (Birkett et al., 1998; Christie et al., 1998).

6. Knowledge gaps and recommendations for further research

1. The provision of biogenic habitat by kelp species globally represents a significant and highly-valuable ecological service, which is increasingly under threat from environmental change. While

the patterns of change and driving processes have been studied extensively over the last 60 years or so, our current knowledge on the ecology of kelp forests is not evenly spread. The majority of research concerns just a few species (namely *Laminaria hyperborea* in the northeast Atlantic, *Macrocystis pyrifera* in the north Pacific and southern Atlantic, and *Ecklonia radiata* in South Africa and Australasia), and information on others is sparse, or even non-existent. Indeed, several areas of kelp distribution seem to be understudied, with very little information from East Asia currently available or accessible.

2. While steps must be taken to form an accurate picture of habitat provision and associated biodiversity patterns from a representative number of kelp species, the experimental design used to do so should also be taken into account. Currently, it is difficult to make overarching inferences or comparisons between kelp species or geographic regions from existing data, due to the different sampling methods, survey designs, habitat metrics (e.g. total habitat volume versus habitable space) and ecological response variables used and presented between studies.

3. A standardised sampling approach would allow comparisons to be made between species and across large spatial scales. Given that several key ecological processes operate at large spatial scales (e.g. climate change, global spread of non-native species), consistent and comparable observations of kelp populations and their associated communities across similar spatial scales are needed to advance understanding and improve management of these highly-valuable ecosystems. Adequately resourced international projects or networks would facilitate these goals.

4. Recent advances in technology should be employed in order to advance understanding of ecological pattern and processes within kelp forests. For example, previous work unravelling the influence of habitat complexity and size have used simplified mimics of biogenic structures (e.g. holdfasts) that do not accurately represent the complexity seen in nature. Developments in 3D modelling and printing, for example, could be used to manipulate aspects of habitat complexity and size in an ecologically-relevant manner to shed new light on their influence on kelp-associated

biodiversity. Similarly, reliable information on the structure and spatial extent of kelp forest habitat is lacking for many regions, partly because shallow rocky reef habitat is logistically-difficult to sample at large spatial scales. Advances in remote sampling technologies, such as Automated Underwater Vehicles (AUVs, see Smale et al., 2012) and Gliders could dramatically increase the spatial and temporal scale of benthic sampling, which would provide more accurate assessment of the structure and distribution of kelp forest habitats. This information would feed into spatial modelling approaches (e.g. Bekkby et al., 2009) and, ultimately, marine management.

5. Kelp-dominated habitats provide a wealth of ecosystem goods and services, both directly (such as harvesting of kelp for food, alginates and other products as well as extraction of associated species including crabs and lobsters) and indirectly (such as biogenic coastal defence and nutrient cycling). However, current understanding of the provision of these goods and services, and their value and importance to human society, is limited. A better appreciation of the direct and indirect value of kelp forests, and marine ecosystems generally, to regional industries such as fishing and tourism will benefit conservation and management of these habitats.

6. Global environmental change factors, such as the spread of invasive species, overfishing and climate change, are impacting the structure and quantity of biogenic habitat provided by kelp species. Targeted field studies on the wider implications (e.g. changes in primary productivity, biodiversity, coastal geomorphology) of the loss or replacement of habitat-forming species, conducted across multiple spatial scales and trophic levels, is urgently needed to document ecological impacts, and to inform management and support conservation.

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Table 1: Summary data from published studies explicitly examining the structure and diversity of kelp-associated assemblages. * indicates the pooled number of species and/or individuals found in a number of samples. • indicates an average. † indicates that only mobile invertebrates were sampled. ‡ indicates that only sessile species were sampled. Christie et al. (1998) refers to samples taken a year after trawling (1 yr), and samples taken from untrawled areas (untrawled).

Species	Location	Month	Year	Kelp Section	No. samples	No. Species	No. Individuals	Reference
L. digitata	Kongsfjorden, Svalbard	5 & 8	2004	Blade	10	15*‡	N/R	**Carlsen et al. (2007)**
S. latissima		5 & 8	2004	Blade	10	17*‡	N/R	
A. esculenta	Kongsfjorden, Svalbard	6 & 7	1997	Entire plant	2 - 4	51*	32*	**Lippert et al. (2001)**
L. digitata		6 & 7	1997	Entire plant	2 - 4	32*	204*	
A. esculenta	Hornsund, Svalbard	7	2003	Blade	122	38*	N/R	**Włodarska-Kowalczuk et al. (2009)**
A. esculenta		7	2003	Stipe	122	16*	N/R	
A. esculenta		7	2003	Holdfast	122	151*	N/R	
L. digitata		7	2003	Blade	79	30*	N/R	
L. digitata		7	2003	Stipe	79	4*	N/R	
L. digitata		7	2003	Holdfast	79	143*	N/R	
S. latissima		7	2003	Blade	155	24*	N/R	
S. latissima		7	2003	Stipe	155	7*	N/R	
S. latissima		7	2003	Holdfast	155	143*	N/R	
L. hyperborea	Norway	8		Stipe	20	N/R	N/R	**Christie et al. (1998)**
L. hyperborea		8		Holdfast	20	N/R	1 yr. 750, untrawled 5000	
L. hyperborea	Norway	8 – 9	1993-97	Stipe	56	29 – 62	288 – 56330	**Christie et al. (2003)**
L. hyperborea		8 – 9	1993-97	Holdfast	56	41 – 77	388 – 5938	
L. hyperborea	Norway	8	1993	Entire plant	3-4	103†	621863†•	**Christie et al. (2009)**
L. hyperborea		8	1993	Entire plant	3-4	107†	24680†•	
L. hyperborea		8	1993	Entire plant	3-4	92†	15320†•	
L. hyperborea		8	1995	Entire plant	3-4	132†	55500†•	
L. hyperborea		8	1995	Entire plant	3-4	106†	84273†•	
L. hyperborea		8	1996	Entire plant	3-4	119†	126596†•	
L. hyperborea		8	1997	Entire plant	3-4	125†	12782†•	
L. hyperborea		8	1996	Entire plant	3-4	90†	25700†•	
S. latissima		8	1996	Entire plant	3-4	62†	110725†•	
S. latissima		8	2008	Entire plant	3-4	49†	22750†•	
S. latissima		8	2008	Entire plant	3-4	64†	75833†•	
L. hyperborea	Norway	6 & 9	1996	Frond	6	34†	2761†	**Jorgensen and Christie (2003)**
L. hyperborea		6 & 9	1996	Stipe	9	69†	39725†	
L. hyperborea		6 & 9	1996	Holdfast	9	89†	23157†	

L. hyperborea	Norway	4 - 11	1995	Stipe & Holdfast		116†	59664†	**Norderhaug et al. (2002)**
Artificial substrata	Norway	4 - 11	1995	ST & HF mimics		99†	38942†	
E. fistulosa	Aleutian Islands	Summer	2009	Holdfast	35	61	N/R	**Schuster and Konar (2014)**
S. polyschides	Isle of Cumbrae, Scotland	1	1981	Holdfast	19	77*	N/R	**McKenzie and Moore (1981)**
L. hyperborea	North Sea, Scotland	Summer	1975	Holdfast	20	33†	676†	**Sheppard et al. (1980)**
L. hyperborea	North Sea, England	Summer	1975	Holdfast	20	27†	1692†	
L. hyperborea	West Coast, England	Summer	1975	Holdfast	20	30†	562†	
L. hyperborea	South Coast, England	Summer	1975	Holdfast	20	35†	1164†	
L. digitata	Ireland, west coast	10/11	2011	Holdfast (benthic)	25	53*	1801*	**Walls et al. 2016**
L. digitata		10/11	2011	HF (suspended)	10	42*	633*	
L. digitata	Southwest UK	9 – 11	2004	Holdfast	15	96*	N/R	**Blight and Thompson (2008)**
L. ochroleuca		9 – 11	2004	Holdfast	15	68*	N/R	
L. ochroleuca	Plymouth Sound, UK	8	2014	Blade & Stipe	100	5*‡	N/R	**Arnold et al. (2016)**
S. latissima		8	2014	Blade & Stipe	100	7*‡	N/R	
S. polyschides		8	2014	Blade & Stipe	100	5*‡	N/R	
U. pinnatifida		8	2014	Blade & Stipe	100	4*‡	N/R	
L. ochroleuca		5 - 8	2014	Holdfast	56	32*‡	N/R	
S. latissima		5 - 8	2014	Holdfast	60	25*‡	N/R	
S. polyschides		5 - 8	2014	Holdfast	60	9*‡	N/R	
U. pinnatifida		5 - 8	2014	Holdfast	60	13*‡	N/R	
L. hyperborea	Plymouth Sound, UK	4	2014	Holdfast	12	61*‡	N/R	**Teagle et al. (in prep)**
L. hyperborea		4	2014	Stipe	15	29*‡	N/R	
L. ochroleuca		4	2014	Holdfast	12	49*‡	N/R	
L. ochroleuca		4	2014	Stipe	15	7*‡	N/R	
L. ochroleuca	Spain, north coast	7 - 8 (4 yr. study)	1996-99	Frond		8.4 (±3.39)	279†	**Arroyo et al. (2004)**
L. ochroleuca			1996-99	Holdfast		13.9 (±13.9)	5089†	
S. polyschides	Portugal	8		Holdfast	30	N/R	18,541*†	**Tuya et al. (2011)**
L. hyperborea		8		Holdfast	30	N/R	5,792*†	
E. radiata	NSW, Australia	2, 8	1987-91	Holdfast	54	386*	125605*†	**Smith et al. (1996)**
E. radiata	Australia			Holdfast		24.78	89.96	**Connell S. (unpublished data)**
E. radiata	New Zealand	1 – 2	2002	Holdfast	80	351*	N/R	**Anderson et al. (2005)**
L. spicata	Chile	4	2011	Holdfast	10	26* (taxa)	N/R	**Ortega et al. (2014)**
M. pyrifera	Chile	1, 4, 7, 9	1999 - 2001	Holdfast	10 - 18	114*	N/R	**Rios et al. (2007)**
M. pyrifera	Southern Chile	1, 4, 6, 9, 11	1980	Holdfast	62	43* (taxa)	N/R	**Ojeda and Santelices (1984)**
U. pinnatifida	Patagonia, Argentina	3	2004	Holdfast	N/R	25*	N/R	**Raffo et al. (2009)**
M. pyrifera	Patagonia, Argentina	3	2004	Holdfast	N/R	21*	N/R	

Table 2. Estimates of the quantity of biogenic habitat provided by kelp species at 2 contrasting study sites near Plymouth, UK. Data are sourced from Arnold et al. (2016), Smale et al. (2015) and unpublished data collected by Teagle and Smale. The approximate area of subtidal rocky reef inhabited by kelps at each study site was conservatively estimated by using a combination of satellite imagery, *in situ* surveys and bathymetry data. At Firestone Bay, mean values were generated from 5 independent surveys for abundance and 3 sampling events for biogenic habitat metrics. For the Mewstone, mean values for abundance and biogenic habitat structure were generated from 2 independent surveys. Abundance values relate to mature sporophytes only and do not include juvenile plants. Metrics shown are: biomass as wet weight (WW), holdfast habitable space (HFLS), surface area (SA; total area available for colonisation including stipe and blade) and abundance (AB). Note differences in units with increasing spatial scale.

Site 1: Firestone Bay (50°21'36.51"N, 04° 9'43.45"W), estimated area of rocky reef habitat = 4500 m^2										
Kelp Species	**Mean WW per plant (g)**	**Mean HFLS per plant (ml)**	**Mean SA per plant (cm^2)**	**Mean AB (inds. m^{-2})**	**Mean WW per m^2 (g)**	**Mean HFLS per m^2 (ml)**	**Mean SA per m^2 (cm^2)**	**Mean WW per site (T)**	**Mean HFLS per site (l)**	**Mean SA per site (m^2)**
L. ochroleuca	248	56	3706	0.9	214	48	3187	0.9	218	1434
S. latissima	265	26	4503	6.1	1631	164	27630	7.3	742	12433
S. polyschides	375	83	5104	1.4	526	116	7167	2.4	525	3225
U. pinnatifida	75	21	1192	2.5	188	52	2967	0.8	235	1335
TOTAL	965	187	14507	10.9	2559	382	40953	11.5	1721	18429

Site 2: West Mewstone (50°18'28.16"N, 04° 6'34.50"W), estimated area of rocky reef habitat = 8610 m^2										
Kelp Species	**Mean WW per plant (g)**	**Mean HFLS per plant (ml)**	**Mean SA per plant (cm^2)**	**Mean AB (inds. m^{-2})**	**Mean WW per m^2 (g)**	**Mean HFLS per m^2 (ml)**	**Mean SA per m^2 (cm^2)**	**Mean WW per site (T)**	**Mean HFLS per site (l)**	**Mean SA per site (m^2)**
L. hyperborea	750	190	3696	6.6	4927	1252	24260	42.4	10786	20888
L. ochroleuca	459	125	3260	3.1	1443	395	10248	12.4	3404	8823
S. latissima	265	26	4503	0.5	132	13	2251	1.1	115	1938
S. polyschides	375	83	5105	0.8	281	62	3828	2.4	537	3296
TOTAL	1851	426	16565	11.0	6784	1724	40588	58.4	14843	34946

Figure legends:

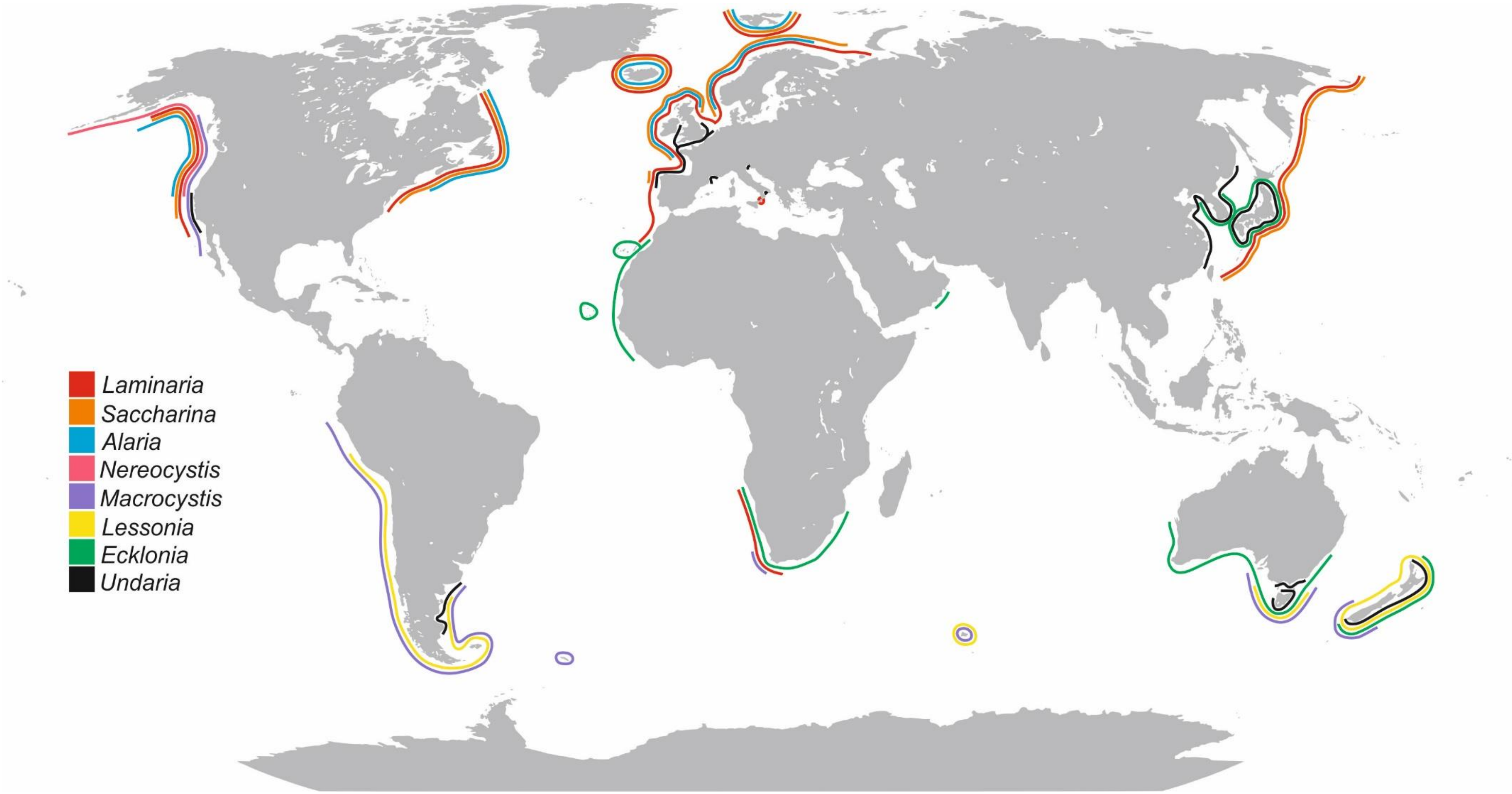
Figure 1. Approximate global distribution of dominant genera of the Laminariales. Modified and adapted from Steneck et al. (2002) and Steneck and Johnson (2013).

Figure 2. Schematic depicting the primary biogenic microhabitats (the blade/lamina, stipe and holdfast) provided by kelps, as well as secondary habitat (epiphytes) and the wider substratum modified by kelp canopies. Model kelp species shown are *Laminaria hyperborea* (left) and *Laminaria ochroleuca* (right). Interspecific variation in kelp morphology, structure and life history strongly influences habitat provision for the associated community.

Figure 3. Interspecific variability in the structure of the holdfast habitat provided by kelps. The 'typical' laminarian holdfast structure is illustrated by (A) *Laminaria ochroleuca* (example shown from Plymouth, UK), which is often colonised by a rich and abundant sessile invertebrate assemblage, and (B) *Laminaria pallida* (South Africa), which provides a highly complex and intricate microhabitat for associated organisms. Other typical laminarian species include (C) *Ecklonia radiata* (Western Australia), shown here supporting a high coverage of ecologically-important encrusting coralline algae, and (D) *Ecklonia maxima* (South Africa), which may support a high biomass of filter-feeding invertebrates. The giant kelp (E) *Macrocystis pyrifera* (California) forms a more massive and intricate structure, with mature holdfasts reaching ~1m in diameter and height. The non-native kelp (F) *Undaria pinnatifida* generates thin, intertwining haptera that form a far smaller holdfast habitat, but does produce an extensive and convoluted sporophyll. The fucoid bull 'kelp' (G) *Durvillaea Antarctica* (New Zealand) does not produce discrete haptera but instead forms a solid, discoid holdfast that provides a distinct habitat. (H) *Saccorhiza polyschides* (Plymouth, UK) is an important canopy-forming alga (order Tilopteridales not Laminariales) in the northwest Atlantic and develops a distinct holdfast structure comprising a large, hollow, bulbous structure and claw-like haptera. The approximate size of the holdfasts is illustrated by means of a 10 cm scale bar.

Figure 4. The number of unique understorey macroalgal taxa (primarily Rhodophyte species) recorded within kelp forests during recent biodiversity surveys in southwest UK (A) and southwest Australia (B). The cumulative number of species is derived for each location from multiple sites (2-6 site surveys per location, 3-15 m depth), with seaweeds identified *in situ* (using scuba) by regional taxonomic experts. Locations shown are (1) Pembrokeshire (2) Lundy Island (3) Fal and Helford Special Area of Conservation (4) Plymouth Sound (5) Isle of Wight (6) Kalbarri (7) Juiren Bay (8) Marmion Marine Park (9) Hamelin Bay. Data were collected by T. Wernberg from Australian sites (presented in Smale et al., 2010) and by F. Bunker and colleagues (2003-2012) at UK sites (Bunker, 2013; Bunker et al., 2005; Mercer et al., 2004 and F. Bunker unpublished data).

Fig 1.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Macrocystis
Lessonia
Ecklonia
Undaria

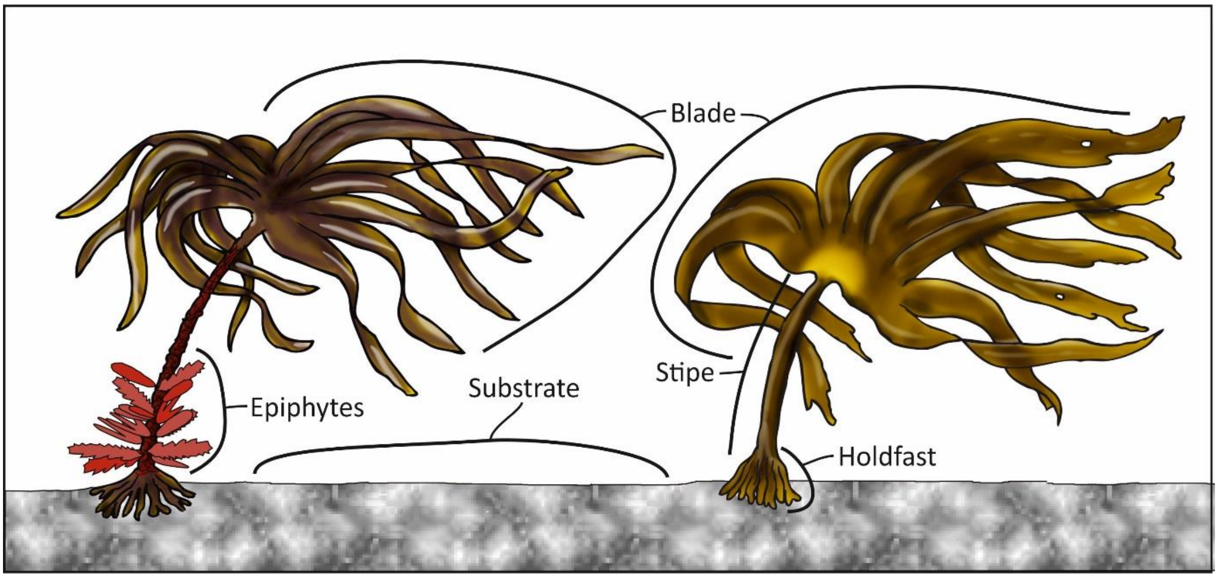
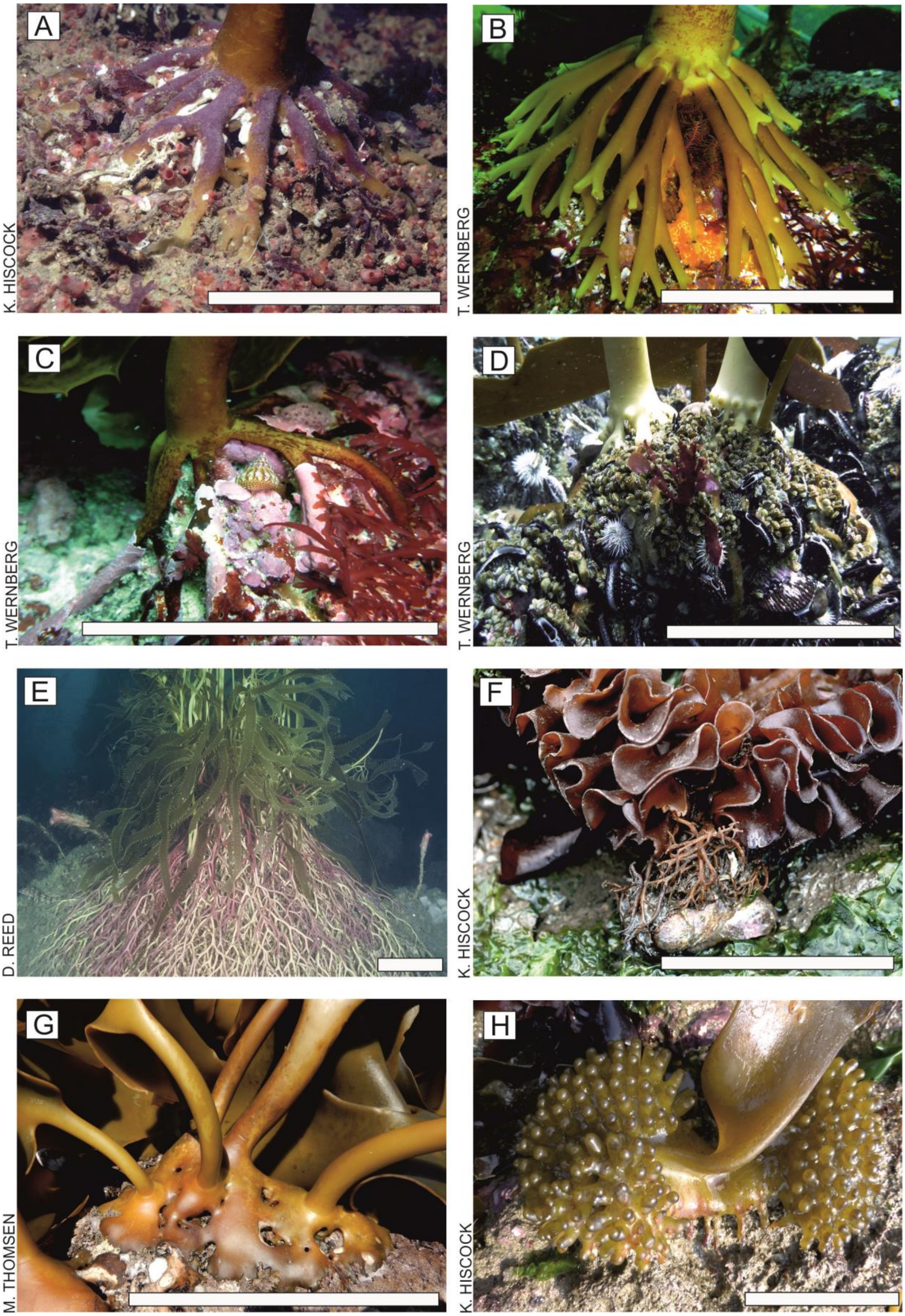


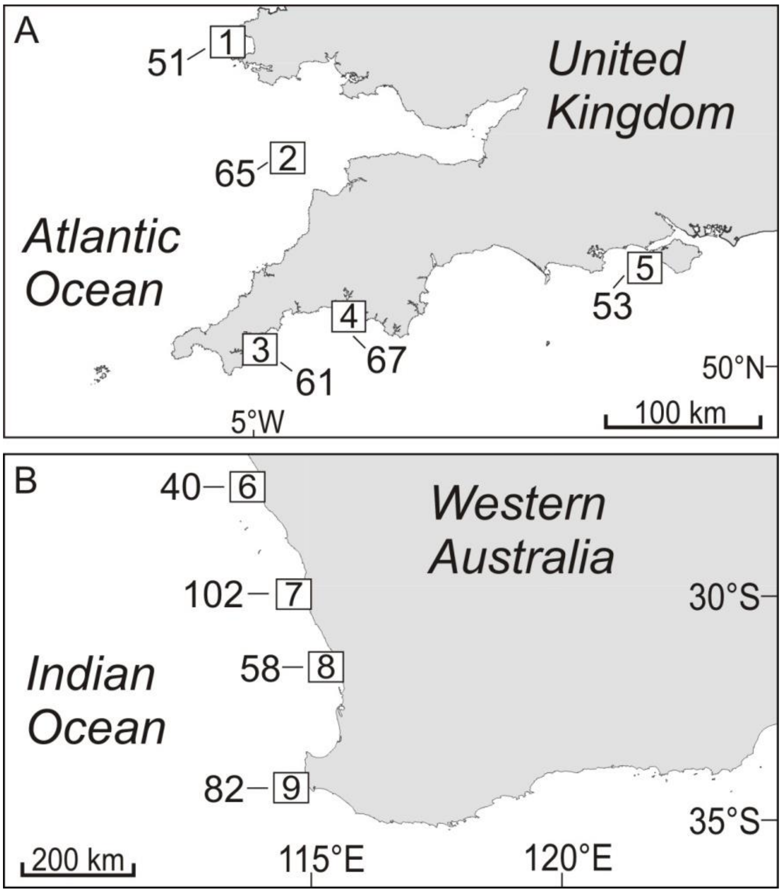
Fig 2.



1601

1602 Fig. 3

1603



1604

1605 Fig. 4

1606