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School of Ocean and Earth Sciences

The influence of ocean warming on the provision of biogenic habitat by kelp species

by

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(BSc Hons, MRes)

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UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES
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THE INFLUENCE OF OCEAN WARMING ON THE PROVISION OF BIOGENIC HABITAT BY KELP SPECIES

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Kelp forests represent some of the most productive and diverse habitats on Earth, and play a critical role in structuring nearshore temperate and subpolar environments. They have an important role in nutrient cycling, energy capture and transfer, and offer biogenic coastal defence. Kelps also provide extensive substrata for colonising organisms, ameliorate conditions for understorey assemblages, and generate three-dimensional habitat structure for a vast array of marine plants and animals, including a number of ecologically and commercially important species. This thesis aimed to describe the role of temperature on the functioning of kelp forests as biogenic habitat formers, predominantly via the substitution of cold water kelp species by warm water kelp species, or through the reduction in density of dominant habitat forming kelp due to predicted increases in seawater temperature. The work comprised three main components; (1) a broad scale study into the environmental drivers (including sea water temperature) of variability in holdfast assemblages of the dominant habitat forming kelp in the UK, *Laminaria hyperborea*, (2) a comparison of the warm water kelp *Laminaria ochroleuca* and the cold water kelp *L. hyperborea* as habitat forming species, and further investigation into the impacts of this subtle climate driven substitution of habitat forming kelps, and (3) experimental manipulation of densities of the dominant intertidal kelp in the UK, *Laminaria digitata*, in order to understand the impacts of climate driven loss of a dominant habitat forming species.

L. hyperborea assemblages varied significantly between study regions spanning ~9° of latitude, as well as between and within sites at a local scale. Patterns in mobile and sessile assemblage structure were driven principally by different environmental factors. Overall patterns in the structure of biogenic habitat and assemblage structure did not vary predictably with latitude, indicating that other processes acting across multiple spatial scales are important drivers of assemblage structure.

L. ochroleuca hosted impoverished assemblages associated with both holdfasts and stipes, compared with *L. hyperborea*. Further, climate driven increases in the relative abundance of *L. ochroleuca* relative to *L. hyperborea* lead to disruption of an important habitat cascade associated with the stipe of *L. hyperborea* and epiphytic algae. *L. ochroleuca* stipes typically lack the dense epiphytic assemblage associated with *L. hyperborea*, and host depauperate faunal assemblages which may have impacts on higher trophic levels.

Experimental reduction in the density of *L. digitata* led to a dramatic shift in dominance from perennial to annual species, particularly the pseudo-kelp *Saccorhiza polyschides* on an exposed rocky shore. Impacts on a sheltered shore were subtler, and may have been tempered by the presence of another perennial kelp, *Saccharina latissima*. Loss of *L. digitata* led to a reduction in the standing stock of macroalgae after ~2.5 years of manipulation on both shores. These findings have significant implications for the structure and functioning of rocky shores in the future.

Overall, anthropogenic climate change is likely to negatively impact the functioning of kelp forests as repositories of biodiversity in the future via the reshuffling of warm- and cold-water kelp species and through an overall loss of algal biomass and associated habitat due to continued increases in seawater temperature in the northeast Atlantic.

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Academic Thesis: Declaration Of Authorship

I, Harry Andrew Teagle declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

The influence of ocean warming on the provision of biogenic habitat by kelp species

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself (see following page);
7. Either none of this work has been published before submission, or parts of this work have been published as:

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Chapter 1:

This chapter has been published as:

Teagle, H., Hawkins, S. J., Moore, P. J., Smale, D. A. (2017) The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and Ecology*. **492**. 81 – 98.

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Chapter 4:

Experimental design and initial conception by Harry Teagle, Dan Smale. Fish gut data supplied by Mathilde Bue. Sample collection by Dan Smale and Pippa Moore. Feedback on the initial drafts from Dan Smale and Steve Hawkins.

Chapter 5:

Experimental design and initial conception by Harry Teagle, Dan Smale and Steve Hawkins. Fieldwork assistance from Anna Yunnie. Feedback on the initial drafts from Dan Smale and Steve Hawkins.

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Doing a PhD is tough, both physically and mentally. It's a long road and there are times when it seems easier to just give up; when the tide isn't low enough and you spend days just staring at the sea, when lab work doesn't work out and you begin to realise that those sponges you've been ignoring for 6 months might actually have to be identified, or when the apparently simple statistics you've been trying to run on your data for 8 hours just. Won't. Work. Its times like these that you need a friend (preferably in the same situation) to turn to and moan at. I was lucky enough to be blessed with not one, but two friends who stuck it out with me throughout this entire process. To Chaz and Sam, it's been tough at times, but I can honestly say it has been a pleasure and a joy to have you guys with me every step of the way. I couldn't be prouder of you both for the work that you've done over the last few years, and for going out and being real adults with real jobs now you've (almost) finished. Thank you for all the awkward giraffes, t**t paddles, laughs, pub sessions, tea breaks and everything in between. It's been a blast, and I'll see you on the other side.

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Chapter 1. General Introduction

The data and bulk of the information in the chapter are published as: Teagle, H., Hawkins, S. J., Moore, P. J. Smale, D. A. (2017) The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and Ecology*. 492. 81 – 98.

1.1. Opening remarks

Kelps dominate rocky reefs in lower intertidal and shallow subtidal zones throughout temperate and sub-polar regions of the world (Fig 1.1, Steneck *et al.*, 2002). Kelp forests represent some of the most productive and diverse habitats on Earth (Mann, 1973; Brady-Campbell *et al.*, 1984; Reed *et al.*, 2008) and provide humans with ecosystem services worth billions of dollars annually (Beaumont *et al.*, 2008).

The work in my thesis aims to provide novel insights into the effects of environmental factors on the functioning of kelps as biogenic habitat formers, with particular focus on the impacts of increases in seawater temperatures associated with anthropogenically-driven climate change. In the remainder of this introductory chapter I briefly outline the ecological roles played by kelps before synthesizing existing knowledge about kelps (and kelp-like canopy-forming brown algae) as biogenic habitat providers, particularly examining the consistency and variability in patterns of associated biodiversity across species and biogeographic regions. I 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 and identify threats to habitat provision by kelps. The rationale, overall aims and structure of the thesis are then outlined.

1.2. Role of kelps in ecosystem structure and functioning

Kelps are a major source of primary production in coastal zones (Mann, 1973; Krumhansl & Scheibling, 2012). 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 (Steneck *et al.*, 2002; Smale *et al.*, 2013). The biogenic habitat structure provided by large canopy-forming seaweeds has been shown to offer protection to several commercial fish species (Bologna & Steneck, 1993), and kelp forests in particular serve as important nursery grounds (Holbrook *et al.*, 1990; Tegner & 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 & Connell, 2006), flow dynamics (Eckman *et al.*, 1989), substratum availability and condition (Christie *et al.*, 2007) and food quantity and quality (Krumhansl & 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 ecological roles are often referred to as kelp in ecological studies, and will be considered as such throughout this thesis. 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 nine accepted families of Laminariales (Agaraceae, Akkesiphycaceae, Alariaceae, Arthrothamnaceae, Aureophycaceae, Chordaceae, Laminariaceae, Lessoniaceae and Pseudochordaceae) represented by 59 genera and 147 species (Guiry & Guiry 2015). At present, 84% of all described species are found within the three most speciose families (Alariaceae, Laminariaceae, and Lessoniaceae) and 63% of all kelp species are found within just five 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 1.1). Other widespread and ecologically important genera include *Macrocystis*, *Nereocystis* and *Undaria* (Fig 1.1). Other non-laminarian species which are commonly referred to as kelps include *Saccorhiza polyschides* and the bull ‘kelp’ *Durvillaea antarctica*.

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 & 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 1.2). These biogenic habitats differ considerably in structure (Fig 1.2) 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

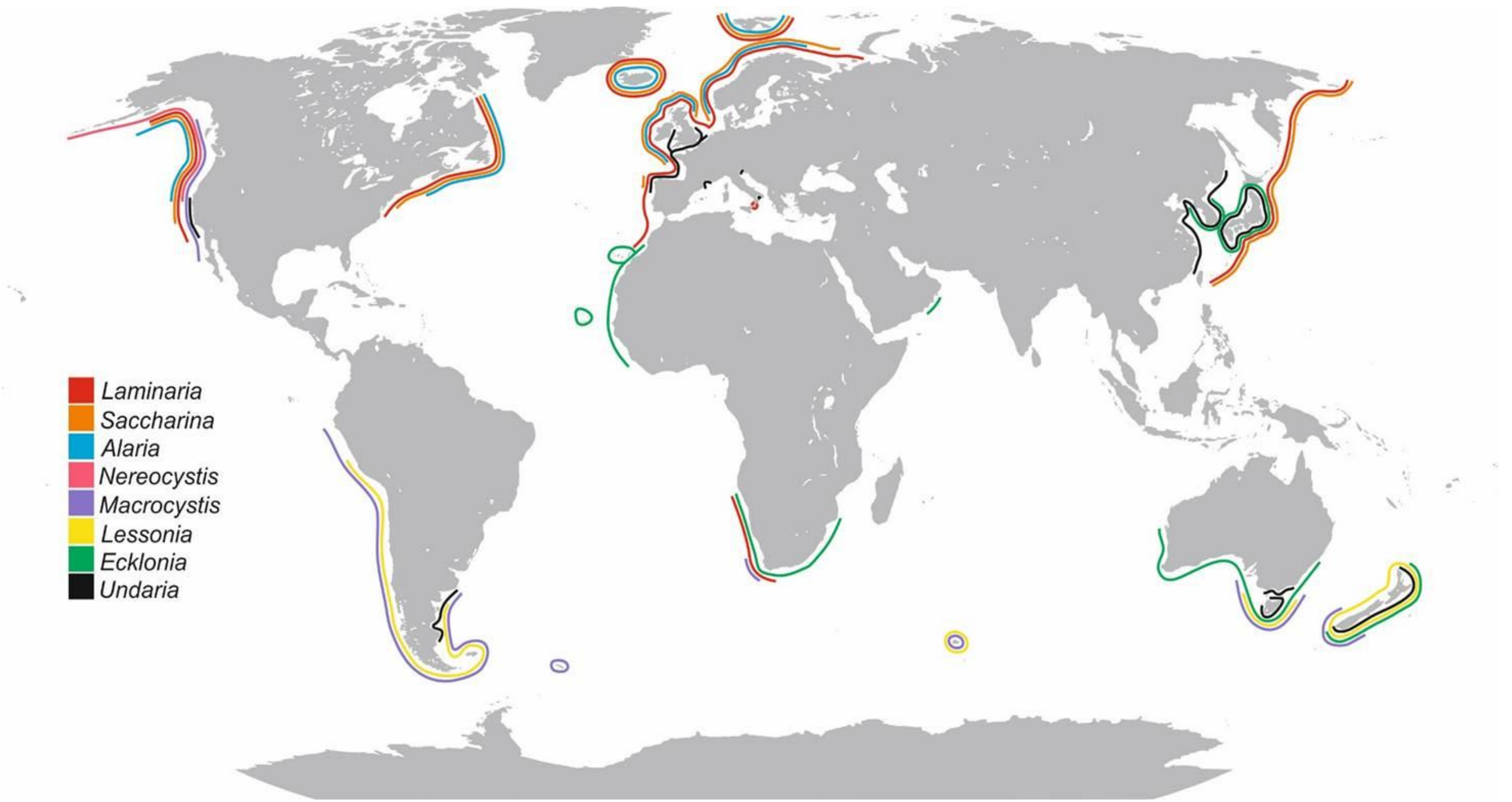

Fig 1.1 Approximate global distribution of dominant genera of the Laminariales. Modified and adapted from Steneck et al. (2002) and Steneck and Johnson (2013).

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.

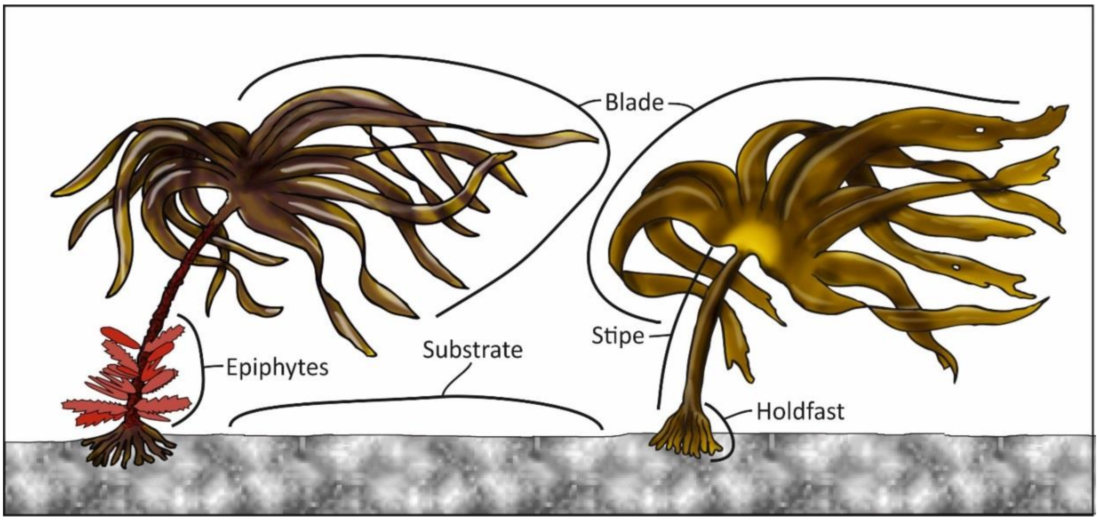

Fig 1.2 Schematic depicting the primary biogenic microhabitats (the blade/lamina, stipe and holdfast) provided by kelps, as well as secondary habitat (epiphytes) and the wider substratum modified by kelp canopies. Model kelp species shown are *Laminaria hyperborea* (left) and *Laminaria ochroleuca* (right). Interspecific variation in kelp morphology, structure and life history strongly influences habitat provision for the associated community.

1.3. Direct provision of biogenic habitat

i. 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 1.3).

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 1.3). 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 1.3). *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 1.3) 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 among populations subjected to different environmental conditions, particularly in response to gradients in wave exposure or current flow (Sjøtun & Fredriksen, 1995). For example, the biomass and internal volume of holdfasts of mature *Laminaria* plants can more than double along a wave exposure gradient (see Chapter 2). 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 via displacement (Sheppard et al., 1980). Recent work by Walls et al. (2016) suggests that

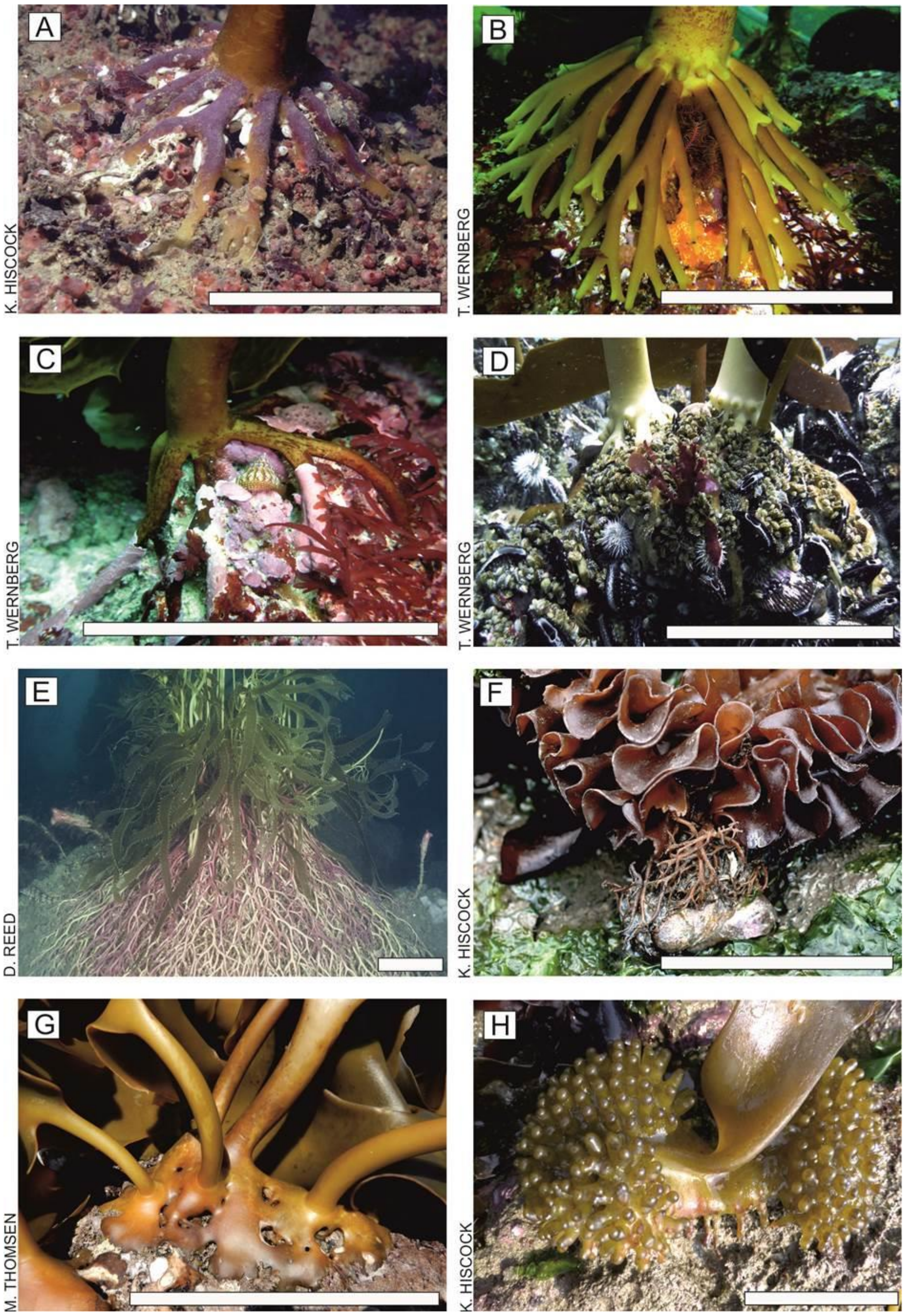

Fig 1.3 Interspecific variability in the structure of the holdfast habitat provided by kelps. The 'typical' laminarian holdfast structure is illustrated by (A) *Laminaria ochroleuca* (example shown from Plymouth, UK), which is often colonised by a rich and abundant sessile invertebrate assemblage, and (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.

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; 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 & 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 (Jones, 1972; Moore, 1972a; Thiel & Vásquez, 2000; Christie *et al.*, 2003). Macro-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 1.1). Even so, holdfast structures consistently support high levels of biodiversity (Table 1.1), with the vast majority of studies concluding 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 (Smith *et al.*, 1996; Anderson *et al.*, 2005). 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 1.1).

Holdfast assemblages are typically dominated by mobile invertebrates taxa including harpactocoid copepods, polychaetes, gastropods and amphipods plus sessile fauna such as bryozoans, bivalves and sponges (Moore, 1972a; Ojeda & Santelices, 1984; Norderhaug *et al.*, 2002; Christie *et al.*, 2003; Arroyo *et al.*, 2004; Anderson *et al.*, 2005; Rios *et al.*, 2007; Blight & Thompson, 2008; Christie *et al.*, 2009; 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, 1973b; Sheppard *et al.*, 1980; Smith & 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

Table 1.1 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 (UT).

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, UT 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	Holdfast (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	

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. In addition local water column turbidity and sedimentation rates are important influences, as many suspension feeding species are susceptible to smothering (Moore, 1973b). Food supply, principally from detrital kelp and other macroalgae and deposited phytoplankton, is rarely thought to be limiting in most kelp forest habitats (Newell *et al.*, 1982; Schaal *et al.*, 2012). Kelp holdfasts (particularly laminarian holdfasts) efficiently trap and accumulate sediment (Moore, 1972b; Arroyo *et al.*, 2004), 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 (Smith *et al.*, 1996; Christie *et al.*, 2003). 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 & McLay, 1983). The specific microhabitat provided by the holdfast structure allows the spider to survive submergence for at least 19 days (McQueen & McLay, 1983).

A range of trophic guilds are represented within holdfasts, including deposit feeders, filter feeders, grazers, scavengers and predators (McKenzie & 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 & Moore, 1981) and the spiny lobster *Panulirus interruptus* (Mai & 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 (Smith *et al.*, 1996; Christie *et al.*, 2003; Anderson *et al.*, 2005). 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 & Simpson, 1998), and sewage outfall effluent (Smith & Simpson, 1992). This has led to feasibility studies on the utility of kelp holdfasts as self-contained units for environmental monitoring (Sheppard *et al.*, 1980; Smith & Simpson, 1992; Anderson *et al.*, 2005).

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). All studies report that the total abundance of holdfast fauna increases with habitat size; but some studies have found this relationship only holds for smaller, younger holdfasts with abundance being independent of habitat size in older plants (Ojeda & Santelices, 1984; Anderson *et al.*, 2005). In contrast, a consistent positive relationship between faunal abundance and habitat size has been observed throughout the entire size range of the kelp holdfast (Smith *et al.*, 1996; Christie *et al.*, 2003; 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 (Ojeda & Santelices, 1984; Anderson *et al.*, 2005) 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 & Santelices, 1984; Smith *et al.*, 1996). This may be because 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 & Vásquez, 2000), making 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. They 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 contributing to 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 (Raffo *et al.*, 2009; Arnold *et al.*, 2016). In Argentina, the larger holdfasts offered by *M. pyrifera* support higher faunal richness and abundance than *U. pinnatifida* (Raffo *et al.*, 2009). In the British Isles 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 among kelp populations (Ojeda & 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).

ii. 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 with some species (e.g. *M. pyrifera*) developing mid-water fronds to facilitate photosynthesis (Graham *et al.*, 2007). Several ecologically-important species, including *Undaria pinnatifida* and *Saccorhiza polyschides* have flattened stipes (Norton, 1969; Norton & Burrows, 1969; Castric-Fey *et al.*, 1999). 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 & 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 (Harlin, 1973; Cattaneo & Klaff, 1979).

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 (Sørlie, 1994; Christie *et al.*, 1998). Whittick (1983), however, found that 95% of epiphyte biomass found on samples of *L. hyperborea* in southeast Scotland comprised just 4 species (*Palmaria palmata*, *Ptilota plumosa*, *Membranoptera alata* and *Phycodrys rubens*). 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 & 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 (Marshall, 1960; Allen & Griffiths, 1981; 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 1.1). 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 (Hacker & Steneck, 1990; Christie *et al.*, 2009). 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 (also see Schmidt & Scheibling, 2006; e.g. Palmaria palmata; Christie *et al.*, 2009). 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).

iii. 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 (Włodarska-Kowalczuk *et al.*, 2009; Arnold *et al.*, 2016). 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 & Harris, 1980). The blade of healthy kelp plants typically supports a low coverage of epiphytic algae, which may 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 & Christie, 2012; Smale & Wernberg, 2012). In perennial species it occurs 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 & 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 & 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 & 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 & 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; Scheibling *et al.*, 1999; Saunders & Metaxas, 2008). 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 & 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 & 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 1.1).

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 called *Helcion pellucidum or Patina pellucida*), is a common and locally abundant grazer found on *Laminaria* spp., where it feeds predominantly on the kelp tissue (Vahl, 1971; Christie *et al.*, 2003). Similarly, the gastropod *Lacuna vincta* can colonise laminae in high densities (e.g. on *Laminaria longicruris* in Nova Scotia; Johnson & 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 & Scheibling, 2011a). 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 (Ingólfsson, 1995; Hobday, 2000; Fraser *et al.*, 2011). 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 (Rueness, 1989; e.g. Sargassum muticum; Kraan, 2008).

iv. 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 & 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 & 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 macroalgae, 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 other 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).

v. The quantity of biogenic habitat provided by kelps

Kelp species are widespread throughout temperate and sub-polar 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, Werner & Kraan, 2004; Burrows *et al.*, 2014). 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 1.2). 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 1.2). To contextualise, the total biomass and surface area of biogenic habitat provided by kelps exceeds maximum reported values for mature seagrass meadows (Larkum *et al.*, 1984; ~95 g dry weight m2 and ~3.7 m2 respectively; Duarte & Sand-Jensen, 1990; 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 1.2). 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 1.2) 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 & Christie, 2012; Wernberg *et al.*, 2013).

Table 1.2. 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. LO = *Laminaria ochroleuca*, SL = *Saccharina latissima*, SP = *Saccorhiza polyschides*, UP = *Undaria pinnatifida*, LH = *Laminaria hyperborea*.

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)**
LO	248	56	3706	0.9	214	48	3187	0.9	218	1434
SL	265	26	4503	6.1	1631	164	27630	7.3	742	12433
SP	375	83	5104	1.4	526	116	7167	2.4	525	3225
UP	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)**
LH	750	190	3696	6.6	4927	1252	24260	42.4	10786	20888
LO	459	125	3260	3.1	1443	395	10248	12.4	3404	8823
SL	265	26	4503	0.5	132	13	2251	1.1	115	1938
SP	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

1.4. Physical and biological regulation of habitat provision

i. 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 (Fincham, 1974; Fenwick, 1976). 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 & 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, 1973b).

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 (Molloy & Bolton, 1996; Wernberg & Thomsen, 2005; Fowler-Walker *et al.*, 2006). Adaptations to exposed environments can result in an increase in holdfast size and volume (Sjøtun & Fredriksen, 1995, Smale, Teagle, unpublished data), increased stipe length (Smale *et al.*, 2016) and thickness (Klinger & De Wreede, 1988), and increased blade thickness (Molloy & Bolton, 1996; Kregting *et al.*, 2016). Such strength-increasing adaptations may reduce the probability of dislodgement, or other damage caused by wave action (Wernberg & Thomsen, 2005). An increase in overall thallus size is also a common adaptation to increased wave exposure in kelps (Klinger & De Wreede, 1988; Wernberg & Thomsen, 2005; Wernberg & Vanderklift, 2010; Pedersen *et al.*, 2012); 'going with the flow' with a long, flexible thallus reduces hydrodynamic forces (Friedland & Denny, 1995; Denny *et al.*, 1998; Koehl, 1999; Denny & Hale, 2003). Some species, however, also exhibit an increase in overall thallus size in very sheltered conditions (and L. digitata; Sundene, 1961; e.g. Laminaria hyperborea; Sjøtun & Fredriksen, 1995). 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 (Schultze *et al.*, 1990; Christie *et al.*, 1998; Christie *et al.*, 2003; Anderson *et al.*, 2005; Norderhaug *et al.*, 2007; Norderhaug & Christie, 2011; Norderhaug *et al.*, 2012; Norderhaug *et al.*, 2014; 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 & 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 (Pugh & Davenport, 1997; Fraser *et al.*, 2009). *Macrocystis pyrifera*, however, will persist in such areas as its holdfast can anchor below the maximum keel depth of ice-bergs (Pugh & 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 & Hernández-Carmona, 2005), and reducing growth rates (Dean & 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 (see Steneck & Johnson, 2013 and references therein). 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 (Vadas & Steneck, 1988; Steneck *et al.*, 2002). 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 due 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).

ii. 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 (Norton *et al.*, 1977; Christie *et al.*, 2003; Bartsch *et al.*, 2008). 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 & 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 (Norton *et al.*, 1977; Christie *et al.*, 2003). 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 & 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 (Jones, 1971; Moore, 1973b, a; Schultze *et al.*, 1990; Christie *et al.*, 2003; Blight & Thompson, 2008). 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 (Santelices, 1980; Ojeda & Santelices, 1984). 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 (Mann, 1988; Fielding & Davis, 1989) and intertidal consumers (Bustamante & Branch, 1996; Krumhansl & 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 & Branch, 1996; Duggins & 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 (Macaya *et al.*, 2005; Norderhaug *et al.*, 2006; Dubois & Iken, 2012). 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 & Fretter, 1947; McGrath & Foley, 2005). As such, this species may cause considerable mortality of host kelps due to the weakening of the holdfast (Kain & 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" (Steneck *et al.*, 2002; Johnson *et al.*, 2011; Filbee-Dexter & Scheibling, 2014; Ling *et al.*, 2015).

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.

1.5. 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 & Thain, 1983) or economical (e.g. the European Lobster; Johnson & 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 (Steneck *et al.*, 2002; Estes *et al.*, 2004; Graham, 2004). 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 (Norton *et al.*, 1977; Maggs, 1986), which provides habitat for an array of invertebrate fauna. Understorey assemblages are generally dominated by red algae, with commonly over 40 species present (Maggs, 1986; Clark *et al.*, 2004; Flukes *et al.*, 2014). 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 1.4). 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 1.4). 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 & Connell, 2001; Watt & 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 (storms; Thomsen *et al.*, 2004; e.g. by grazing; Bulleri & Benedetti-Cecchi, 2006; Ling, 2008; or localised warming events; Smale & Wernberg, 2013; Wernberg *et al.*, 2013), and

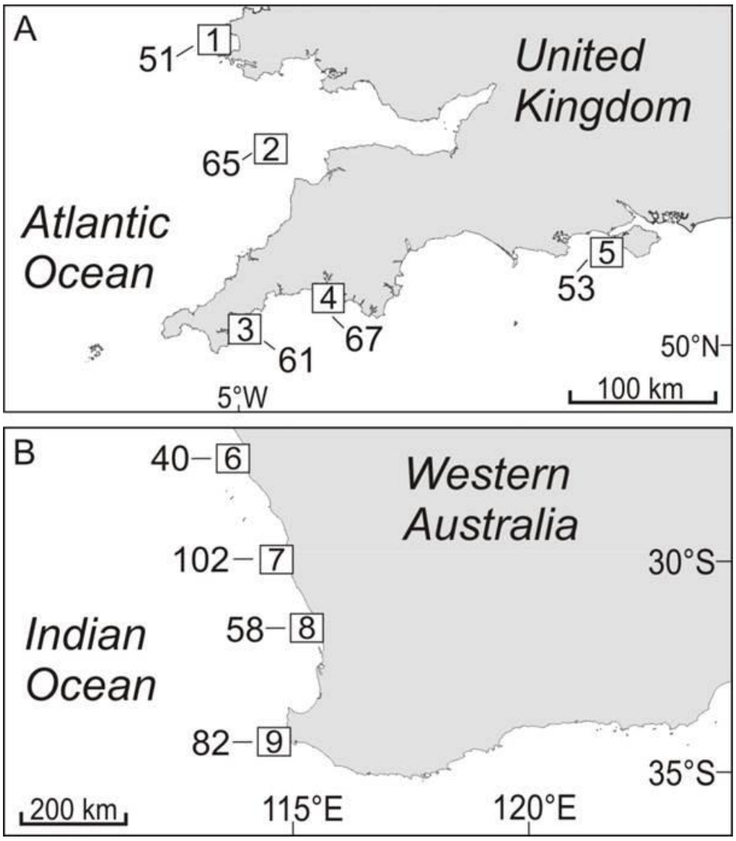

Fig 1.4 The number of unique understorey macroalgal taxa (primarily Rhodophyte species) recorded within kelp forests during recent biodiversity surveys in southwest UK (A) and southwest Australia (B). The cumulative number of species is derived for each location from multiple sites (2-6 site surveys 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 (Mercer *et al.*, 2004 and F. Bunker unpublished data; Bunker *et al.*, 2005; Bunker, 2013)

experimentally by *in situ* removal experiments (Reed & Foster, 1984; Hawkins & Harkin, 1985; Melville & Connell, 2001; Clark *et al.*, 2004; Toohey *et al.*, 2007; Flukes *et al.*, 2014). The structure, abundance and diversity of understorey assemblages is regulated by shading (Foster, 1982; Reed & Foster, 1984; Kennelly, 1987; Arkema *et al.*, 2009) 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 & 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 & Corner, 1963; Norton *et al.*, 1977), and suffer mortality at higher irradiances (see Jones & 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 (Leichter & Witman, 1997; Knights *et al.*, 2012) and increased sedimentation has been shown to have a negative impact on the recruitment and survival of sessile invertebrates (Irving & Connell, 2002; Airoldi, 2003). 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 & 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 (Dayton, 1973; Blanchette, 1996). *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 & Foster, 1984). Indeed, within Californian *M. pyrifera* systems the abundance of understorey algae beneath the canopy may be light-limited (Rosenthal *et* *al.*, 1974; Foster, 1982), so that removal of the canopy can lead to increases in both abundance and richness of understorey assemblages (Kimura & Foster, 1984; Reed & Foster, 1984). In Chile, however, similar canopy removal experiments deliver a comparatively muted ecological response (Santelices & Ojeda, 1984).

Unlike in *M. pyrifera* dominated systems, sessile invertebrates are conspicuously absent from the understorey assemblages in temperate Australia (Fowler-Walker & 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 & 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 & 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 does not 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 & 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 & Johnson, 2003). *U. pinnatifida* has also been shown to host a less diverse and structurally distinct epibiotic assemblage when compared with native algae (Raffo *et al.*, 2009; Arnold *et al.*, 2016). Thus invasion of native reef assemblages by non-native species may result in impoverished kelp associated assemblages and overall lower local biodiversity (Casas *et al.*, 2004; Arnold *et al.*, 2016). 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; Firth *et al.*, 2016). Such structures differ from natural reefs in a number of ways (Moschella *et al.*, 2005), including their composition, complexity and orientation, and have been shown to support distinct assemblages from those found on natural substrates (Glasby, 1999; Bulleri *et al.*, 2005). Recently there has been a focus on elevating the ecological value of such structures, including the 'gardening' of habitat-forming species (Perkol-Finkel *et al.*, 2012; Firth *et al.*, 2014). Habitat-forming species growing on artificial substrates, however, support different associated assemblages compared to those growing on natural substrate (People, 2006; Marzinelli *et al.*, 2009). 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 role 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.

1.6. *Ecological goods and services provided by kelp forests*

Aside from altering the physical environment and forming considerable three-dimensional habitat for a vast array of marine life, healthy kelp forests also provide a range of ecological goods and services throughout their geographic range. Kelp forests represent some of the most productive habitats on Earth (Mann, 1973; Reed *et al*., 2008) and are a major source of primary production in temperate and sub-polar coastal environments (Steneck *et al*., 2002). While a proportion of kelp material is consumed *in situ* by grazers, the majority of kelp production enters the food chain as detritus or dissolved organic matter (Krumhansl & Scheibling, 2012). Fresh growth of kelp material occurs at the meristematic tissue, generally located at the blade-stipe junction. As such kelp plants act as “conveyor belts” of biomass production (Smale *et al*., 2013) with new material being passed distally with continued growth. The distal tips of the blade are gradually eroded to form fragments ranging in size from small particles to large sections of blade. During periods of increased water movement, such as those experienced during storm events, entire kelp plants can be detached from the substrate following dislodgement of the holdfast or breakage of the stipe. This kelp detritus is either retrained within the forest or exported to adjacent systems. Rates of export exhibit significant spatiotemporal variability as they are governed a complex suite of interacting factors (i.e. water flow, seabed topography, substratum type, and the size, weight and buoyancy, and species of kelp from which it is derived; Smale *et al*., 2013). Thus, kelps underpin a continuous export of material to adjacent systems.

There is increasing evidence that marine vegetated systems support significant rates of organic carbon burial (Duarte *et al*., 2005). However, kelp forests (and other macroalgae dominated habitats) have generally been discounted in the discussion regarding marine carbon sinks (Krause-Jensen & Duarte, 2016) as they typically grow on rocky substrate where burial of organic material is unlikely. Recently however, pathways for the export and sequestration of kelp derived carbon in coastal and deep-sea sediments have been identified (Krause-Jensen & Duarte, 2016). Initial estimates of annual kelp derived carbon sequestration are greater than those previously suggested for angiosperm based coastal habitats (e.g. seagrass beds and mangroves) and suggest that these habitats are of global significance (Krause-Jensen & Duarte, 2016).

Kelp forests alter water motion and can provide a buffer against storms through wave damping and attenuation, and by reducing the velocity of breaking waves (Lovas & Torum, 2001). In this way, kelp forests impede the movement of sand and pebbles to adjacent beaches and reduce coastal erosion (Lovas & Torum, 2001). The effectiveness of kelps as a biogenic coastal defence will be dependant on the morphology of the dominant kelp species involved, as well as on the spatial extent, density, and composition of the kelp forest itself (Gaylord *et al*., 2007), as well as any associated understorey assemblages (Eckman *et al*., 1989).

The secondary production characteristic of kelp forests has been exploited for human consumption for centuries and continues to this day. Kelp forests serve as nursery grounds for a number of commercially important species of fish including Atlantic Cod (*Gadus morhua*), pollack (*Pollachius pollachius*) and conger eels (*Conger conger*). The American lobster (*Homarus americanus*) has been shown to be affiliated with kelp forests and will preferentially aggregate under *Laminaria* canopies (Bologna & Steneck, 1993). A similar relationship exists in the northeast Atlantic between kelp forests and the European lobster (*Homarus gammarus*), a fishery worth around £30 million per year to fisheries in the UK alone (Smale *et al*., 2013).

Kelp plants also hold significant economic value in and of themselves, and are harvested as a source of alginate, a gel-forming polysaccharide used in numerous industries (e.g. textiles, food, and pharmaceuticals; Billot *et al*., 2003), as well as food for human consumption (Mabeau & Fleurence, 1993; Kolb *et al*., 2004). As the demand for ‘clean’ alternatives to more traditional fossil feuls increases, kelp have been highlighted as a potential source of biofuels (Adams *et al*., 2011a; Adams *et al*., 2011b; Jung *et al*., 2013). Kelps can grow extremely quickly (up to 50 cm per day), are rich in polysaccharides and do no compete with land-based crops for space, fertilizers or water (Smale *et al*., 2013). There is therefore increasing interest in the largescale harvesting and culturing of kelps globally. Estimates of the carbon footprint of the production of fuel from macroalgae however, indicate that production of biofuels from other sources (e.g. corn, wheat, sugar cane) is more efficient (Fry *et al*., 2012). Large scale harvest of kelps for biofuels in the future will likely have significant ecological impacts on coastal ecosystems (see section 1.7), but the long-term impacts of such harvesting will likely be dependent on the species involved. In southern California *Macrocystis pyrifera* populations have been harvested extensively for algin since the 1920s, with minimal impact on kelp survivorship (Graham *et al*., 2007).

Coastal biodiversity is of significant socioeconomic value globally. In the UK for example, leisure and recreation industries directly reliant on marine coastal biodiversity contribute >£11 billion to the economy each year (Beaumont *et al*., 2008). Diverse kelp dominated habitats also offer a range of diverse recreational activities (e.g. snorkelling, scuba diving, kayaking, wildlife watching, and angling) which contribute significantly to local economies and have other non-monetary benefits for human health and wellbeing (Beaumont *et al*., 2008).

1.7. *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 (Steneck *et al.*, 2002; Smale *et al.*, 2013; Steneck & Johnson, 2013; Brodie *et al.*, 2014). 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 & Vance, 2015), extreme wave action can cause damage to kelps and associated fauna, leading to high rates of mortality and widespread loss of habitat (Krumhansl & Scheibling, 2011b; Filbee-Dexter & Scheibling, 2012). 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. Thomsen *et al.*, 2004; Reed *et al.*, 2011). 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 (Santelices & Ojeda, 1984; Hawkins & Harkin, 1985; Connell, 2003b; Clark *et al.*, 2004; Flukes *et al.*, 2014). Furthermore, increased storminess and physical disturbance may interact with other environmental change factors, such as climate-driven range shifts of species (Smale & 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 & Mann, 1976b; Hagan, 1983; Steneck *et al.*, 2002; Johnson *et al.*, 2011; Filbee-Dexter & Scheibling, 2014; Ling *et al.*, 2015). 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 & Schiel, 1982) can all influence sea urchin abundances, but predators are the single most important regulator of sea urchin populations (Estes & Duggins, 1995; Sala *et al.*, 1998; Steneck, 1998; Johnson *et al.*, 2011; Ling *et al.*, 2015). Where key sea urchin predators (e.g. lobster; Breen & Mann, 1976a; and cod; Tegner & Dayton, 2000; Ling *et al.*, 2009) 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. Christie *et al.*, 1998; Anderson *et al.*, 2006), 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 & 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 (Wernberg *et al.*, 2010; Merzouk & Johnson, 2011; Harley *et al.*, 2012). Both increased frequency and severity of extreme warming events (Dayton & Tegner, 1984; Smale & Wernberg, 2013) and longer-term gradual warming (Wernberg *et al.*, 2011c) 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 & 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 & 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 & Schaffelke, 1996), and affect depth distributions (Schaffelke *et al.*, 1996). The virulence of many marine microbes is temperature-regulated (Harvell *et al.*, 2002; Eggert *et al.*, 2010). 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 and the climate driven range expansion of the barren forming long-spined sea urchin, *Centrostephanus rodgersii*, (Johnson *et al.*, 2005; 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 & 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 & 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).

1.8. *Rationale and Aims of Thesis*

The overarching aim of this research is to assess the impact of climate change on the habitat provision by kelps in the wider context of biodiversity in kelp beds of the northeast Atlantic, especially the UK. I also look to make inferences on the effect of changes to habitat provision by key kelp species on wider biodiversity patterns. I then attempt to link these changes to trophic interactions involved in ecosystem functioning. A primary focus of this work is the impacts of climate driven shifts in kelp forest composition, especially the consequences of subtle changes in the abundances of different kelp species and loss of key canopy forming species. The rational and aims of each chapter are outlined below.

It is widely accepted that kelps harbour significant biodiversity. However, our current understanding of the spatiotemporal variability in kelp-associated assemblages, and the key environmental factors which drive variability patterns remain limited. The work in *Chapter 2* aims to benchmark the diversity, abundance, biomass and structure of assemblages found in association with the holdfasts of *Laminaria hyperborea* across its entire latitudinal range in the UK. Spatial variability in the structure of these assemblages are also examined. Finally this chapter explicitly links the observed variability in assemblage structure with key environmental drivers. Thus this chapter furthers our knowledge of the biodiversity associated with kelp forests in the UK, a subject which has been critically understudied.

Climate change is driving a global redistribution of species, potentially with significant effects on local community structure. In *Chapter 3* I examine the impacts of observed climate-driven shifts in the relative abundance of two apparently similar habitat-forming kelps, the warm water *Laminaria ochroleuca* and the cool water *Laminaria hyperborea*. First temporal trends in the relative abundance of these kelp species at key monitoring sites are examined. Secondly, biodiversity patterns associated with each kelp species where they are both found in Plymouth Sound are quantified at high taxonomic resolution. These kelp communities are proposed, more generally, as useful model systems to examine how thermally driven shifts in habitat-forming species may influence the structure of associated assemblages and local biodiversity patterns.

Chapter 4 builds on the previous by examining the wider impacts of the relative shift in abundance of these subtly different habitat-forming kelps. Specifically I examine the consequences of such a shift of foundation species on the important habitat cascade associated with *Laminaria hyperborea* (i.e. kelp – epiphytic algae – mobile invertebrates). This chapter aims to test whether the strength of the facilitative interaction between kelp and stipe associated algae is greater for *L. hyperborea* than *Laminaria ochroleuca*, across a range of environmental conditions. I also investigate whether the decreased secondary habitat associated with *L. ochroleuca* leads to depauperate assemblages. Finally this chapter provides insight into whether changes in the structure or abundance of mobile invertebrates may have impacts on higher trophic levels, in this case predatory fish.

While the previous chapters are concerned with the subtle shift in relative species composition of kelp forests, in *Chapter 5* I examine the impacts a climate driven reduction in density or the total loss of a key canopy forming kelp species may have on the composition of kelp canopies in the southwest UK. By utilising experimentally manipulated clearance plots on the intertidal rocky shore, this chapter aims to test whether the reduction or loss of *Laminaria digitata* canopy leads to overall changes in canopy composition. I also examine the impacts of canopy loss on the understorey algal assemblage, and ask whether the responses of canopy and understorey algae will differ according to wave exposure.

Finally, in *Chapter 6* the main findings are summarised and synthesised. The ecological consequences of changes in major ecosystem engineering kelp species for biodiversity and ecosystem functioning are discussed. Conservation and management implications are also explored. Knowledge gaps are highlighted and suggestions are made for further research.

Chapter 2. Spatial variability in the diversity and structure of faunal assemblages associated with kelp holdfasts (*Laminaria hyperborea*) in the northeast Atlantic

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2.1. *Abstract*

Kelp species are ecologically-important habitat-formers in coastal marine ecosystems, where they alter environmental conditions and promote local biodiversity by providing complex biogenic habitat for an array of associated organisms. While it is widely accepted that kelps harbour significant biodiversity, our current understanding of spatiotemporal variability in kelp-associated assemblages and the key environmental drivers of variability patterns remains limited. Here we examined the influence of ocean temperature and wave exposure on the structure of faunal assemblages associated with the holdfasts of *Laminaria hyperborea,* the dominant habitat-forming kelp in the northeast Atlantic. We sampled holdfasts from 12 kelp-dominated open-coast sites nested within four regions across the UK, spanning ~9° in latitude and ~2.7° C in mean sea surface temperature. Overall, holdfast assemblages were highly diverse, with 261 taxa representing 11 phyla recorded across the study. We examined patterns of spatial variability for sessile and mobile taxa separately, and documented high variability between regions, between sites within regions, and between replicate holdfasts for both assemblage types. Mobile assemblage structure was more strongly linked to temperature variability than sessile assemblage structure, which was principally structured by site-level variability in factors such as wave exposure. Patterns in the structure of both biogenic habitat and associated assemblages did not vary predictably along a latitudinal gradient in temperature, indicating that other processes acting across multiple spatial and temporal scales are important drivers of assemblage structure. Overall, kelp holdfasts in the UK supported high levels of diversity, that were similar to other kelp-dominated systems globally and comparable to those recorded for other vegetated marine habitats (i.e. seagrass beds), which are perhaps more widely recognised for their high biodiversity value.

2.2. *Introduction*

In the marine environment, the distribution of species and the structure of communities are regulated by a range of biotic and abiotic factors that operate over multiple spatial and temporal scales (Osman, 1977; Watanabe, 1984; Harrold & Reed, 1985; Richmond & Seed, 1991; Christie *et al.*, 2003; Bulleri & Chapman, 2010). Understanding the relative influence of key processes in structuring populations and communities is a central goal of ecology, and is of elevated importance given that abiotic and biotic factors are being altered by human activities (Steneck *et al.*, 2002; Parmesan & Yole, 2003; Smale *et al.*, 2013; Steneck & Johnson, 2013; Brodie *et al.*, 2014; Scheffers *et al.*, 2016). By examining patterns of variability in ecological structure over multiple spatial and temporal scales, insights can be gained into the relative importance of processes that vary across similar scales. For example, repeated regional-scale observations conducted across latitudinal gradients in ocean temperature can elucidate the influence of temperature on the ecophysiological performance of populations and species (Wernberg *et al.*, 2010; Moy & Christie, 2012), the biogeographical distributions of species (Mieszkowska *et al.*, 2006; Hawkins *et al.*, 2009; Sunday *et al.*, 2012) and, in turn, the structure of communities (Wernberg *et al.*, 2011a; Moy & Christie, 2012; Tuya *et al.*, 2012; Smale & Moore, 2017). Similarly, examining biodiversity patterns across smaller spatial scales that encapsulate natural gradients in other factors (e.g. wave exposure, grazing pressure, turbidity) can provide insights into their relative importance in structuring communities (Ballantine, 1961; Brattström, 1968; Moore, 1973b; Loya, 1976; Pedersen *et al.*, 2012; Norderhaug *et al.*, 2014; Ling *et al.*, 2015). Establishing baselines of biodiversity patterns at multiple scales within key ecosystems is vital, given the rate at which species' distributions and abundances are changing in the current period of anthropogenic environmental change (Burrows *et al.*, 2011; Wernberg *et al.*, 2013).

Foundation species exert strong influence over other organisms by altering environmental conditions and, in many cases, creating or modifying habitat for other species (Jones *et al.*, 1994; Jurgens & Gaylord, 2017). Kelps, large brown seaweeds of the order Laminariales, are the dominant foundation species along temperate and subpolar rocky coastlines in both hemispheres (Steneck *et al.*, 2002). Kelps are amongst the fastest growing autotrophs on Earth (Mann, 1972; Jupp & Drew, 1974; Reed *et al.*, 2008) and, as such, represent a major source of primary production and an important food source in coastal environments (Krumhansl & Scheibling, 2012). Kelps also promote secondary productivity through the provision of three-dimensional habitat structure, which supports a myriad of associated organisms including species of commercial and ecological importance (Bologna & Steneck, 1993; Steneck *et al.*, 2002; Smale *et al.*, 2013). They support increased levels of biodiversity by offering greater habitat space, heterogeneity and complexity, as well as through direct and indirect (via epibionts) provision of food (Teagle *et al.*, 2017). A recent review of the role of kelps as biogenic habitat formers found that individual plants often support highly abundant invertebrate assemblages, often numbering in the high tens of thousands per kelp plant (see Teagle *et al.*, 2017 and references therein). As habitat formers, mature kelp thalli provide three distinct micro-habitats; the blade (lamina), the stipe, and the holdfast, all of which differ considerably in form and structure, and consequently support assemblages of differing composition, diversity and abundance (Teagle *et al.*, 2017). Of these micro-habitats, the holdfast generally supports the most diverse and temporally persistent assemblage, and has received greatest attention in the literature (see Teagle *et al.*, 2017 and references therein).

The interstitial space between the underlying hard substratum and the haptera (the root-like structures which form the holdfast) of kelp holdfasts represents favourable habitat for colonising fauna, primarily because (i) the surface area and volume of habitat available for colonisation is increased; (ii) the structure offers protection from adverse environmental conditions and predators, and (iii) food availability is enhanced through accumulation of organic matter (Moore, 1972b, 1978; Cancino & Santelices, 1980; Ojeda & Santelices, 1984). In general, the living space within kelp holdfasts offers a range of niches that may differ from adjacent habitats. Assemblages associated with kelp holdfasts are often diverse and abundant, with up to 90 macrofaunal species (Jones, 1972; Moore, 1972a; Christie *et al.*, 2003) and 10,000 individuals inhabiting a single holdfast (Christie *et al.*, 2003; Schaal *et al.*, 2012). Variability in the structure of holdfast-associated assemblages is driven by a range of biotic and abiotic factors, including the size and complexity of the holdfast itself (Smith *et al.*, 1996; Christie *et al.*, 2003; Christie *et al.*, 2009; Tuya *et al.*, 2011), hydrodynamic forces (Fincham, 1974; Fenwick, 1976), sedimentation rates and sediment content (Smith, 1996b; Schaal *et al.*, 2012), food and larval supply (Moore, 1973b; Marzinelli, 2012), pollution (Jones, 1973; Smith & Simpson, 1992, 1998), turbidity (Moore, 1973b; Sheppard *et al.*, 1980) and depth (Smith, 1996b; Coleman *et al.*, 2007). In addition, kelps are cool-water species and the structure of kelp populations is known to vary along large-scale gradients in ocean temperature (Wernberg *et al.*, 2010; Smale *et al.*, 2016). Marginal equatorward populations, in particular, are stressed by increases in temperature (Voerman *et al.*, 2013; Wernberg *et al.*, 2016) and, as such, observed and predicted ocean warming trends will likely impact upon kelp populations and affect their functioning as habitat-forming foundation species. It seems likely, therefore, that ocean climate will be a key driver of holdfast assemblage structure, because (i) biogenic habitat structure is likely to vary with temperature as kelp populations respond to climatic conditions, (ii) the biogeographic distributions of marine species are strongly constrained by temperature (Sunday *et al.*, 2012) and (iii) the structure of populations of kelp-associated fauna (i.e. abundances) is likely to vary with ocean climate (Foster *et al.*, 2014). However, as very few studies have examined variability in holdfast assemblages across spatial scales large enough to encompass natural temperature gradients, the influence of ocean climate on biodiversity patterns remains unclear.

In the northeast Atlantic, wave-exposed subtidal rocky reefs are generally dominated by the kelp *Laminaria hyperborea* (Gunnerus) Foslie 1884; a large, stipitate kelp which attaches to rocky substratum by a well formed, typically 'laminarian' holdfast (Teagle *et al.*, 2017), from the extreme low intertidal to depths of up to 40 m in clear oceanic waters (Tittley *et al.*, 1985). *L. hyperborea* is a boreal species, distributed from northern Portugal to its poleward range edge in northern Norway, Iceland and the Russian Murmansk coast. *L. hyperborea* is the foremost canopy former on shallow, wave exposed rocky reefs throughout this region (Bekkby *et al.*, 2009; Yesson *et al.*, 2015), and represents an important habitat for coastal biodiversity and other ecosystem services (Smale *et al.*, 2013). In the UK, recent work has shown that *L. hyperborea* is spatially extensive, forms dense canopies and offers a high quantity and quality of biogenic habitat (Smale & Moore, 2017; Fig 2.1). In general, however, kelp ecosystems in the UK have been relatively understudied since the pioneering work of the 1960s and 70s (e.g. Kain, 1963; Moore, 1972a; Jupp & Drew, 1974), particularly when compared to the volume of work conducted in other research-intensive nations (e.g. Australia and the USA; Smale *et al.*, 2013). Perhaps surprisingly, fundamental information on biodiversity patterns associated with *L. hyperborea*, and the potential multi-scale drivers of variability in holdfast assemblage structure, are still lacking.

Here, we examined the structure of holdfast assemblages at 12 sites within 4 regions of the UK to better understand spatial variability in kelp-associated biodiversity. The specific aims of the study were to (1) benchmark the diversity, abundance, biomass, and structure of holdfast assemblages across the latitudinal distribution of *L. hyperborea* in the UK; (2) examine multiscale spatial variability patterns in holdfast assemblage structure; and (3) explicitly link variability in ecological pattern with potential environmental drivers. Recent work on the kelp canopies themselves has documented high between-site variability in population and habitat structure, as well as regional differences between northerly and southerly locations in the UK (Smale *et al.*, 2016; Smale & Moore, 2017). Given that holdfast assemblages are likely to be strongly influenced by the population structure of host kelp species (Smith *et al.*, 1996; Anderson *et al.*, 2005; Teagle *et al.*, 2017), we predicted that they would also exhibit high levels of small-scale variability (i.e. between

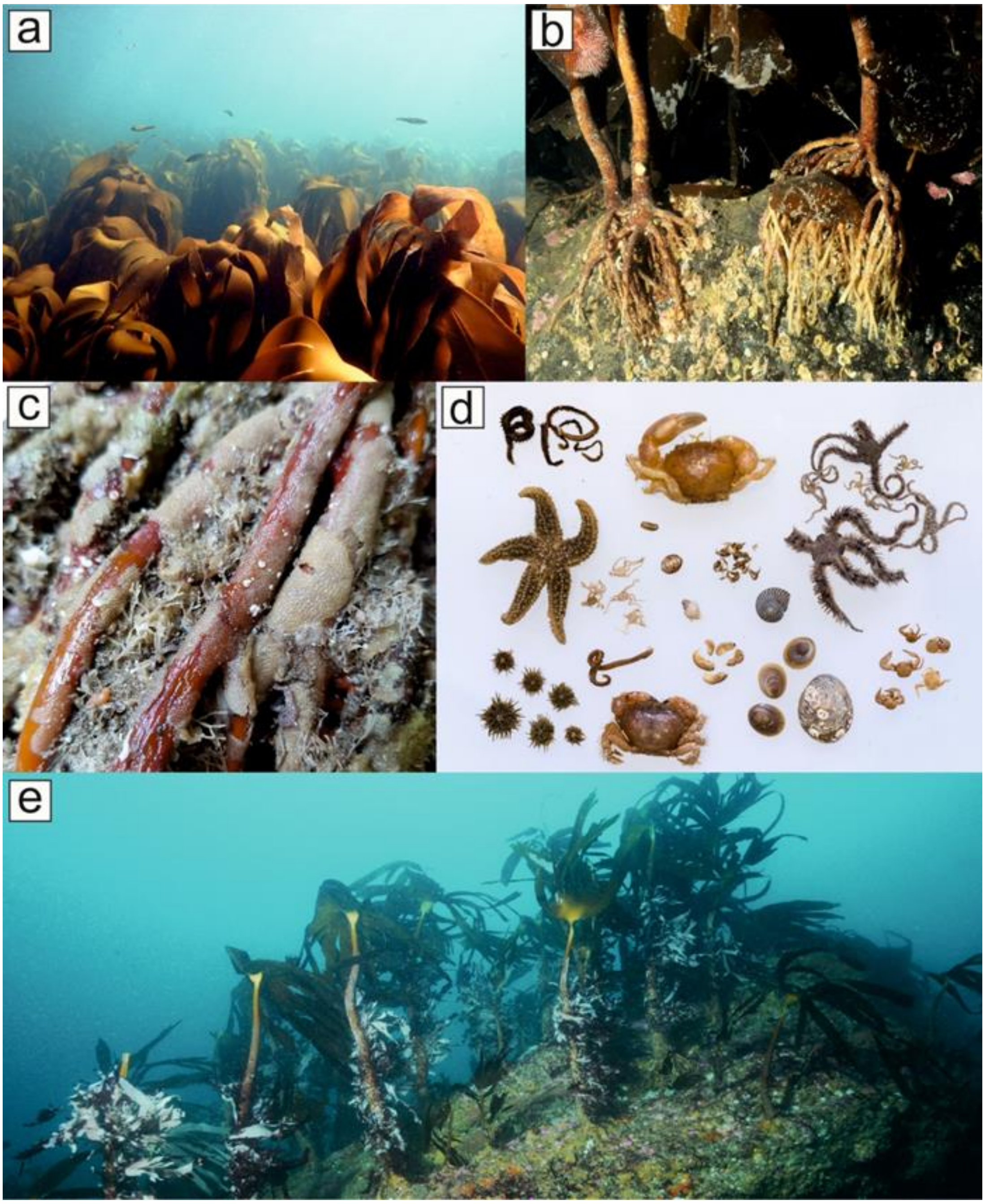

Fig 2.1 (a) *Laminaria hyperborea* is a dominant kelp species in the northeast Atlantic, where it forms dense, extensive macroalgal canopies. (b) It forms a large, complex holdfast structure, which anchors the plant to rocky substrata and provides biogenic habitat for associated organisms. (c) Holdfasts sampled were typically encrusted by a high coverage of sessile invertebrates. (d) The interstitial space between the reef surface and the holdfast was utilised by a high diversity of mobile invertebrates. (e) Dense stands of *L. hyperborea* may serve as ecologically-significant repositories of biodiversity.

plants and sites), as well as some structuring across larger spatial scales (i.e. between regions).

2.3. *Methods*

i. Study area

Laminaria hyperborea holdfasts were sampled by scuba divers from 12 sites nested within four regions in the UK (Fig 2.2); north Scotland (region 'A'), west Scotland (B), southwest Wales (C) and southwest England (D). All sites were located on the exposed west coast of the UK, where kelp forest habitat is abundant, and span 9° of latitude (~50° to ~59° N), and encompass a temperature gradient of ~2.7°C (Table 2.1). All study sites within these regions were 'open coast', moderately to fully exposed to wave action and were characterised by extensive subtidal rocky reef at depths of 0 to >5 m (below chart datum). All sites were also deemed to be representative of the wider region, in terms of coastal geomorphology, and were not strongly influenced by local anthropogenic activities.

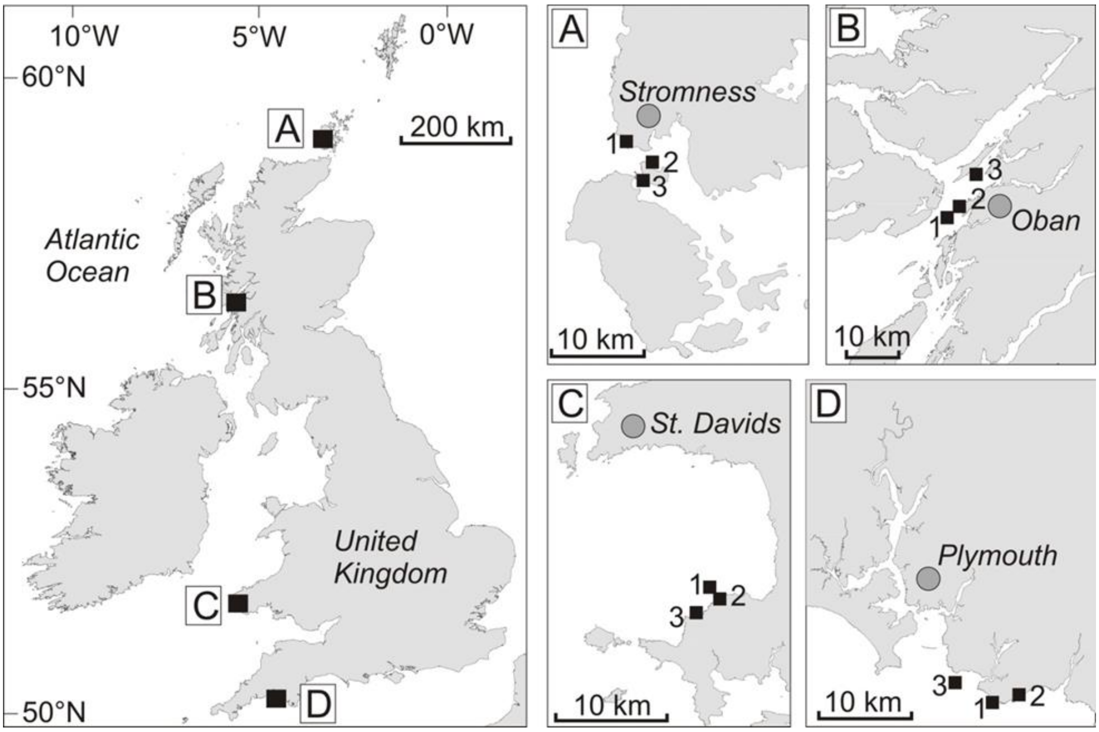

Fig 2.2 Map indicating the locations of the four study regions in the UK, northeast Atlantic: (A) northern Scotland, (B) western Scotland, (C) southwest Wales and (D) southwest England. Smaller panels show the positions of the 3 study sites within each region.

Table 21. Predictor variables recorded at 12 study sites within 4 distinct regions in the UK. ‘Mean SST’ is the annual mean temperature calculated from satellite-derived sea surface temperature (SST) data (2005-2014). ‘Log wave fetch’ is a broad-scale metric of wave exposure, derived by summing fetch values calculated for 32 angular sectors surrounding each site (see Burrows, 2012). ‘Log chl *a* mean’ is the average annual concentration of chlorophyll *a* (log10 mg m^{-3} from MODIS Aqua satellite data, 2002-2012). ‘Peak summer max (mean) temp’ is the maximum (average) daily temperature recorded between 26 July and 18 August 2014, when all sensor array deployments overlapped. ‘Summer daylight’ is the average daytime (08:00-20:00) light intensity during a 14 d deployment of light loggers. ‘Tidal water motion’ is a proxy for water movement driven by tidal flow, derived from the range in water motion values recorded during a 24 h period, averaged over the 45 d accelerometer deployment. ‘Wave water motion’ is a proxy for water movement driven by waves, derived from averaging the 3 highest-magnitude water motion values observed during the 45 d accelerometer deployment (following correction for tidal-movement). ‘PO_4^{3-}’ and ‘NO_3^- +NO_2^-’ indicate averaged spring and summer concentrations of phosphate and nitrite + nitrate respectively (n = 4 water samples taken from ~1 m above the kelp canopy).

Region	**Site**	**Locality**	**Mean SST (°C)**	**Log wave fetch (km)**	**Log chl *a* mean (mg m^{-3})**	**Peak summer temp (°C)**		**Summer daylight (lumens m^{-2})**	**Tidal water motion (m s^{-1})**	**Wave water motion (m s^{-1})**	**NO_3^- +NO_2^- (µM)**	**PO_4^{3-} (µM)**
						Max	Mean					
N Scot (A)	A1	Warbeth	9.7	3.8	0.21	13.99	13.69	7124	0.18	1.02	1.66	0.17
	A2	N Graemsay	9.8	3.5	0.26	13.68	13.49	4835	0.20	0.30	1.92	0.23
	A3	S Graemsay	9.7	3.4	0.26	13.87	13.65	5144	0.26	0.16	2.58	0.19
W Scot (B)	B1	Dubh Sgeir	10.8	3.3	0.59	13.96	13.69	4794	0.15	0.22	2.93	0.30
	B2	W Kerrera	10.7	3.1	0.65	13.93	13.68	3094	0.05	0.08	2.52	0.26
	B3	Pladda Is.	10.8	2.8	0.73	14.52	14.06	4874	0.19	0.11	1.96	0.27
Wales (C)	C1	Stack Rock	11.7	3.7	0.43	17.06	16.54	1861	0.13	0.73	3.17	0.16
	C2	Mill Haven	11.8	3.5	0.43	17.15	16.62	3657	0.08	0.34	2.68	0.22
	C3	St. Brides	11.8	3.4	0.43	17.13	16.63	2960	0.08	0.23	3.09	0.14
SW Eng (D)	D1	Hillsea Pt.	12.4	4.1	0.28	17.62	16.80	2746	0.15	0.42	3.41	0.17
	D2	E Stoke Pt.	12.4	3.9	0.28	18.31	17.09	2840	0.11	0.22	2.41	0.11
	D3	N Mewstone	12.5	3.5	0.38	17.71	17.06	4432	0.06	0.20	3.05	0.35

ii. Environmental variables

Environmental sensors were deployed on a small sub-surface buoy, suspended in the water column immediately above the reef surface by a 0.65 m rope, which was attached to a clump weight and allowed free movement of the sensor in response to water motion (Appendix 1). Sensors were deployed within a 4-week period in July and August 2014 and retrieved ~6 weeks later. Each sensor array was deployed for >45 days at each site, and any surrounding kelp plants (~2 m radius) were removed to negate any shading and/or impediment of water movement around the buoy. These arrays recorded temperature, light levels, and relative water motion at fine temporal resolutions. In order to quantify water motion driven by wave exposure and/or tidal regimes, an accelerometer (HOBO Pendant G Logger, Onset, attached to the buoy) recorded its position in three axes every 5 minutes (see Figurski *et al.*, 2011). A temperature and light level sensor was also attached to the buoy and captured data every 15 minutes (see Smale *et al.*, 2016 for further details). Relative water motion was calculated from the accelerometer data by extracting movement data in the planes of the x- and y-axes, after first subtracting the modal average of the entire dataset from each value to account for any latent static 'acceleration' resulting from the accelerometer not sitting exactly perpendicular to the seabed (caused by imprecise attachment of the logger to the buoy or the buoy to the tether).

Accelerometer data were converted to water motion following Evans and Abdo (2010), and then used to generate two separate metrics, one for water movement induced by tidal flow, and one by wave action. For tidal flow, all values above the 90th percentile (i.e. those most likely related to turbulent, wave driven water movement) were removed. The range of water motion values recorded within each 12 h period (representing ~1 complete tidal cycle) was then calculated and averaged over the 45 d deployment. Following subtraction of average water motion induced by tidal flow, wave-induced water movement was calculated by taking an average of the 3 highest magnitude values recorded for each site. Recorded temperature data was converted to daily mean temperatures; a 24 h period during peak summer temperatures, where all sensor array deployments overlapped was then used to generate maximum daily means and average daily temperature for each study site. To establish average summer daytime (08:00 - 20:00 h) light levels for each site, data for the first 14 d of deployment were used, in order to limit the potential of fouling by biofilms and epiphytes to affect light measurements.

In addition, nutrient levels at each site were assessed by collecting 2 independent seawater samples from immediately above the kelp canopy with duplicate 50 ml syringes. Samples were passed through a 0.2 µm syringe filter and kept on ice without light, before being frozen and analysed (within 2 months) for nutrients (nitrate+nitrite; NO_3^-+NO_2^-, and phosphate; PO_4^{3-}) using standard analytical techniques (see Smyth *et al.*, 2010 and references therein). Nutrient concentrations were quantified twice at each site (in summer 2014 and spring 2015) and mean values are presented here. In addition to these fine-scale variables, average sea temperatures (2005-2014) were calculated from satellite-derived SSTs (9 km resolution AVHRR data), wave fetch was calculated for each site following Burrows *et al.* (2008) and Burrows (2012), and estimates of chlorophyll *a* (chl *a*) concentrations were generated from optical properties of seawater derived from satellite images (collected by the MODIS Aqua satellite at 9 km resolution, averaged for the period 2002 to 2012).

iii. Sample collection and processing

Six holdfast samples were collected in late summer (i.e. August/September 2014) from each site (72 samples in total). Mature, canopy forming *L. hyperborea* plants (see Fig 2.1) were haphazardly selected from within dense kelp stands at depths of 2-4 m (below chart datum). Divers cut the stipe of each plant just above the holdfast, which was immediately covered with a fine-mesh cotton bag to prevent the loss of mobile fauna, and then gently prised the holdfast from the reef before sealing the bag with a cable tie. Kelp plants were situated >2 m apart and samples were all individual, rather than fused, holdfasts. Samples were immediately treated with a 1% propylene phenoxytol solution for ~30 minutes, in order to relax soft invertebrate specimens to aid in later identification, and stored in 70% industrial methylated spirit (IMS) solution until processing. To process, holdfasts were rinsed with freshwater, and any mobile fauna was collected in a 1 mm sieve and returned to 70% IMS solution for subsequent identification. The total holdfast volume was then quantified by displacement; the entire holdfast structure was wrapped in plastic kitchen wrap and submerged in freshwater. Haptera (the root-like structures which make up the holdfast) were then removed to reveal the internal holdfast structure and any sessile fauna within, which were identified immediately. The volume of the cleaned haptera were then measured (using displacement), subsequently being subtracted from total holdfast volume to give the volume of the potential habitable space within the holdfast, and wet weight was recorded. All fauna was identified to the lowest taxonomic level possible, in most cases species (~67% of taxa). Sessile fauna was weighed (tissue-dried fresh weight) to establish biomass, whereas mobile fauna were enumerated for abundance. Finally, each kelp sampled was aged by sectioning the stipe immediately above the holdfast and counting seasonal growth rings, as described by Kain (1963).

iv. Statistical analysis

All analysis was conducted using univariate and multivariate permutational analyses using the PERMANOVA add on (Anderson *et al.*, 2008) for Primer v7 software (Clarke & Gorley, 2015). Metric multidimensional scaling (mMDS) ordinations were constructed to visualise multivariate patterns. Variability in assemblage structure was examined with multivariate PERMANOVA using a 2-factor design, with region (4 levels) as a fixed factor and site (3 levels) as a random nested factor. To examine correlations with habitat size, habitable holdfast space was included as a co-variate in all analyses. Permutations (4999 under a reduced model) were based on a Bray-Curtis similarity matrix constructed from fourth root transformed biomass data (for sessile assemblages) and fourth root transformed abundance data (for mobile assemblages). Fourth root transformation was chosen to down weight the influence of large sponges and colonial ascidians and high abundances of amphipods, respectively. Pair-wise tests between regions were conducted wherever the main effect was significant ($P < 0.05$). Differences in multivariate dispersion between assemblages were examined using the PERMDISP routine. Where significant differences in assemblage structure between regions were detected, SIMPER analysis was performed to determine which taxa contributed most to the observed dissimilarity. We also conducted a multivariate analysis based on relative abundance data, in order to remove any overriding effect of holdfast living space and to effectively standardise for habitat size. First, each taxa was converted to a proportional biomass/abundance value for each sample, and then sessile and mobile taxa were summed to yield a ‘combined assemblage’ for each holdfast. Variability patterns were then examined using the same model described above, but with untransformed data and without the co-variate. Univariate assemblage metrics (i.e. total biomass and species richness) were examined using the same model, but with permutations based on resemblance matrices generated from Euclidean distances between untransformed data. The biogenic structure of holdfasts (i.e. total volume, living space, age) was examined using the same univariate model but without the co-variate.

Relationships between environmental variables and assemblage structure were examined using the DISTLM (distance-based linear models) routine in PERMANOVA. Predictor variables included the environmental data shown in Table 2.1, as well as the habitat characteristics of holdfast age and habitable space. Prior to analysis, draftsman's plots were generated from normalised data, and Pearson's correlation coefficient was used to check for colinearity between variables. All temperature measures were highly correlated ($r > 0.9$), so only mean summer temperature was retained in the analysis. Mean nitrate+nitrite (NO_3^-+NO_2^-) and chl *a* concentration were also highly correlated with other variables and were excluded from the analysis. The DISTLM routine was then used to obtain the most parsimonious model using a stepwise selection procedure and AICc selection criterion (McArdle & Anderson, 2001; Anderson *et al.*, 2008).

To examine the biogeographic affinities of individual species comprising holdfast assemblages, all fauna identified to species level (174 species) were classified based on the southernmost limit (i.e. warm-water equatorward range edge) of their recorded distributions. Species were categorised in bins of 10° latitude (which ranged from the 'warmest' bin of 20°-30°N to the 'coolest' bin of 50°-60°N) based on data from the Ocean Biogeographic Information System (OBIS), the Global Biodiversity Information Facility (GBIF), and the World Register of Marine Species (WoRMS). We hypothesised that our northernmost study regions would support a greater proportion of species with higher latitude equatorward range edges (i.e. Arctic or Boreal species) whereas southernmost regions would support more species with lower latitude equatorward range edges (i.e. Lusitanian species).

2.3. *Results*

i. Environmental variables

Seawater temperature differed across study regions, with a clear distinction between northern (A, B) and southern regions (C, D; Table 2.1). Mean sea temperatures in southern regions were ~2.7°C higher than in northern regions. Wave fetch was generally comparable between sites and regions, although the greatest values were recorded for sites in northern Scotland and southwest England (Table 2.1). Water motion associated with tidal flow was most pronounced in northern Scotland (sites A2 and A3). Light intensity was variable, both within and among regions (Table 2.1), with maximum light intensity (site A1) ~3 times greater than minimum light intensity (site C1). Nitrate and nitrite (NO_3^-+NO_2^-) and phosphate (PO_4^{3-}) concentrations were broadly comparable across sites and regions, although nitrate and nitrite values were slightly higher in Wales and southwest England and phosphate values were higher in west Scotland (Table 2.1).

ii. Biogenic habitat structure

The average age of kelp plants varied to some degree (Fig 2.3a), with a maximum mean age of 8.83 ± 0.48 SE recorded in north Scotland (site A1) and a minimum mean age of 5 ± 0.37 SE in west Scotland (site B3). Overall, the age of individual kelp plants ranged from 4 years (sites C2, B2 and B3) to 12 years (site B2). Statistically, significant differences between sites were detected, but there was no overall effect of region (Table 2.2). Regional-scale variability was more pronounced for both total volume and habitable space (i.e. the living space contained within the holdfast), which tended to be highest in north Scotland and

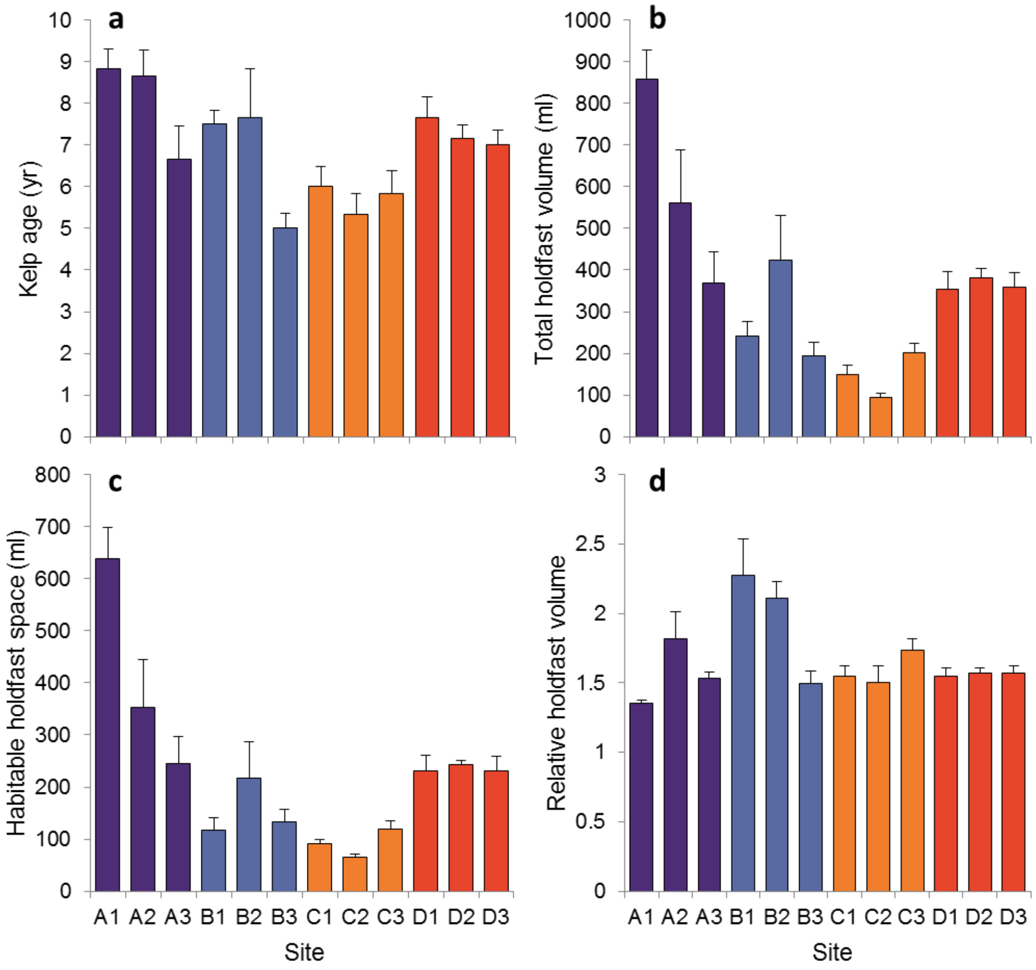

Fig 2.3 Biogenic habitat structure provided by *Laminaria hyperborea* holdfasts: (a) kelp age, (b) total holdfast volume (THV), (c) habitable holdfast space (HHS) and (d) relative holdfast space (THV/HHS). Values are means of 6 replicate holdfasts per site (± SE).

lowest in southwest Wales (Fig 2.3b,c). Significant variability was recorded both between regions and between sites (Table 2.2). Pairwise tests within the significant region factor showed that holdfast size (in terms of both total holdfast volume and habitable space) differed significantly between all regions, with the exception total holdfast volume at west Scotland and southwest England, where no difference was observed. In general, holdfasts from north Scotland (sites A1 and A2) were the largest observed, with those from southwest Wales being consistently the smallest (Fig 2.3b, c). The ratio of total volume to habitable space provided an estimate of internal complexity, with a higher ratio indicating relatively greater interstitial spacing. This metric was more consistent across regions, but did exhibit marked between-site variability in north and west Scotland (Fig 2.3d). Statistically, variability between sites was significant but no effect of region was detected (Table 2.2).

Table 2.2 Results of univariate PERMANOVA to test for differences in habitat metrics (a. kelp age, b. total holdfast volume, c. habitable holdfast space and d. relative holdfast space). Permutations were based on a Euclidean distance similarity matrix generated from untransformed data. All tests used a maximum of 4999 permutations under a reduced model; significant effects (P<0.05) are shown in bold.

Source	a. Kelp age				b. Total holdfast volume			
	df	MS	*F*	P	*df*	MS	*F*	P
Region	3	17.333	2.943	0.123	3	6.36E+05	5.404	**0.007**
Site(Region)	8	5.8889	2.928	**0.007**	8	1.18E+05	5.216	**0.001**
Residual	60	2.0111			60	22551		
Total	71				71			
	c. Habitable holdfast space				d. Relative holdfast space			
Region	3	3.48E+05	5.105	**0.002**	3	0.6768	1.901	0.212
Site(Region)	8	68098	5.864	**0.001**	8	0.3544	4.412	**0.001**
Residual	60	11612			60	0.0803		
Total	71				71			

iii. Overall biodiversity patterns

Across the study (72 holdfasts), 261 taxa representing 11 phyla were recorded, with just over 70% classed as mobile fauna (Appendix 2). In total 146 taxa were recorded from north Scotland (Region A), 134 taxa from western Scotland (B), 142 taxa from southwest Wales (C) and 136 from southwest England (D). Overall, taxa exhibited limited regional-scale specificity, with 33.7% of taxa being recorded in more than one region and >50% recorded in all four study regions. Over 8,000 individual mobile organisms were identified and counted, and the sessile fauna identified weighed ~500g.

iv. Sessile assemblages

In total, 74 taxa were recorded from the 72 holdfasts (Appendix 2). Typically, the haptera structures forming the holdfast were colonised by a high coverage of sessile organisms (Fig2.1). Taxon richness varied from nine species per holdfast (samples from sites B3 and A1) to 25 species per holdfast (samples from site D3). The sessile assemblage was dominated by bryozoans (35 taxa), with the remainder comprised of bivalve molluscs (11 taxa), hydroids (eight taxa), barnacles (six taxa) and polychaetes (three taxa). Porifera (nine groups) were identified to morphological groups, while ascidians (split into colonial and solitary) and anthozoa (anemones) were broadly grouped, due to difficulty in identifying these taxa to species level. The proportion of major taxonomic groups found in the holdfasts was more or less consistent across sites, with the exception of sites B3 and C3,

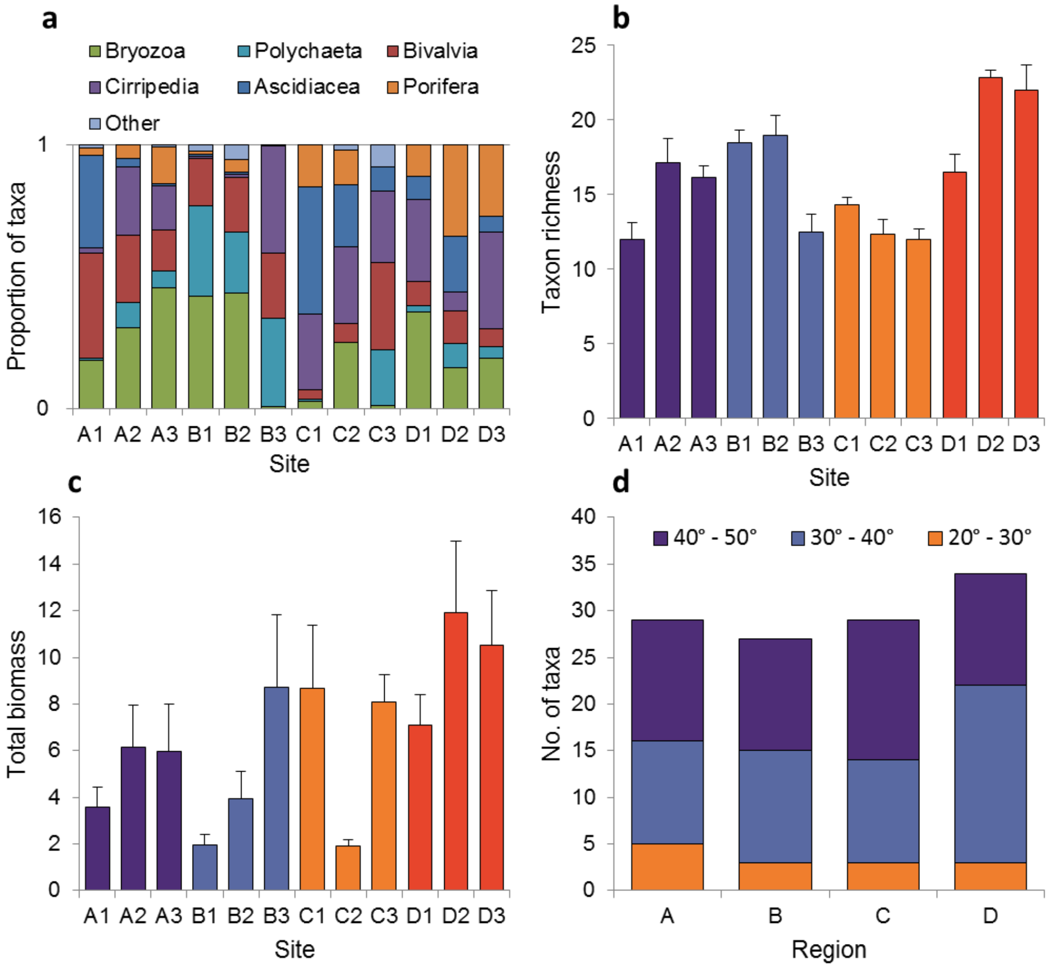

Fig 2.4 Univariate assemblage-level metrics for sessile holdfast assemblages: (a) the proportion of major taxonomic groups, (b) sessile assemblage taxon richness, (c) total biomass of sessile organisms, (d) taxa equatorward range edge. Values for (b) and (c) are means of 6 replicate holdfasts per site (±SE).

which lacked the high biomass of bryozoans characteristic of other sites, and of site C1, where holdfasts supported a high biomass of ascidians, and very low biomass of polychaetes and bryozoans (Fig 2.4a).

Metric MDS plots indicated some degree of partitioning between regions and, in some cases, between sites within regions (Fig 2.5a). Sites within regions A and D were distinctly

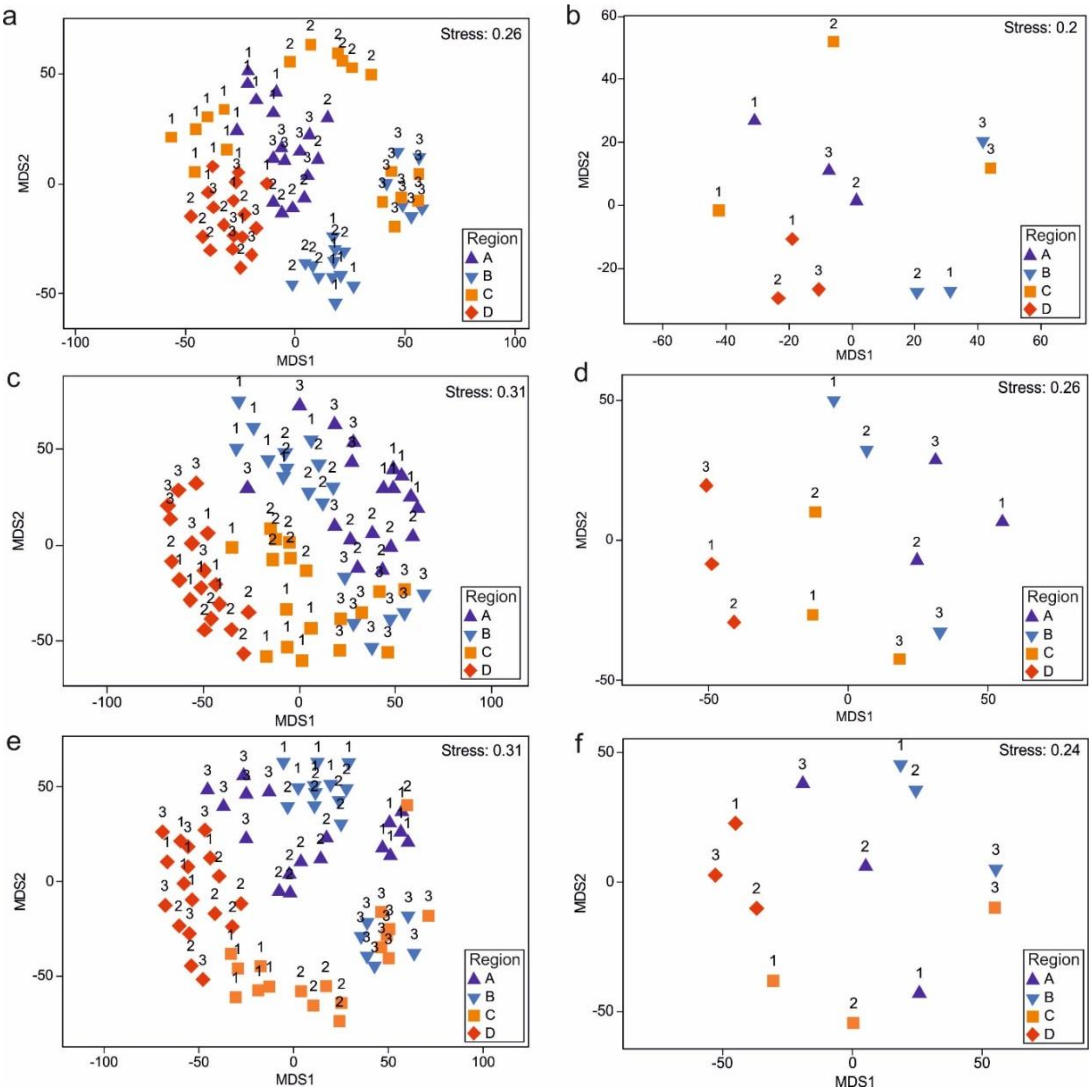

Fig 2.5 mMDS plots depicting the structure of sessile faunal assemblages, with centroids representing (a) individual holdfast samples (b) and site averages. Similarly mMDS plots depicting the structure of mobile faunal assemblages, with centroids representing (c) individual holdfasts and (d) site averages). Plots (e) and (f) indicate multivariate structure of the combined assemblage (based on proportional abundances of both sessile and mobile assemblages) at the scale of holdfast and site, respectively. Labels indicate sites and symbols indicate regions.

grouped, but regions B, and particularly C, exhibited considerable variability between sites (Fig 2.5a). There was limited evidence of partitioning in structure between the cool northern regions and the warmer southern regions, even when centroids were averaged by site (Fig 2.5b). PERMANOVA detected significant variability between regions and between sites nested within regions, as well as a significant effect of the co-variate (Table 2.3). Pairwise tests within the region factor showed that assemblages in north Scotland were

Table 2.3 Results of multivariate PERMANOVA to test for differences in holdfast sessile (a) and mobile (b) assemblage between regions (fixed) and sites (random, nested within region). Habitable holdfast space (HHS) was included as a covariable in the analysis. Permutations were based on a Bray-Curtis similarity matrix generated from fourth-root transformed biomass/abundance data. Results of univariate PERMANOVA to test for differences in assemblage-level univariate metrics (taxon richness and total biomass) in holdfast assemblages are also shown (c–f). Permutations for univariate analysis were based on a Euclidean distance similarity matrix generated from untransformed diversity data. Results of multivariate analysis on the combined assemblage (based on proportional data) are also shown (g). All tests used a maximum of 4999 permutations under a reduced model; significant effects (P<0.05) are shown in bold.

Source	**a. Sessile Assemblage**				**b. Mobile Assemblage**			
	df	MS	*F*	P	*df*	MS	*F*	P
HHS	1	9222.1	2.084	**0.027**	1	9555.6	1.822	**0.017**
Region	3	10942	1.935	**0.031**	3	14436	2.219	**0.005**
Site(Region)	8	5824.1	10.83	**0.001**	8	6682.7	5.329	**0.001**
Residual	59	537.67			59	1254.1		
Total	71				71			
	c. Sessile Taxon Richness				d. Mobile Taxon Richness			
HHS	1	24.958	0.534	0.477	1	49925	5.705	**0.032**
Region	3	176.35	2.954	0.116	3	1733.9	0.178	0.867
Site(Region)	8	61.503	10.48	**0.001**	8	9942.1	650.1	**0.001**
Residual	59	5.8712			59	15.294		
Total	71				71			
	e. Sessile Total Biomass				f. Mobile Total Abundance			
HHS	1	91.856	4.230	0.062	1	3.09E+05	10.74	**0.005**
Region	3	99.772	3.581	0.065	3	43348	1.389	0.310
Site(Region)	8	28.714	12.67	**0.001**	8	31763	4.681	**0.001**
Residual	59	2.2670			59	6785.5		
Total	71				71			
	g. Combined Assemblage							
HHS	1	11256	1.799	**0.015**				
Region	3	18036	2.298	**0.012**				
Site(Region)	8	8069.2	6.596	**0.001**				
Residual	59	1223.4						
Total	71							

distinct from those in west Scotland and southwest England, which were also dissimilar from one another. PERMDISP showed significant differences between regions in within-factor multivariate dispersion ($F_{3,86} = 29.22$, $P < 0.001$), with variability between holdfast samples from Wales (region C) considerably greater than elsewhere.

SIMPER analysis indicated that the observed differences between regions were driven primarily by a shift in the dominance of barnacle species from north to south, with samples from southwest England dominated by *Verruca stroemia*, and *Balanus crenatus* (and to a lesser extent *Balanus balanus*) becoming more common in northerly regions (Table 2.4). Further dissimilarity was caused by high biomass of sponges and colonial ascidians in southwest England and a particularly high abundance of *Mytilus* spp. (Mollusca) in north Scotland. Holdfasts from west Scotland supported a reduced biomass of common bryozoan species found abundantly in both southwest England and north Scotland (Table S2).

Taxon richness varied between sites within regions but, in general, the values tended to be highest in southwest England and lowest in Wales (Fig 2.4b). Total biomass exhibited high variability between replicate holdfasts and between sites, but no clear regional patterns (Fig 2.4c). Indeed, univariate PERMANOVA detected significant differences between sites but no effect of region for these metrics, and no significant effect of the co-variate (Table

Table 2.4 Percentage contributions of individual taxa to observed differences in sessile holdfast assemblages between regions, as determined by SIMPER analysis.

Species	Av. abund	Av. abund	Av. diss	Diss/SD	Contrib%	Cum%
	N Scot (A)	**W Scot (B)**				
Celleporina hassalii	0.79	0.06	4.33	3.38	7.15	7.15
Mytilus spp.	0.70	0.16	3.37	1.73	6.04	13.19
Verruca stroemia	0.75	0.24	3.18	1.65	4.59	17.78
Spirobranchus spp.	0.56	0.98	3.04	1.19	4.58	22.36
Escharoides coccinea	0.72	0.54	2.87	1.45	4.39	26.75
	N Scot (A)	**SW Eng (D)**				
Demosponge A	0.24	0.89	3.61	1.62	7.15	7.15
Mytilus spp.	0.70	0.09	3.05	2.10	6.04	13.19
Didemnidae spp.	0.44	0.84	2.32	1.42	4.59	17.78
Demosponge F	0.03	0.50	2.32	1.23	4.58	22.36
Verruca stroemia	0.75	1.12	2.22	1.23	4.39	26.36
	W Scot (B)	**SW Eng (D)**				
Verruca stroemia	0.24	1.12	4.35	2.21	7.22	7.22
Demosponge A	0.00	0.89	4.14	2.01	6.86	14.08
Celleporina hassallii	0.06	0.69	3.19	2.03	5.29	19.37
Didemnidae spp.	0.20	0.84	3.15	1.80	5.22	24.58
Demosponge F	0.00	0.50	2.42	1.25	4.01	28.60

2.3). The biogeographic affinities of species within the assemblages were fairly consistent across the regions, with similar proportions of 'warm' and 'cool' water species (Fig 2.4c).

The DISTLM routine was used to determine links between environmental predictor variables and variability in sessile assemblage structure. Marginal tests showed that wave fetch, wave-driven water motion and kelp holdfast age were, individually, the most important predictor variables. The stepwise selection procedure indicated that the most parsimonious model included all environmental variables, which explained 54% of the total observed variability in sessile assemblage structure (Table 2.5).

Table 2.5 DISTLM marginal test results for each environmental predictor variable selected for the most parsimonious model for sessile assemblages. The best solution based on stepwise selection and AICc criteria is shown. SS = sum of squares (trace), Prop. = proportion of variation explained.

Variable	SS	Pseudo-*F*	P	Prop.
Wave fetch	16127	10.83	0.001	0.134
Wave driven water motion	14886	9.879	0.001	0.124
Kelp age	14268	9.414	0.001	0.119
Holdfast habitable space	10606	6.765	0.001	0.088
Summer temperature	9665	6.112	0.001	0.080
Tidal driven water motion	5489	3.345	0.002	0.046
Summer light intensity	6390	3.925	0.001	0.053
Phosphate concentration	4846	2.937	0.005	0.040
Best solution: All variables (R^2: 0.54, AICc: 499.8)				

v. Mobile assemblages

Study-wide, a total of 187 mobile taxa were recorded from 72 holdfasts (Appendix 2) and, typically, holdfasts supported an array of mobile taxa (Fig 2.1). Of all the groups recorded, polychaete worms dominated by richness, making up over a third of the taxa identified (64 taxa). Crustacean groups were also numerous and diverse: gammaridean amphipods (infraorder Gammarida; 37 taxa), Decapoda (order; 13 taxa), Isopoda (order; 11 taxa), Mysida (order; three taxa), Leptostraca (order; one taxon) and Tanaidecea (order; one taxon). Mollusca were also well represented: Gastropoda (class; 34 taxa) and Polyplacophora (class; four taxa). The remainder of the assemblage comprised echinoderms (class Ophiuroidea, class Asteroidea, class Echinoidea, and class Holothuroidea; eight taxa), Pycnogonida (class; four taxa), and three other groups (class Turbellaria, phylum Nemertea, and phylum Sipuncula; four taxa). A sample from southwest

England (D1) included a fish (family Gobiesocidae). Mobile fauna were most abundant in northern Scotland (a maximum of >800 individuals per holdfast), which were characterised by high abundances of a few amphipod taxa (namely *Jassa* spp., *Parajassa pelagica* and *Ampithoe* spp.). Study-wide abundances of mobile fauna were, however, highly variable with the lowest value (16 individuals per holdfast) recorded in southwest England. Numerically, amphipods dominated all sites with the notable exception of sites in SW England (D1-D3), which were characterised by high relative abundances of polychaetes and decapod crustaceans (Fig 2.6a).

Metric MDS plots showed some partitioning between regions, but these patterns were not as clear as those observed in the sessile assemblage data (Fig 2.5c). Similarly, while the mMDS plots showed some partitioning between sites, within regions, this is less evident than those observed for sessile assemblages; generally, there is considerably more variation in mobile assemblages, both within regions, and within sites. Interestingly, there was some evidence of partitioning between the two southern regions (C & D) and the two northern regions (A & B), a pattern not observed for sessile assemblages (Fig 2.5d). PERMANOVA identified significant differences between regions and sites, as well as a significant effect of the co-variate (Table 2.3). Pairwise tests within the region factor showed that assemblages in southwest England were statistically distinct from those in other regions. PERMDISP did not detect any significant differences in multivariate dispersion between regions ($F_{3,68}$ = 0.92, P = 0.486).

SIMPER analysis showed that the observed differences between regions were driven primarily by a lower abundance of the amphipod *Jassa* spp. within southwest England compared to the other regions (Table 2.6). Samples from southwest England were also characterised by high abundances of the crab *Pisidia longicornis* and the sabellid polychaete *Branchiomma bombyx* compared to all other regions (Table 2.6).

Taxon richness varied markedly between sites within regions, with values across regions being comparable (Fig 2.6b). Total abundance varied by a factor of ~8 within a single region (north Scotland), with the lowest values recorded at sites in southwest England (Fig 2.6c). For both metrics, we recorded a significant effect of site and the co-variate, but no overall effect of region (Table 2.3). As with the sessile assemblage, the biogeographic affinities of

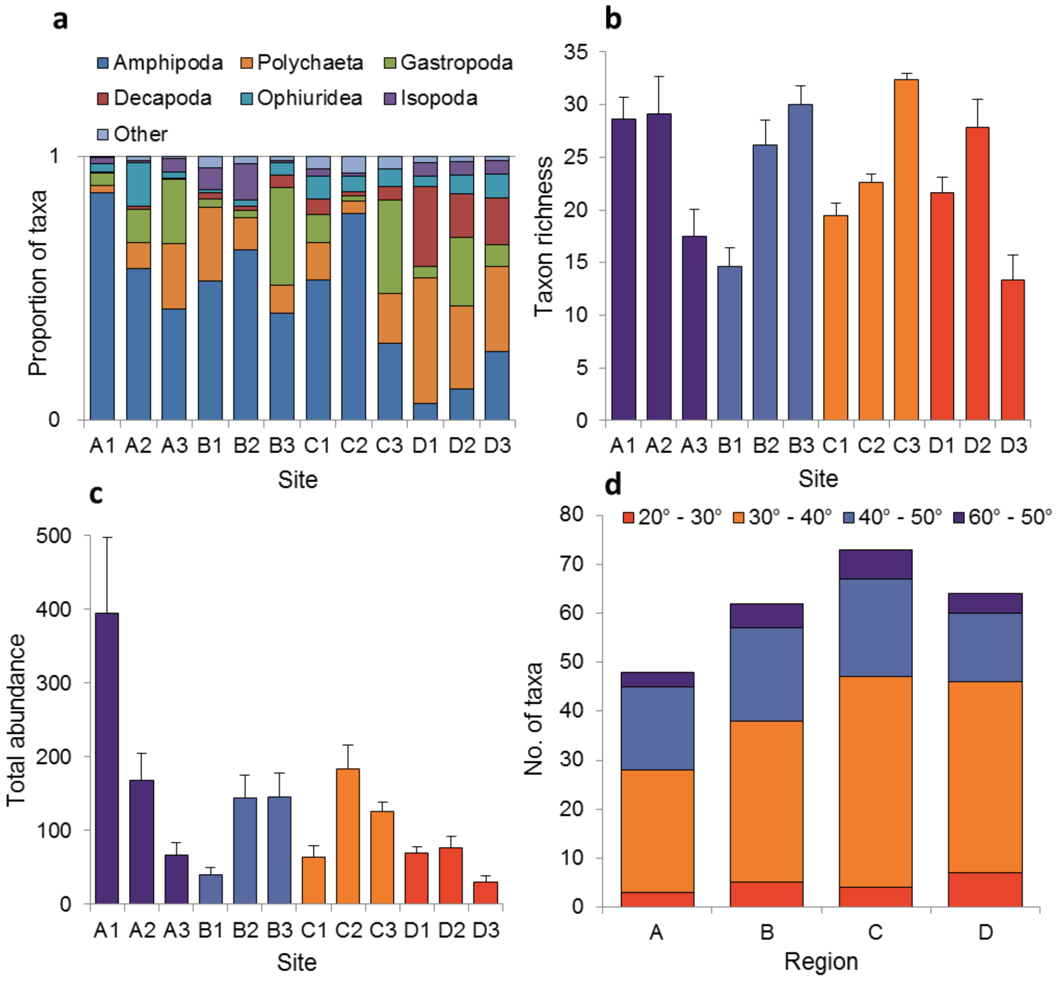

Fig 2.6 Univariate assemblage-level metrics for mobile holdfast assemblages: (a) the proportion of major taxonomic groups, (b) mobile assemblage taxon richness, (c) total biomass of mobile organisms, (d) taxa equatorward range edge. Values for (b) and (c) are means of 6 replicate holdfasts per site (±SE).

species within the assemblages was fairly consistent across the regions, with similar proportions of 'warm' and 'cool' water species (Fig 2.6d).

The DISTLM routine showed that, based on marginal tests, summer temperature, wave fetch and summer light intensity were the most important predictors of mobile assemblage structure (Table 2.7). The stepwise selection procedure indicated that the most

Table 2.6 Percentage contributions of individual taxa to observed differences in mobile holdfast assemblages between regions, as determined by SIMPER analysis.

Species	Av. abund	Av. abund	Av. diss	Diss/SD	Contrib%	Cum%
	N Scot (A)	**SW Eng (D)**				
Jassa spp.	2.62	0.18	1.24	2.65	5.42	5.42
Pisidia longicornis	0.06	1.45	2.48	1.95	3.18	8.60
Ampithoe spp.	1.43	0.00	2.31	1.05	2.96	11.56
Branchiomma bombyx	0.00	1.18	2.02	1.88	2.58	14.14
Lembos websteri	1.09	0.18	1.83	1.25	2.34	16.48
	W Scot (B)	**SW Eng (D)**				
Jassa spp.	1.85	0.18	3.28	1.95	4.17	4.17
Pisidia longicornis	0.49	1.45	2.21	1.40	2.81	6.99
Branchiomma bombyx	0.00	1.18	2.15	1.89	2.74	9.73
Erichthonius brasiliensis	1.19	0.25	1.89	1.45	2.41	12.14
Caprella sp. A	0.89	0.06	1.84	1.14	2.35	14.49
	Wales (C)	**SW Eng (D)**				
Jassa spp.	1.57	0.18	2.67	1.50	3.60	3.60
Monocorophium sextonae	1.52	0.21	2.55	1.69	3.43	7.03
Branchiomma bombyx	0.00	1.18	2.03	2.04	2.73	9.76
Caprella sp. complex	1.01	0.00	1.79	0.84	2.40	12.16
Syllis spp.	0.62	1.51	1.75	1.45	2.36	14.52

Table 2.7 DISTLM marginal test results for each environmental predictor variable selected for the most parsimonious model for mobile assemblages. The best solution based on stepwise selection and AICc criteria is shown. SS = sum of squares (trace), Prop. = proportion of variation explained.

Variable	SS	Pseudo-*F*	P	Prop.
Summer temperature	21147	9.299	0.001	0.117
Wave fetch	15245	6.464	0.001	0.085
Summer light intensity	14745	6.234	0.001	0.082
Holdfast habitable space	12673	5.291	0.001	0.070
Kelp age	10553	4.351	0.001	0.059
Tidal driven water motion	9813	4.029	0.001	0.054
Wave driven water motion	8477	3.453	0.001	0.047
Phosphate concentration	6525	2.629	0.003	0.036
Best solution: All variables (R^2: 0.47, AICc: 539.0)				

parsimonious solution, which explained 47% of the total observed variability in assemblage structure, included all the predictor variables (Table 2.7).

vi. Combined assemblage

Multivariate patterns based on the structure of combined assemblages (i.e., proportional data of both sessile and mobile taxa) were not dissimilar to those based on sessile and mobile assemblages individually, in that there was some partitioning between regions as well as pronounced between-site variability, particularly in southwest Wales (Fig 2.5e). Site-level averages indicated that assemblages in southwest England were somewhat clustered and distinct from other regions (Fig 2.5f). PERMANOVA detected significant variability between both regions and sites, as well as a significant effect of the co-variate (Table 2.3). PERMDISP showed significant differences between regions in within-factor multivariate dispersion ($F_{3,86} = 10.14$, $P = 0.001$), with variability between holdfast samples from Wales (region C) considerably greater than elsewhere. Pairwise tests within the region factor showed that assemblages in southwest England were statistically distinct from those in other regions. A SIMPER analysis showed that these differences were largely driven by the barnacles *Ballanus crenatus* and *Verruca stroemia*, which tended to be lower and higher in abundance, respectively, in southwest England compared to other regions (Table 2.8). Moreover, the amphipod *Jassa* spp. tended to be relatively less abundant and an unidentified sponge more abundant in southwest England and compared to other regions (Table 2.8). Finally, the DISTLM routine indicated that summer temperature, wave fetch and kelp holdfast age were important predictors of assemblage structure, and that the best solution explained 50% of variability and included all the predictor variables (Table 2.9).

Table 2.8 Percentage contributions of individual taxa to observed differences in combined assemblages (based on proportional data) between regions, as determined by SIMPER analysis.

Species	Av. abund **N Scot (A)**	Av. abund **SW Eng (D)**	Av. diss	Diss/SD	Contrib%	Cum%
Jassa spp.	31.72	0.42	7.82	1.78	10.28	10.28
Verruca stroemia	12.40	23.05	4.39	1.12	5.77	16.05
Demosponge A	2.69	13.87	3.54	0.85	4.65	20.70
Escharoides coccinea	14.83	12.16	3.42	1.26	4.49	25.19
Pisidia longicornis	0.05	12.93	3.22	1.35	4.23	29.43
	W Scot (B)	**SW Eng (D)**				
Spirobranchus spp.	28.21	5.55	5.76	1.71	7.04	7.04
Verruca stroemia	0.81	23.05	5.56	1.25	6.79	13.83
Jassa spp.	21.35	0.42	5.26	1.39	6.43	20.26
Demosponge A	0.00	13.87	3.47	0.81	4.24	24.50
Balanus crenatus	13.51	0.05	3.38	0.65	4.13	28.63
	Wales (C)	**SW Eng (D)**				
Verruca stroemia	7.34	23.05	5.07	1.21	6.26	6.26
Balanus crenatus	19.43	0.05	4.85	1.07	5.99	12.25
Didemnid spp.	17.29	8.92	4.47	0.97	5.53	17.78
Demosponge A	7.70	13.87	4.30	0.86	5.31	23.09
Syllis spp.	0.93	13.73	3.24	1.26	4.00	27.09

Table 2.9 DISTLM marginal test results for the environmental predictor variables selected for the most parsimonious model for the combined assemblage (based on proportional data) based on AICc selection criteria. SS = sum of squares (trace), Prop. = proportion of variation explained.

Variable	SS	Pseudo-*F*	P	Prop.
Summer temperature	23672	9.287	0.001	0.117
Wave fetch	22170	8.625	0.001	0.109
Kelp age	19666	7.546	0.001	0.097
Wave driven water motion	17441	6.612	0.001	0.086
Holdfast habitable space	15456	5.797	0.001	0.076
Summer light intensity	14222	5.299	0.001	0.070
Tidal driven water motion	9296	3.375	0.001	0.045
Phosphate concentration	6334.8	2.265	0.012	0.031
Best solution: All variables (R^2: 0.50, AICc: 541.9)				

2.5. *Discussion*

Kelp holdfasts are important repositories of biodiversity in coastal marine ecosystems. The assemblages sampled in this study were highly diverse, in some cases highly abundant, and fairly typical of *Laminaria hyperborea* holdfasts described in previous research (Sheppard *et al.*, 1980; Christie *et al.*, 2003; Jorgensen & Christie, 2003; Schaal *et al.*, 2012). We recorded a study-wide richness value of 261 distinct taxa, while average richness per holdfast was ~40 taxa (i.e. combined averages for sessile and mobile richness). These values are comparable to, but notably higher, than most previous reports of holdfast richness, with the exception of *Ecklonia radiata* holdfasts in Australasia and *L. hyperborea* holdfasts in Norway (see Teagle *et al.*, 2017 for a comprehensive review). These values are also comparable to study-wide richness values for macroinvertebrate assemblages associated with seagrass beds (and in Western Australia; Edgar, 1990a; e.g. in the Mediterranean; Como *et al.*, 2008), which are widely regarded as habitats with high biodiversity value (Unsworth & Cullen-Unsworth, 2014). With regards to faunal densities, average mobile invertebrate abundance exceeded ~400 individuals per holdfast at one study site but was typically >150 individuals per holdfast, while mean biomass of sessile assemblages was typically ~10g per holdfast. Given that densities of mature *L. hyperborea* plants are in the order of 10 plants m^{-2} at these study sites (Smale *et al.*, 2016), a simple approach to 'scaling up' would yield estimates of faunal abundance of 1500 $inds.m^{-2}$ and faunal biomass of 100 g m^{-2} for holdfast assemblages alone. As *L. hyperborea* populations in the UK are predicted to inhabit an area in the region of 8,100 (Smale *et al.*, 2016) to

16,000 km^2 (Yesson *et al.*, 2015), holdfast associated assemblages are likely to play a significant role in trophic processes and wider coastal ecosystem functioning.

We recorded marked between-region and between-site variability in the structure of both sessile and mobile macrofaunal assemblages, as well as the combined assemblages based on proportional data. In general, mobile assemblages were more diverse than their sessile equivalents, and tended to be more heterogeneous and spatially variable. Although we observed considerable regional-scale variability, we did not record predictable shifts in assemblage diversity or structure with latitude. That is, differences between regions did not generally correspond with sequential shifts in latitude or temperature. For sessile taxa, holdfast assemblages in north Scotland, west Scotland and southwest England were all distinct from one another, whereas assemblages from Wales were far more heterogeneous and were not dissimilar to other regions. For mobile assemblages, there was some indication of latitudinal shifts in structure (see below) and, despite high site-level variability, assemblages in southwest England were statistically distinct from those in other regions. Evidence of regional-scale variability contrasts with a comparable study on *E. radiata* holdfasts in New Zealand (Anderson *et al.*, 2005), which found holdfast assemblages structure to be relatively consistent and predictable along a gradient of 2° in latitude and >300 km of coastline. As our study encompassed a larger spatial gradient, it is likely that between-region variability in key drivers of ecological pattern such as temperature, wave exposure and primary productivity in the overlying water column are important.

For example, while wave fetch and local water motion were broadly comparable between regions, overall wave exposure values were slightly greater in north Scotland and southwest England compared to west Scotland and southwest Wales (except C1). *L. hyperborea*, like many other kelp species, exhibits morphological adaptations to hydrodynamic forcing, including the development of larger holdfasts under wave exposed conditions (Sjøtun & Fredriksen, 1995), which was perhaps reflected in the generally larger holdfasts in north Scotland and (to a lesser extent) southwest England. The size and shape of the holdfast habitat can be an important driver of diversity and abundance of associated assemblages in some systems (Moore, 1978; Sheppard *et al.*, 1980; Smith, 1996b), although this relationship has been shown to break down elsewhere (e.g. Christie *et al.*, 2003; Walls *et al.*, 2016), and may be more important for smaller, younger holdfasts (Ojeda & Santelices, 1984; Anderson *et al.*, 2005). Here, differences in holdfast structure may also be driven, at least in part, by regional-scale variability in biogenic habitat structure. Other possible drivers of variability operating across regional scales include patterns of dispersal and connectivity, coastal geomorphology and differences in proximal habitat types and potential source populations.

Similarly, regional scale variability in turbidity, sedimentation and the supply of organic matter may be important in determining holdfast assemblage structure. In this case, holdfasts from southwest England were largely distinct from those elsewhere, primarily because of markedly lower abundances of amphipods, and higher relative abundances of crabs, polychaetes, and sponges. The marine environments around Wales (i.e. the Irish Sea) and West Scotland (i.e. the Firth of Lorne) are typically more turbid, with higher levels of suspended material (Moore, 1978; Smale *et al.*, 2016), and holdfasts here were characterised by high silt deposition. A considerable proportion of the mobile assemblages at these sites was composed of filter and deposit feeding amphipods (e.g. *Jassa* spp., *Monocorophium sextonae*), which would conceivably benefit from high levels of particulate organic matter. In contrast, the less turbid waters in southwest England could favour different taxa, and could explain a lower dominance of amphipod deposit feeders and a higher dominance of omnivorous crabs. As such, regional-scale differences in turbidity or the deposition of organic matter from riverine inputs or pelagic primary production may influence the development of holdfast assemblages and trophic structuring (Moore, 1973b; Smith, 1996b). Unfortunately, we did not directly measure the sediment content of each holdfast, which would have been a useful predictor variable given that previous research has shown correlations between the abundances of taxa and sediment loads (Smith, 1996b). Given that coastal development and maritime activities (e.g. dredging) can alter sedimentation rates, further investigation into the influence of sediment content on holdfast assemblages would be useful.

The structure of mobile assemblages did exhibit some latitudinal patterns, with some distinction in multivariate structure between northernmost (north and west Scotland) and southernmost (southwest Wales and southwest England) sites, and sea temperature emerging as an important explanatory variable. This was largely driven by a general increase in the relative abundance of amphipods from south to north and, in contrast, an increase in the relative abundance of decapods and polychaetes from north to south. Conversely, sessile species were widely distributed across the regions and sessile assemblages were more influenced by wave exposure and local water motion. Such differences in variability patterns between mobile and sessile fauna may be linked to dispersal potential. The most abundant mobile fauna, in this instance gammaridean amphipods, tend to brood their offspring and may have relatively limited dispersal potential compared to many commonly found sessile fauna, which have a planktonic larval stage (Moore, 1981; Borowsky, 1983; Dick *et al.*, 1998; Goldson *et al.*, 2001). Moreover, recent work has shown that the structure of kelp forests varies with latitude along the gradient encapsulated in this study (Smale & Moore, 2017) and, as different kelp species may harbour distinct associated assemblages (e.g. Blight & Thompson, 2008; Raffo *et al.*, 2009, Teagle and Smale, unpublished data; Tuya *et al.*, 2011), the composition of the wider kelp forest may potentially play a role in the development of distinct, regional holdfast assemblages. This may be particularly important for mobile assemblages, as some common taxa (e.g. amphipods and isopods) have been shown to move freely throughout kelp forests and even to emigrate to adjacent systems (Jorgensen & Christie, 2003; Bartsch *et al.*, 2008). As such, the structure and configuration of surrounding habitats, and their associated species pools, is likely to play an important role in the structuring of holdfast assemblages and may vary somewhat predictably with latitude.

Pronounced site-level variability was an important component of the observed spatial variation in holdfast community structure and diversity, suggesting that environmental factors varying across similar spatial scales, such as wave exposure, could be important in determining ecological pattern. Previous research has highlighted the importance of hydrodynamic forces (i.e. the action of waves and the tide) in structuring marine communities (Ballantine, 1961; Brattström, 1968; Knights *et al.*, 2012), including kelp systems (Sjøtun & Fredriksen, 1995; Molloy & Bolton, 1996; Wernberg & Thomsen, 2005; Pedersen *et al.*, 2012; Bekkby *et al.*, 2014), and in relation to kelp-associated assemblages in particular (Norderhaug & Christie, 2011; Norderhaug *et al.*, 2012; Norderhaug *et al.*, 2014). The effect of wave exposure on the morphology of *L. hyperborea* is well documented (e.g. development of larger, more complex holdfasts; Sjøtun & Fredriksen, 1995), and as faunal diversity is often (but not always) related to habitat size, a relationship exists between wave exposure and kelp associated faunal diversities (Schultze *et al.*, 1990; Christie *et al.*, 1998; Christie *et al.*, 2003; Anderson *et al.*, 2005; Norderhaug *et al.*, 2007; Norderhaug & Christie, 2011; Norderhaug *et al.*, 2012; Norderhaug *et al.*, 2014; Walls *et al.*, 2016). Intense wave action represents a physical disturbance to algal associated fauna, and may result in considerable loss of fauna due to dislodgement and mortality (Fincham, 1974; Fenwick, 1976). The reduced diversity and abundances of communities associated with holdfasts from the most wave exposed sites (i.e. A1) in this study suggest this process may play a role within kelp holdfasts. The largest holdfasts, by some margin, were found at site A1, the most exposed site in north Scotland. While the mobile assemblage associated with these holdfasts was diverse and abundant, as one would expect, the sessile assemblage was comparatively depauperate in relation to the apparent habitable space available. Holdfasts from this site were missing the high abundances and biomass of common bryozoan species in particular, and were characterised by a high sediment load made of coarse sand, and had an almost ‘sand-blasted’ look. It is likely that the strong wave motion characteristic of this site, coupled with the large, open nature of the holdfasts, caused smothering of delicate filter-feeding organisms, such as the bryozoans so characteristic of other sites.

Interestingly, the potential effects of wave exposure seemed to be more pronounced on sessile, rather than on mobile assemblages. This impact is potentially due to the influence of sedimentation, which can smother delicate filter-feeding sessile organisms (Moore, 1973b) but may have exert a positive influence over other taxa (Smith, 1996b). Site-level variability may also be promoted by differences in reef structure and substratum characteristics. Topographic complexity, the prevalence of large boulders versus pavement-like platforms, and reef rugosity may influence kelp population structure (Toohey *et al.*, 2007; Toohey & Kendrick, 2008; Azzarello *et al.*, 2014). As such, variation in holdfast morphology (i.e. relative holdfast volume) driven by site-level differences in reef structure may have influenced the development and richness of associated assemblages. Other factors that have been identified as important drivers of site-level variability in holdfast assemblages include pollution (Smith, 1996a), kelp harvesting and farming (Vasquez & Santelices, 1990; Walls *et al.*, 2016) and grazing pressure (Hagan, 1983; Tegner *et al.*, 1995). However, given the negligible impact of these activities and processes across the current study area (Smale *et al.*, 2013), they were unlikely to be important in this case.

In addition to the variability between regions and between sites, we recorded pronounced small-scale variability between individual holdfasts separated by a few meters. Marine benthic communities generally exhibit considerable small-scale variability (e.g. Fraschetti *et al.*, 2005; Smale *et al.*, 2010), which is driven by a range of processes operating across multiple spatial, and temporal scales (Foster *et al.*, 2014). Combined with the highly variable nature of supply-side ecology (Underwood & Fairweather, 1989), the inter-holdfast variability recorded here is perhaps not surprising. Small-scale variations in food availability, protection from predation, water movement and sedimentation (e.g. due to proximity to topographical reef features which may attenuate wave action), and differences in species' tolerance to smothering or dislodgement may also influence assemblage structure (Edgar, 1990b; Edgar & Robertson, 1992; Foster *et al.*, 2014). Indeed, much of the variability observed in holdfast community structure throughout this investigation was unexplained by the environmental factors measured. It is likely that these factors were measured at a spatial scale too large to account for within-site variation, highlighting the need for more research into the small, local scale drivers of holdfast assemblage development and maintenance.

In conclusion, faunal assemblages associated with *L. hyperborea* holdfasts are highly diverse and exhibit considerable structural variability over multiple spatial scales. Crucially, the sessile and mobile components of holdfast assemblages exhibited slightly different patterns and may be influenced by key environmental drivers, specifically variability in wave exposure and temperature, to differing degrees due to divergence in life histories or growth strategy. It is evident that *L. hyperborea* serves as a critical foundation species in shallow rocky habitats in the northeast Atlantic by providing biogenic habitat, altering environmental conditions and exerting a strong influence over local biodiversity and community structure. Within UK waters, our study suggests that local scale environmental variability is more important in structuring kelp-associated assemblages than latitudinal-scale variation in sea temperature. However, given that sea water temperatures around the UK have significantly increased in recent decades (Belkin, 2009), and are predicted to continue to rise through the next century (Philippart *et al.*, 2011), it is likely that temperature will begin to play a larger role in structuring the biogenic habitat provided by *L. hyperborea*, and thereby its associated assemblages, in the near future. The ecophysiology of *L. hyperborea* is adversely impacted by temperatures above 20°C (Müller *et al.*, 2009), and as the southernmost regions of the UK currently experience temperatures of this magnitude during anomalous warming events (Joint & Smale, 2017) and are projected to experience such temperatures more frequently in the coming decades (Philippart *et al.*, 2011), the continued provision of biogenic habitat is at risk from future climate change. Any climate-driven reduction in the biomass, density, spatial extent or longevity of *L. hyperborea* will likely result in a reduction of habitat available for colonisation and consequent changes to community structure and local biodiversity. Indeed, further south on the Iberian Peninsula, *L. hyperborea* has retracted its equatorward range edge as marginal populations have responded to ocean warming (Tuya *et al.*, 2012;

Voerman *et al.*, 2013), and key ecological functions including habitat provision and benthic primary productivity have been lost or altered. Changes in habitat provision will likely influence holdfast assemblage structure, and in doing so, affect the usefulness of kelp holdfasts for biodiversity monitoring and detecting local environmental impacts (Smith, 2000). Clearly, a better understanding of the drivers of kelp community structure, including an improved appreciation of species interactions in a rapidly changing environment, is required to predict the structure and conserve the diversity of these ecosystems in the coming decades.

Chapter 3. Climate-driven substitution of habitat-forming species leads to reduced biodiversity within a temperate marine community

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3.1. *Abstract*

In marine ecosystems, habitat-forming species (HFS) such as reef-building corals and canopy-forming macroalgae alter local environmental conditions and can promote biodiversity by providing biogenic living space for a vast array of associated organisms. Climate change is directly altering ecological communities by driving shifts in species distributions and abundances as they occupy favourable thermal habitats. Here I examine community-level impacts of observed climate-driven shifts in the relative abundances of two superficially similar HFS, the warm-water kelp *Laminaria ochroleuca* and the cool-water kelp *Laminaria hyperborea* in the southwest British Isles. Algal and invertebrate assemblages associated with kelp stipes and holdfasts were compared across multiple sites and sampling events. Significant differences were recorded in the structure of assemblages between the host kelp species at each site and event. Assemblages associated with stipes of the cool-water HFS were, on average, >12 times more diverse and >3600 times more abundant (in terms of biomass) compared with the warm-water HFS. Holdfast assemblages also differed significantly between species, although to a lesser extent than those associated with stipes. Overall, assemblages associated with the warm-water HFS were markedly impoverished and comprised far fewer rare or unique taxa. While previous research has shown how climate-driven *loss* of HFS can cause biodiversity loss, our study demonstrates that climate-driven *substitutions* of HFS can also lead to impoverished assemblages. The indirect effects of climate change remain poorly resolved, but shifts in the distributions and abundances of HFS may invoke widespread ecological change, especially in marine ecosystems where facilitative interactions are particularly strong.

3.2. *Introduction*

Anthropogenic climate change is a threat to marine ecosystems. The upper layers of the ocean have warmed by 0.11°C per decade since the mid-20th century (IPCC., 2013) and are now on average more acidic and less oxygenated, and have altered salinity and wave regimes (Bijma *et al.*, 2013; IPCC., 2013). Ocean warming, in particular, has resulted in a global redistribution of species with biogeographic ranges generally shifting polewards in line with changing isotherms (Parmesan, 1996; Burrows *et al.*, 2011; Wernberg *et al.*, 2011b; Sunday *et al.*, 2012; Pinsky *et al.*, 2013; Poloczanska *et al.*, 2013). However, the rate of species' redistributions is not uniform (Poloczanska *et al.*, 2013; Sunday *et al.*, 2015), leading to a reshuffling and reorganisation of communities and ecosystems, which are increasingly structured by novel ecological interactions (Kordas *et al.*, 2011; Verges *et al.*, 2014b). Indirect effects of oceanic climate change manifest when a range-shifting species influences other species and populations within a novel community, through changes in herbivory (Zarco-Perello *et al.*, 2017), predation (Ferrari *et al.*, 2015) or competition (Sorte & White, 2013), for example.

As different species exert different degrees of influence within communities, the indirect effects of some species redistributions will likely be greater than others. For example, the climate-mediated range expansion of a keystone grazer, the sea urchin *Centrostephanus rodgersii*, resulted in extensive barren formation in kelp forests in Tasmania (Ling, 2008), whilst a recent rapid range contraction of canopy-forming macroalgae in southwest Australia induced major alterations in community structure due to habitat loss (Smale & Wernberg, 2013). Habitat forming species (HFS), such as seagrasses, corals and kelps, function as ecological engineers (Jones *et al.*, 1994) by modifying the physical environment and providing biogenic structure for other organisms (Jones *et al.*, 1997). As such, quantifying the indirect effects of climate-driven redistributions of HFS is needed for a holistic understanding of climate change impacts.

Kelps are large brown seaweeds of the order Laminariales. They dominate lower intertidal and shallow subtidal reefs along temperate and subpolar coastlines globally, as well as Arctic coastlines in the northern hemisphere (Steneck *et al.*, 2002; Teagle *et al.*, 2017). They form some of the most productive and diverse habitats on Earth (Mann, 1973; Reed *et al.*, 2008; Smale *et al.*, 2013) and provide human societies with ecosystem services worth billions of pounds annually (Beaumont *et al.*, 2008; Bennett *et al.*, 2016; Filbee-Dexter & Wernberg, 2018). Kelp forests are also a major source of primary production in coastal zones (Steneck *et al.*, 2002), and kelp-derived organic matter may either enter food webs *in situ* or be exported many kilometres into adjacent habitats (Vanderklift & Wernberg, 2008; Krumhansl & Scheibling, 2012). In addition to this primary productivity, kelps also support elevated biodiversity and secondary productivity through the provision of three-dimensional habitat structure (Teagle *et al.*, 2017), which is utilised by a vast array of marine organisms including commercially important species (Bertocci *et al.*, 2015). Due to their high biodiversity value and their socioeconomic importance (e.g. fisheries habitat, direct harvesting for food, alginate and other products), kelp forests are managed and protected in many temperate regions (e.g. in France; Birkett *et al.*, 1998; and Norway; Christie *et al.*, 1998).

Kelps are mostly cool-water HFS and, as such, marginal populations found towards trailing range edges are particularly susceptible to seawater warming. In recent years, climate-driven losses of several kelp populations have been reported (Fernandez, 2011; Verges *et al.*, 2014b; Filbee-Dexter *et al.*, 2016; Wernberg *et al.*, 2016), with wider consequences for associated communities and ecosystems (Tuya *et al.*, 2012; Voerman *et al.*, 2013; Wernberg *et al.*, 2013; Wernberg *et al.*, 2016). In the northeast Atlantic, sea temperatures have increased significantly in recent decades (Belkin, 2009; Smyth *et al.*, 2010), with many areas predicted to warm by >2°C this century (Philippart *et al.*, 2011). In response to this warming trend several more northerly-distributed kelp species (e.g. *Alaria esculenta*, *Laminaria digitata*, *Laminaria hyperborea*) have contracted, or are expected to contract, their equatorward range edges (Hiscock *et al.*, 2004; Müller *et al.*, 2009; Raybaud *et al.*, 2013). On the other hand, recent evidence suggests that more southerly-distributed kelp species have increased in abundance at their poleward range edge (e.g. *Laminaria ochroleuca*; Smale *et al.*, 2015). Any changes in the distributions or relative abundances of these HFS could have significant impacts on the structure and functioning of kelp-associated communities (Blight & Thompson, 2008), but this is likely to be dependent on both the characteristics of the HFS and the environmental context (Tuya *et al.*, 2011; Smale *et al.*, 2013).

Within the wider context of global climate change, the implications of shifts in the relative abundances of HFS for biodiversity are almost entirely unknown in marine systems. We examined community-level responses to climate-driven shifts in the relative abundances of HFS by comparing flora and fauna associated with the stipes and holdfasts of two kelp HFS: *Laminaria hyperborea* and *Laminaria ochroleuca*. These species differ in their geographical distributions and environmental requirements, but are similar in their morphology (Fig 3.1 a-c). *L. hyperborea* is the dominant HFS on wave-exposed shallow reef habitats in the northeast Atlantic, where it supports a diverse array of flora and fauna within its holdfast, and on its blade and stipe (Christie *et al.*, 2003). *L. hyperborea* is a cool temperate species distributed from the Arctic southwards to northern Portugal (Tuya *et al.*, 2012), while *L. ochroleuca* is a warm-temperate Lusitanian species, extending from its poleward range edge in southwest UK southwards to Morocco and into the Mediterranean (Franco *et al.*, 2017). *L. ochroleuca* has recently proliferated at its poleward range edge; it was first documented in the UK in 1946, in Plymouth Sound (Parke, 1948b; John, 1969), and has since spread throughout the southwest coast of the UK (Norton, 1985; Smirthwaite, 2006;

Hargrave *et al.*, 2017). Species distribution models predict a further poleward range expansion in coming decades (Franco *et al.*, 2017).

The magnitude and spatial extent of proliferation at the range edge by *L. ochroleuca* has not yet been quantified with any certainty, and community-level implications are almost entirely unknown. We examined temporal trends in the relative abundances of these HFS

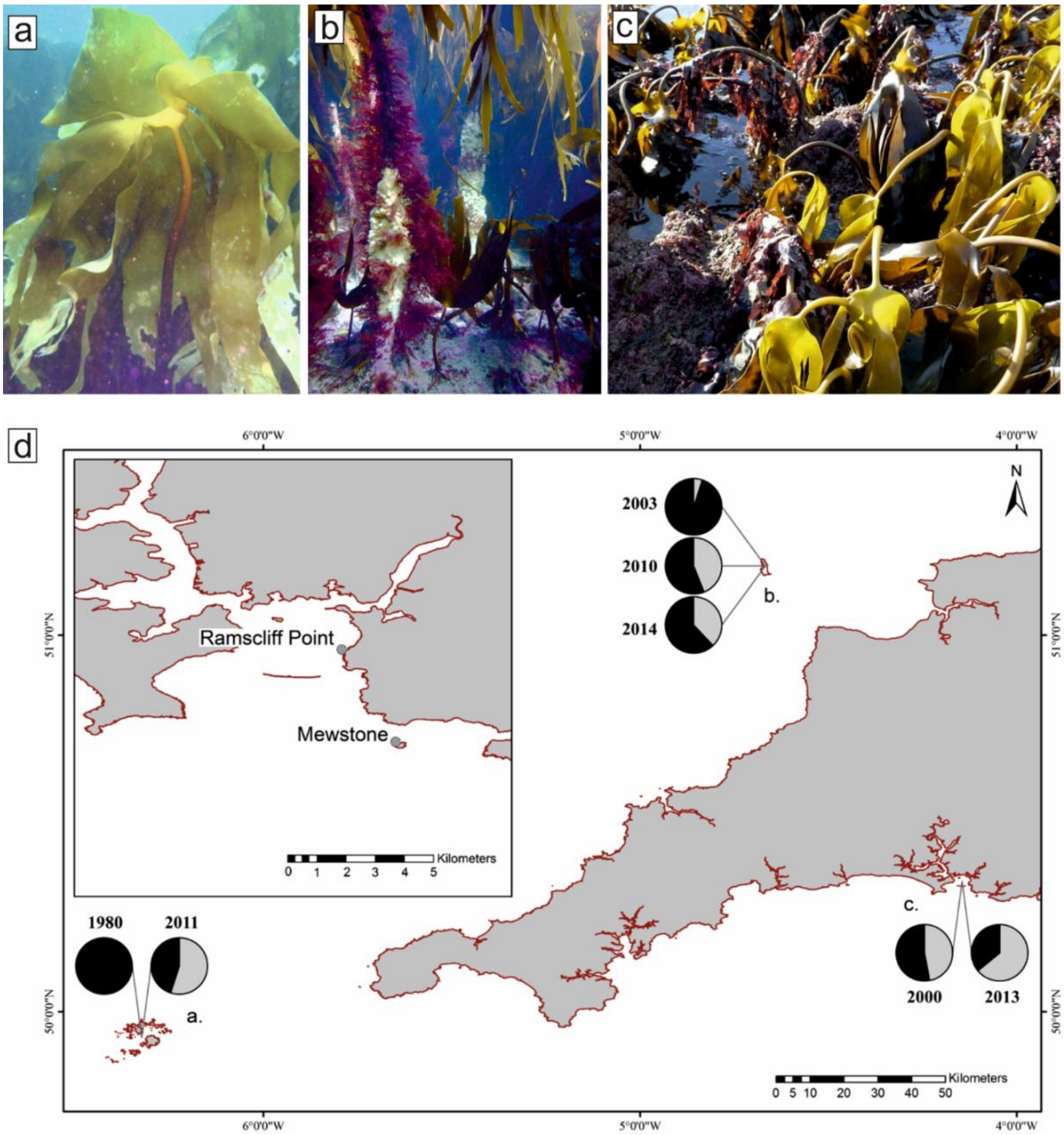


Fig 3.1 Representative examples of (a) the warm-water HFS *L. ochroleuca* and (b) the cool-water HFS *L. hyperborea,* depicting differences in stipe-associated assemblages between the two kelp species. *L. ochroleuca* is typically devoid of all epibionts, whereas *L. hyperborea* tends to support rich and abundant assemblages of red algae and sessile invertebrates. The two HFS co-exist at many locations in southwest UK; (c) rocky reef habitat exposed during spring low tides reveals a mixed bed of *L. hyperborea* (top left) and *L. ochroleuca* (bottom right). Also shown are (d) the temporal trends in the relative abundance of *Laminaria ochroleuca* (grey) and *Laminaria hyperborea* (black), at three locations in the southwest UK: (1) the Isles of Scilly, (2) Lundy Island and (3) Plymouth Sound, indicating the recent proliferation of *L. ochroleuca* at the range edge. Inset map indicates the positions of the two principal study sites, Ramscliff Point and the Mewstone, within Plymouth Sound.

from key monitoring locations and then quantified biodiversity patterns associated with each kelp species. Our overarching aim was to examine how shifts in the relative abundances of HFS, driven by ocean warming, may influence the structure of associated assemblages and local biodiversity patterns.

3.3. *Methods*

i. Temporal trends in the relative abundances of kelp HFS

Historical data were collated from three monitoring sites in the southwest UK: Plymouth Sound, the Isles of Scilly and Lundy Island (Fig 3.1). Data were extracted from a variety of sources including reports commissioned by government agencies (Mercer *et al.*, 2004; Irving & Northern, 2012; Axelsson *et al.*, 2014), historical survey data (e.g. the Marine Natural Conservation Review dataset complied by the Joint Nature Conservation Committee) and from the published literature (e.g. Smale *et al.*, 2015). All data were originally collected using comparable traditional ecological methods (i.e. *in situ* identification and quantification by scuba divers using transects and quadrats; see cited sources for more information). Within each location 2-3 shallow subtidal survey sites, which were moderately exposed to wave action, supported mixed kelp beds and were sampled at least twice between 1980 and 2014, were used to examine the relative proportion of *L. ochroleuca* to *L. hyperborea.*

ii. Environmental variables

Environmental sensors were deployed at each site, to quantify water motion, temperature and light. Water motion was quantified with an accelerometer (HOBO® Pendant G Logger), attached to a subsurface pellet buoy which was tethered to the seabed by a 0.65 m rope and clump weight, to measure water movement in three axes every 5 minutes (Figurski *et al.*, 2011; see Appendix 1). An additional sensor (HOBO® Temperature/Light Weatherproof Pendant Data Logger 8k) was attached to the buoy, facing upwards, and collected and logged temperature and light intensity data every 20 minutes. Due to overgrowth by epiphytic algae, light sensors were cleaned after 8 weeks, and only data from 3 weeks post deployment/clearing were used. Environmental data were recorded for 11 weeks, between April and June 2014.

iii. Sample collection

Kelp samples were collected from two sites in southwest UK; northwest Mewstone (50°18.485′ N, 04°06.521′ W) and Ramscliff Point (50°20.572′ N, 04°07.766′ W), both within the wider Plymouth Sound region (Fig 3.1d). The sites fall within the Plymouth Sound Special Area of Conservation (SAC), within which kelp forest communities are recognised as important conservation features. Both sites support mixed stands of *L. hyperborea* and *L. ochroleuca*, extensive subtidal rocky reef habitat, and are moderately exposed to wave action, although the Plymouth Sound breakwater offers some protection to the Ramscliff Point site (Fig 3.1d). The Mewstone, being situated further offshore, was characterised by slightly higher light availability and water movement than Ramscliff Point, whereas temperature regimes were comparable between sites (Fig 3.2). Sampling was undertaken on two occasions by scuba divers (in April and June 2014) as kelp-associated assemblages exhibit strong seasonality and, as such, any differences between HFS may vary between seasons. Twelve mature canopy-forming sporophytes of both *L. hyperborea* and

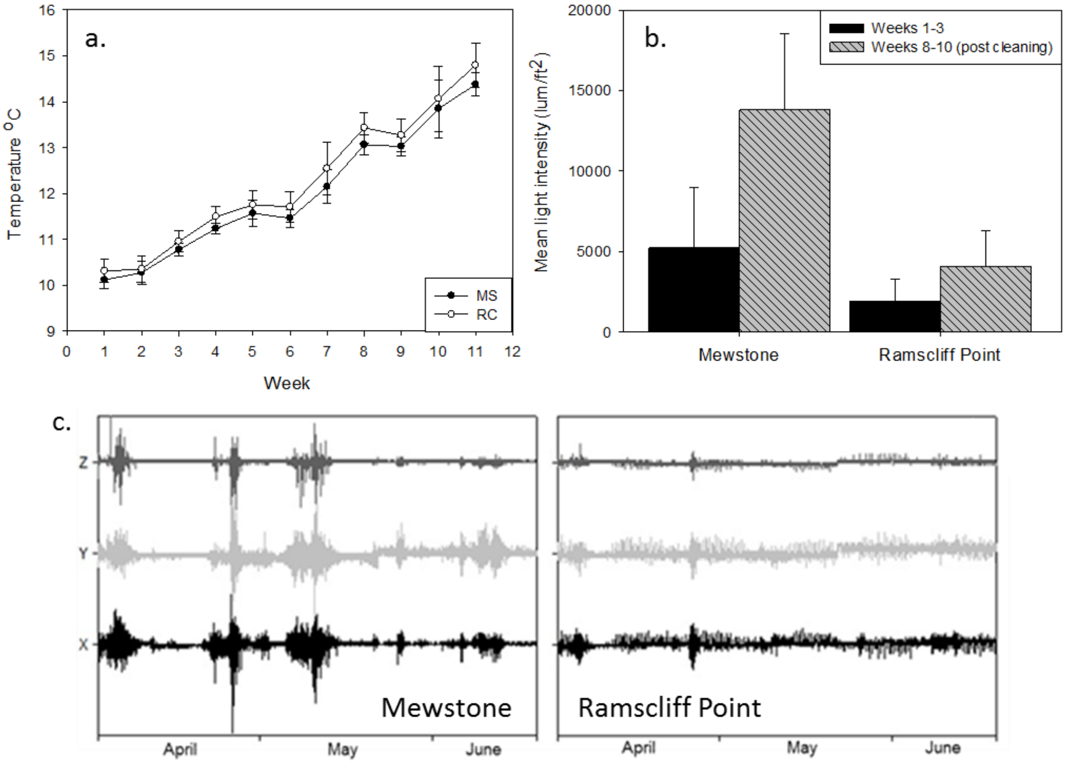


Fig 3.2. Environmental data recorded at each study site: (a) temperature, (b) light availability and (c) water motion. All error bars indicate standard deviation.

L. ochroleuca were collected haphazardly from within mixed stands at each site during each sampling event. Samples were collected from within kelp stands on relatively flat rocky platforms at 2-4 m depth (below chart datum). Following removal of the blade, a fine cotton bag was placed over the stipe of each specimen, which was then cut approximately 5 cm above the holdfast and the bag carefully sealed with a cable tie to retain all attached organisms. The holdfast was then covered with a second cotton bag and was carefully removed from the substrate before being sealed. Samples were immediately returned to the laboratory.

iv. Sample processing

Morphology and biomass (fresh weight) of stipe and holdfast samples were quantified in the laboratory. Sessile fauna and flora on the stipes were identified and weighed to quantify biomass (tissue-dried fresh weight). Holdfast specimens were placed into a 1% propylene phenoxytol solution for ~30 minutes, in order to relax any associated fauna to aid identification. The holdfast specimens were then transferred to a 70% industrial methylated spirit (IMS) solution for preservation. Holdfast volume was determined by displacement, wrapping each holdfast in plastic food wrap to establish total holdfast volume (see Blight & Thompson, 2008); holdfast haptera were then removed to expose the inner structure of the holdfast and any associated flora and fauna. Haptera volume was determined by measuring displacement of the removed and cleaned haptera; subsequently being subtracted from total holdfast volume to give the volume of the potential habitable space amongst the haptera of the holdfast. Identification of all organisms was to species level wherever possible, and all sessile taxa (mobile fauna were not quantified in this study) were carefully removed and weighed to establish biomass (tissue-dried fresh weight). Kelp samples collected in summer were also aged by cross-sectioning the basal section of the stipe and counting annual growth rings (as per Kain, 1963).

v. Statistical analysis

All analysis was conducted with univariate/multivariate permutational analyses using the PERMANOVA add on (Anderson *et al.*, 2008) for Primer v7 software (Clarke & Gorley, 2015); assemblages associated with stipes and holdfasts from each site were analysed separately. Variability in multivariate structure was initially examined with a 3-factor design, with kelp species (2 levels), site (2 levels) and sampling event (2 levels) all as fixed factors. To examine the influence of habitat availability, holdfast volume/stipe surface area was also included in the analysis as a co-variate. Permutations (4999 under a reduced model) were based on a Bray-Curtis similarity matrix constructed from fourth-root transformed biomass data (chosen to downweight the influence of large sponges). Differences in multivariate dispersion between kelp species were examined with the PERMDISP routine, and multivariate patterns were visualised with PCO (principal coordinate analysis) plots, with each site shown separately for clarity. Univariate metrics (i.e. taxon richness and total biomass) were examined using the 3-factor model described above but with permutations based on Euclidian distances between untransformed data. Where significant main effects or interaction terms involving the main factor of interest (i.e. 'species') were detected (at $P < 0.05$), pairwise comparisons within each level of the relevant factors were conducted. Where significant differences in assemblage structure between kelp species were detected (at $P < 0.05$), a SIMPER analysis was performed to determine which taxa contributed most to the observed dissimilarity. The factors 'site' and 'sampling event' were treated as fixed to test *a priori* expectations that assemblages would be different between sites (as they differed in wave exposure) and between sampling events (due to seasonal succession of epiphytic assemblages). However, the inference space of this approach is limited, compared with a mixed model involving random factors, as the analysis tested for differences specifically between these two sites and events, rather than for more general patterns (see discussion). Univariate assemblage metrics were plotted as mean values (± SE) for each site and sampling event, to visualise any trends in dissimilarity between the host kelp species. Finally, we examined the relationship between habitat availability (i.e. stipe surface area and holdfast living space) and associated taxon richness and abundance for each HFS, using scatterplots and linear regression.

3.4. *Results*

i. Temporal trends in the relative abundances of kelp HFS

Data extracted from various sources showed that the relative abundance of *L. ochroleuca* has increased in relation to *L. hyperborea* at all locations (Fig 3.1d). At moderately wave-exposed monitoring sites in the Scillies and Plymouth Sound, *L. ochroleuca* is now more abundant than *L. hyperborea* (Fig 3.1d).

ii. Biogenic habitat structure

The two HFS provided somewhat similar biogenic habitat for associated communities, although interspecific differences in habitat provision varied between sites (Fig 3.3). For the

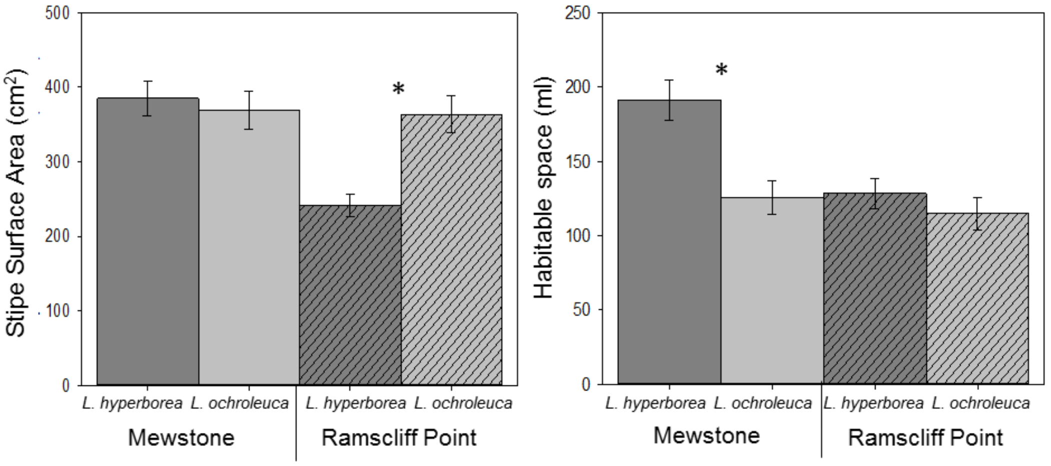


Fig 3.3 Biogenic habitat metrics for kelp stipes (surface area – left plot) and holdfasts (internal living space – right plot). Dark grey bars indicate *L. hyperborea*, light grey bars indicate *L. ochroleuca*; solid bars indicate individuals from the Mewstone, hashed bars indicate samples from Ramscliff Point. Bars represent mean values (± SE).

stipe habitat, the surface area did not differ between the kelp species at the Mewstone (one-way permutational ANOVA; $F_{1,53} = 0.21$, $P = 0.625$) whereas *L. ochroleuca* provided a greater surface area for colonisation than *L. hyperborea* at Ramscliff Point ($F_{1,53} = 18.33$, $P = 0.001$). For the holdfast habitat, *L. hyperborea* offered a greater volume of living space than *L. ochroleuca* at Mewstone ($F_{1,46} = 13.68$, $P = 0.001$), whereas no differences were observed at Ramscliff Point ($F_{1,46} = 0.86$, $P = 0.356$). The age of the sporophytes differed between the 2 kelp species, with the *L. hyperborea* population being slightly, and significantly, older than *L. ochroleuca* (average age: *L. hyperborea* = 6.0 ± 1.1 yr, *L. ochroleuca* = 4.6 ± 1.1 yr; $F_{1,46} = 19.84$, $P < 0.001$).

iii. Stipe assemblages

From 96 kelp stipes, 49 unique taxa (59% of all taxa were identified to species level) were recorded. Rhodophytes dominated the algal assemblage, representing 13 of the 14 species recorded. The sessile faunal assemblage comprised Bryozoans (10 species), Porifera (7 taxa), Ascidians (5 species), Molluscs (mainly bivalves, 5 species), Crustaceans (cirripedia, 4 species), Polychaetes (2 species) and Hydroids (2 species). Across the study, all taxa recorded were found associated with *L. hyperborea* stipes, whereas only ~50% of both floral and faunal taxa were found on *L. ochroleuca* stipes.

PCO plots depicting multivariate assemblage structure indicated clear partitioning between kelp species, although the degree of partitioning was greater at Ramscliff Point than at the

Mewstone (Fig 3.4). Variability in assemblage structure was greater for *L. ochroleuca* than *L. hyperborea*, which supported relatively homogenous stipe assemblages (Fig 3.4). PERMANOVA detected a significant 3-way interaction between species, site and event, as well as highly significant variability associated with species as both a main effect and within higher order interactions (Table 3.1). Pairwise tests within the 3-way interaction term showed that differences between species were significant for every combination of site and event, although the magnitude of dissimilarity was greatest for Mewstone in summer (Table 3.2). The PERMDISP routine indicated that the multivariate dispersion did not differ

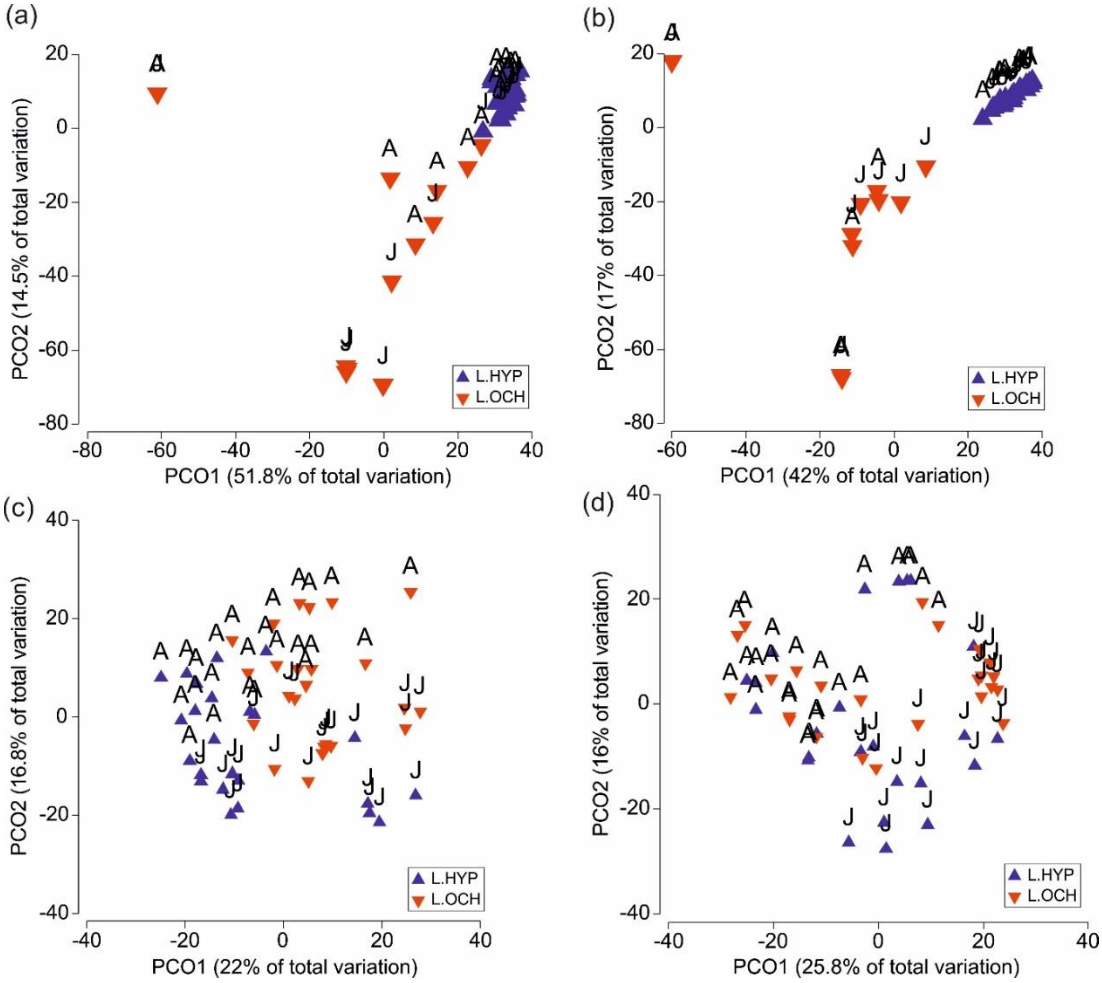


Fig 3.4. Principle component ordinations (PCO plots) depicting the multivariate structure of assemblages associated with kelp stipes and holdfasts. Stipe assemblages are shown separately for (a) Mewstone and (b) Ramscliff Point; holdfast assemblages also shown separately for (c) Mewstone and (d) Ramscliff Point. Samples labelled with an 'A' were collected in April; 'J' indicates samples collected in June. Blue triangles represent *L. hyperborea*, red inverted triangles represent *L. ochroleuca*.

Table 3.1 (a) Results of multivariate PERMANOVA to test for differences in stipe assemblage between kelp species (Sp, fixed), sites (Si, fixed) and sampling event (Ev, fixed). Stipe surface area was included as a co-variate (CO) in the analysis. Permutations were based on a Bray-Curtis similarity matrix generated from fourth-root transformed biomass data. Results of univariate PERMANOVA to test for differences in the assemblage-level univariate metrics (a) taxon richness and (b) total biomass are also shown. Permutations for univariate analysis were based on a Euclidean distance similarity matrix generated from untransformed diversity data. All tests used a maximum of 9999 permutations under a reduced model; significant effects (P<0.05) are shown in bold. The first significant lower order effect of interest (i.e. an interaction or main effect involving the species factor, marked with an asterisk) was examined further with pairwise tests (see text and Table 3.2).

Source	*df*	a. Multivariate assemblage structure			b. Taxon Richness			c. Total Biomass		
		MS	Pseudo-F	P	MS	Pseudo-F	P	MS	Pseudo-F	P
CO	1	10033	6.30	**0.001**	22.0	3.17	0.090	55.6	0.11	0.754
Sp	1	145690	91.70	**0.001**	3021	434.63	**0.001**	31213	64.3	**0.001**
Si	1	13025	8.18	**0.001**	44.5	6.40	**0.014**	4787	9.87	**0.003**
Ev	1	5255	3.30	**0.002**	11.3	1.63	0.237	1384	2.85	0.106
Sp x Si	1	10334	6.49	**0.001**	27.0	3.88	**0.050***	5775	11.90	**0.002**
Sp x Ev	1	3929	2.47	**0.013**	1.34	0.19	0.653	2165	4.46	**0.036***
Si x Ev	1	4960	3.11	**0.002**	130	18.79	**0.001**	2207	4.55	**0.037**
Sp x Si x Ev	1	5501	3.45	**0.001***	22.7	3.27	0.080	384	0.79	0.387
Residual	102	1591			6.94			485		
Total	110									

significantly between the host kelp species ($F_{1,109} = 1.98$, *P* = 0.232). However, while the mean multivariate distance between samples was comparable between species, the variability in distance was ~3 times greater for assemblages associated with *L. ochroleuca* compared with *L. hyperborea* (LH = 39.1 ± 0.9, LO = 43.3 ± 2.8).

Table 3.2 Pairwise tests within significant main effects and interaction terms involving the species factor, for stipe-associated assemblages (see Table 3.1 for outputs of full PERMANOVA). The t and P values relating to the pairwise tests between *L hyperborea* and *L. ochroleuca* are shown for each combination of factors within a significant interaction or main effect. MS= Mewstone, RAM = Ramscliff Point.

Response variable	Site	Event	t	P
Multivariate assemblage	MS	Spring	4.49	0.001
	MS	Summer	5.46	0.001
	RAM	Spring	5.42	0.001
	RAM	Summer	4.76	0.001
Taxon richness	MS	-	13.60	0.001
	RAM	-	14.62	0.001
Total biomass	-	Spring	5.64	0.001
		Summer	6.15	0.001

SIMPER analysis indicated that the differences in multivariate structure between species at the Mewstone was principally driven by the red alga *Phycodrys rubens*, and to a lesser extent the bryozoan *Electra pilosa*, and the red algae *Lomentaria articulata* and *Membranoptera alata*, all of which were more abundant on *L. hyperborea* (Table 3.3). At Ramscliff Point differences were driven primarily by the red alga *Palmaria palmata*, which was abundant on *L. hyperborea*, but absent from *L. ochroleuca* altogether (Table 3.3). Further differences were caused by *Phycodrys rubens* and *Cryptopleura ramosa*, which again were more abundant on *L. hyperborea* (Table 3.3).

Table 3.3 Percentage contributions of individual taxa to the observed difference in stipe assemblage structure between each kelp species at each site, as determined by SIMPER analysis.

	L. hyperborea	*L. ochroleuca*				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Mewstone						
Phycodrus rubens	1.61	0.06	16.89	2.70	17.97	17.97
Electra pilosa	0.87	0.10	9.50	1.39	10.11	28.08
Lomentaria articulata	0.81	0.01	8.43	1.74	8.97	37.04
Membranoptera alata	0.67	0.05	7.52	1.42	8.00	45.05
Celleporina hassallii	0.72	0.04	7.22	1.90	7.68	52.72
Ramscliff						
Palmaria palmata	1.55	0.00	20.48	1.30	20.80	20.80
Phycodrus rubens	1.27	0.01	14.69	1.87	14.92	35.72
Cryptopleura ramosa	0.88	0.03	10.24	1.14	10.40	46.12
Electra pilosa	0.60	0.01	8.47	1.45	8.60	54.73

Mean values of taxon richness and total biomass were markedly higher for *L. hyperborea,* across both sites and sampling events, compared to *L. ochroleuca* (Fig 3.5). Over the entire study, *L. hyperborea* supported on average >12 times as many taxa and >3600 times as much biomass on its stipes compared with *L. ochroleuca*. Moreover, 55.5% of *L. ochroleuca* stipes were completely devoid of any epiphytic material (compared to 0% for *L. hyperborea*). Univariate PERMANOVA detected a significant interaction between species and event (for total biomass) and between species and site (both metrics), as well as a significant main effect of species and of the covariate (Table 3.1). Pairwise tests for taxon richness returned highly significant differences between species, with the magnitude of dissimilarity being greater at Ramscliff Point (Table 3.2). Pairwise tests for total biomass again detected highly significant differences between species, with the magnitude of dissimilarity being greater in summer compared to spring (Table 3.2). We recorded a significant linear relationship between habitat size and taxon richness for *L. hyperborea* at

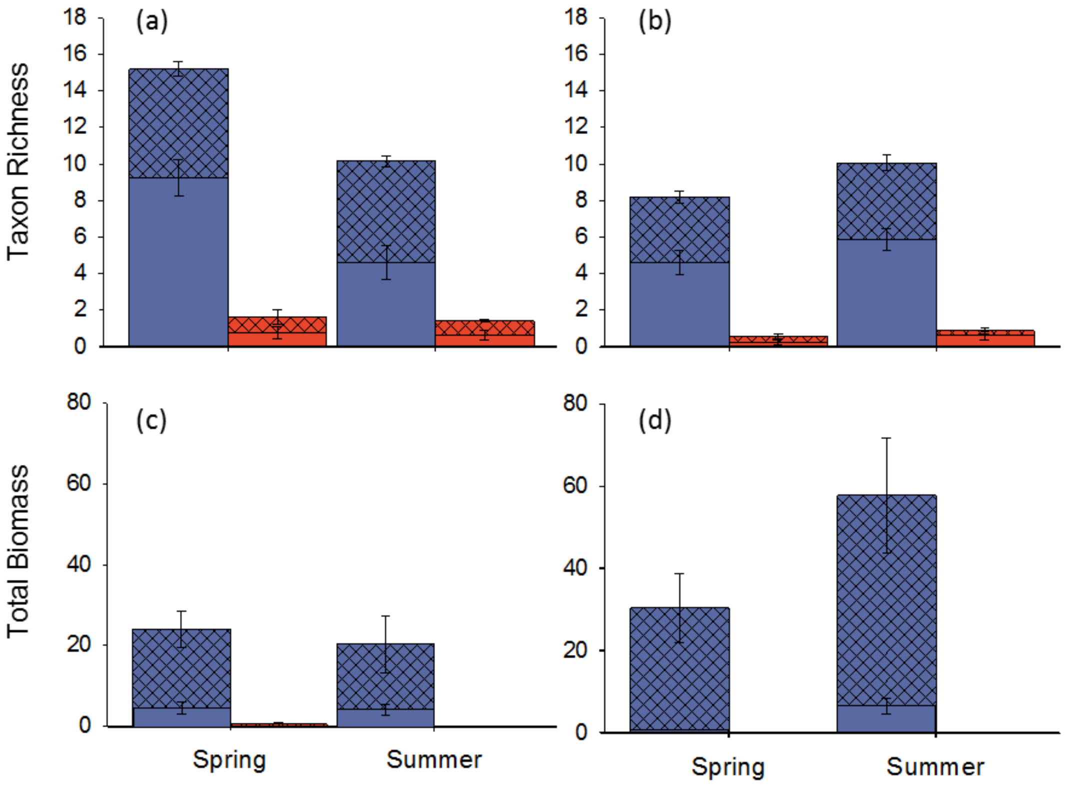


Fig 3.5 Univariate assemblage-level metrics for stipe assemblages: (a) taxon richness at Mewstone, (b) taxon richness at Ramscliff Point, (c) total biomass at Mewstone, (d) total biomass at Ramscliff Point. Blue bars indicate *L. hyperborea*; red bars indicate *L. ochroleuca.* Solid bars indicate sessile faunal assemblage, hashed bars indicate algal assemblage. Values are means of 15 stipes per site/season/species (± S.E).

both sites, with the number of epibiont taxa increasing with increasing stipe surface area, but no such relationships were recorded for *L. ochroleuca* (Fig 3.6).

iv. Holdfast assemblages

From 96 holdfasts, 75 unique taxa of sessile fauna were recorded (64% of all taxa were identified to species level), representing seven phyla. Of these, the Bryozoa were the most speciose (26 species), followed by Chordata (ascidians, 9 species), Mollusca (bivalves, 11 species), Cnidaria (hydroids, 8 species) and Arthropoda (cirripedia, 4 species). Annelida (polychaetes) were identified to family (Serpulidae only), and Porifera were separated into morphospecies based on physical appearance and analysis of spicules (15 distinct taxa). In total 91% of all taxa recorded were found on *L. hyperborea* and 79% were found on *L. ochroleuca*.

PCO plots indicated that holdfast assemblages were far more comparable between host species, although there was some partitioning between species, which was greater at the

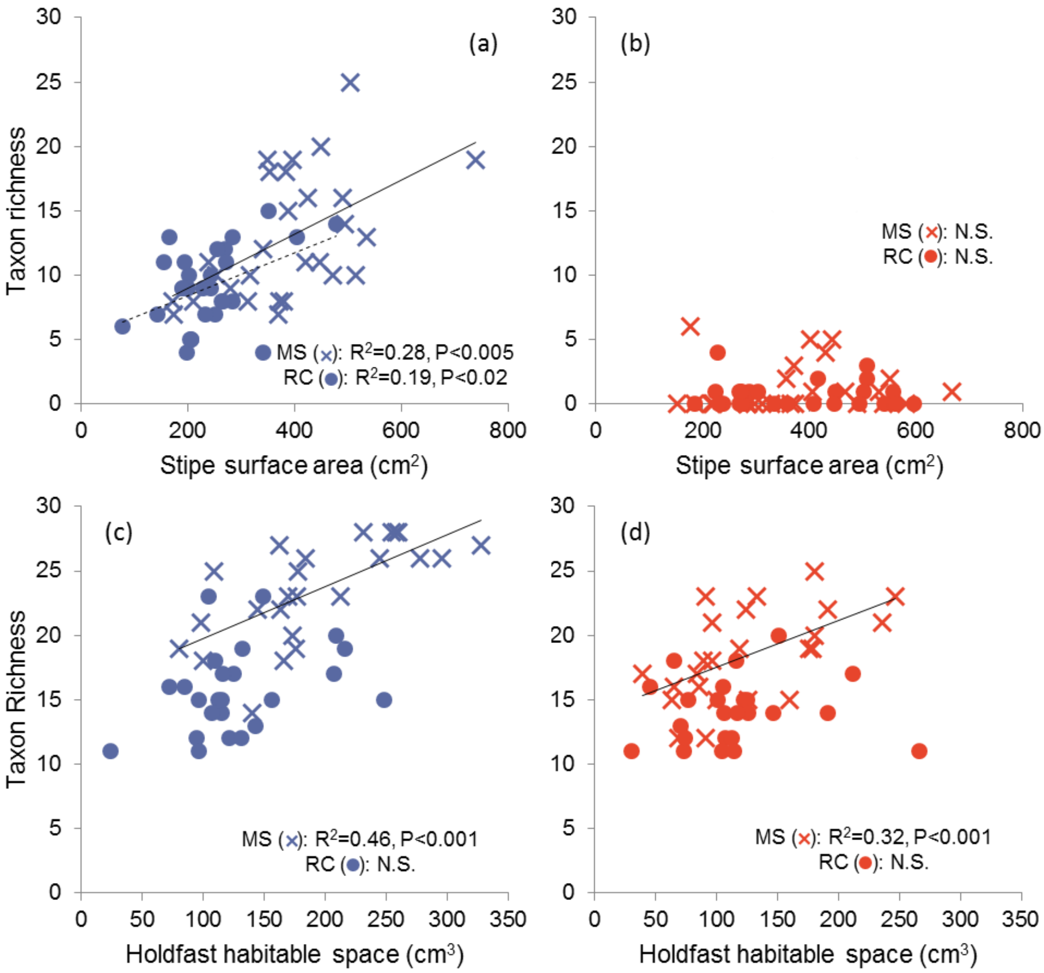


Fig 3.6 Observed relationships between habitat size and taxon richness for both stipe assemblages (a & b) and holdfast assemblages (c & d) for each site and HFS separately. Blue symbols (a & c) indicate *L. hyperborea*; red symbols (b & d) indicate *L. ochroleuca*, crosses represent samples from Mewstone and circles from Ramscliff Point.

Mewstone compared with Ramscliff Point (Fig 3.4). Variability in assemblage structure was also more comparable between host species (Fig 3.4). PERMANOVA again detected a significant 3-way interaction between species, site and event, as well as highly significant variability associated with species as both a main effect and within higher order interactions (Table 3.4). Pairwise tests within the 3-way interaction term showed that differences between species were significant for every combination of site and event, although the magnitude of dissimilarity tended to be greater at the Mewstone than at Ramscliff Point and in summer compared with spring (Table 3.5). PERMDISP found no significant differences in multivariate dispersion between host species, and mean dispersion distances were comparable ($F_{(1,94)}$ = 0.06, p = 0.805, LH = 32.9 ± 0.8, LO = 33.2 ± 0.8).

Table 3.4 (a) Results of multivariate PERMANOVA to test for differences in holdfast assemblage between kelp species (Sp, fixed), sites (Si, fixed) and sampling event (Ev, fixed). Holdfast living space was included as a co-variate (CO) in the analysis. Permutations were based on a Bray-Curtis similarity matrix generated from fourth-root transformed biomass data. Results of univariate PERMANOVA to test for differences in the assemblage-level univariate metrics (a) taxon richness and (b) total biomass are also shown. Permutations for univariate analysis were based on a Euclidean distance similarity matrix generated from untransformed diversity data. All tests used a maximum of 9999 permutations under a reduced model; significant effects (P<0.05) are shown in bold. The first significant lower order effect of interest (i.e. an interaction or main effect involving the species factor, marked with an asterisk) was examined further with pairwise tests (see text and Table 3.5).

Source	*df*	a. Multivariate assemblage structure			b. Taxon Richness			C. Total Biomass		
		MS	Pseudo-F	P	MS	Pseudo-F	P	MS	Pseudo-F	P
CO	1	9675	13.60	**0.002**	834	100.9	**0.001**	396	57.74	**0.001**
Sp	1	3675	5.16	**0.002**	59.8	7.22	**0.008***	40.4	5.88	**0.017***
Si	1	17003	23.91	**0.002**	504	61.00	**0.001**	10.4	1.52	0.234
Ev	1	12258	17.41	**0.002**	37.8	4.57	**0.042**	44.4	6.47	**0.011**
Sp x Si	1	2438	3.42	**0.002**	17.7	2.13	0.154	12.4	1.79	0.221
Sp x Ev	1	1543	2.17	**0.011**	12.6	1.52	0.222	14.0	2.03	0.170
Si x Ev	1	2608	3.66	**0.002**	31.2	3.77	0.052	0.44	0.06	0.813
Sp x Si x Ev*	1	1868	2.62	**0.002***	17.7	2.14	0.146	0.66	0.97	0.749
Residual	87	710			8.30			6.86		
Total	95									

SIMPER analysis indicated that the differences in assemblage structure at the Mewstone were driven primarily by high abundances of demosponge groups (which contributed to ~25% of the observed dissimilarity) and the barnacle *Verruca stroemia* on *L. hyperborea,* compared to *L. ochroleuca* (Table 3.6). Demosponges were also major contributors to the observed dissimilarity between kelp species at Ramscliff Point, although here the barnacles

Table 3.5 Pairwise tests within significant main effects and interaction terms involving the species factor, for holdfast-associated assemblages (see Table 3.4 in main text for outputs of full PERMANOVA). The t and P values relating to the pairwise tests between *L hyperborea* and *L. ochroleuca* are shown for each combination of factors within a significant interaction or main effect. MS= Mewstone, RAM = Ramscliff Point.

Response variable	Site	Event	t	P
Multivariate assemblage	MS	Spring	2.21	0.001
	MS	Summer	2.45	0.001
	RAM	Spring	1.38	0.048
	RAM	Summer	1.89	0.002
Taxon richness	-	-	2.68	0.006
Total biomass	-	-	2.42	0.020

Table 3.6 Percentage contributions of individual taxa to the observed difference in holdfast assemblage structure between each kelp species at each site, as determined by SIMPER analysis.

Species	*L. hyperborea* Av.Abund	*L. ochroleuca* Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Mewstone						
Halicondriidae spp.	0.73	0.23	2.77	1.51	6.18	6.18
Hemedesmiidae spp.	0.64	0.27	2.46	1.43	5.49	11.67
Verruca stroemia	1.03	0.59	2.22	1.40	4.95	16.62
Microcionidae spp.	0.48	0.00	2.15	1.70	4.79	21.41
Mycalidae spp.	0.64	0.59	2.11	1.22	4.70	26.12
Didemnidae spp.	0.72	0.59	1.71	1.17	3.81	29.93
Flat Sponge	0.46	0.37	1.69	1.29	3.77	33.70
Crisia denticulata	0.41	0.19	1.54	1.36	3.43	37.13
Scrupocellaria reptans	0.40	0.26	1.47	1.30	3.28	40.41
Escharoides coccinea	0.78	0.60	1.24	1.31	2.76	43.17
Pomatoceros spp.	0.69	0.58	1.23	1.05	2.74	45.91
Polycarpa pomaria	0.19	0.14	1.21	0.79	2.69	48.60
Anomia sp.	0.59	0.50	1.19	1.10	2.66	51.26
Ramscliff						
Halicondriidae spp.	0.54	0.40	3.02	1.27	6.72	6.72
Balanus crenatus	0.62	0.58	2.57	1.26	5.73	12.45
Hemedesmiidae spp.	0.30	0.34	2.11	1.33	4.69	17.14
Verruca stroemia	0.75	0.56	2.09	1.13	4.65	21.78
Flat Sponge	0.26	0.12	1.84	0.96	4.10	25.88
Escharoides coccinea	0.37	0.49	1.82	1.29	4.06	29.95
Mycalidae spp.	0.30	0.00	1.82	1.27	4.05	33.99
Didemnidae spp.	0.24	0.16	1.76	0.98	3.92	37.91
Celleporina hassallii	0.35	0.34	1.72	1.29	3.83	41.75
Callopora lineata	0.24	0.42	1.71	1.37	3.81	45.55
Pomatoceros spp.	0.56	0.71	1.67	1.09	3.71	49.27
Demosponge E	0.18	0.10	1.55	0.52	3.44	52.71

Balanus crenatus and *Verruca stroemia*, and the bryozoan *Escharoides coccinea* were also important as discriminatory taxa identified by SIMPER as contributing most to the observed differences (Table 3.6). All taxa across both sites, with the exception of *Hemedesmiidae* spp. and *E. coccinea*, were more abundant (in terms of biomass) on or within *L. hyperborea* holdfasts compared with *L. ochroleuca* (Table 3.6).

Mean values of taxon richness and total biomass were markedly higher for *L. hyperborea* than *L. ochroleuca* at the Mewstone, whereas values were more comparable at Ramscliff Point, with the expectation of total biomass in summer (Fig 3.7). Even so, univariate PERMANOVA detected a significant main effect of species on both metrics, with richness and biomass values associated with *L. hyperborea* being greater than *L. ochroleuca* (Table 3.4). At the Mewstone, we recorded significant positive linear relationships between holdfast habitable space and taxon richness for both species, although the strength of this relationship was weaker for *L. ochroleuca* assemblages compared with *L. hyperborea* assemblages (Fig 3.6). Conversely, no significant relationships were recorded at Ramscliff Point for either species (Fig 3.6).

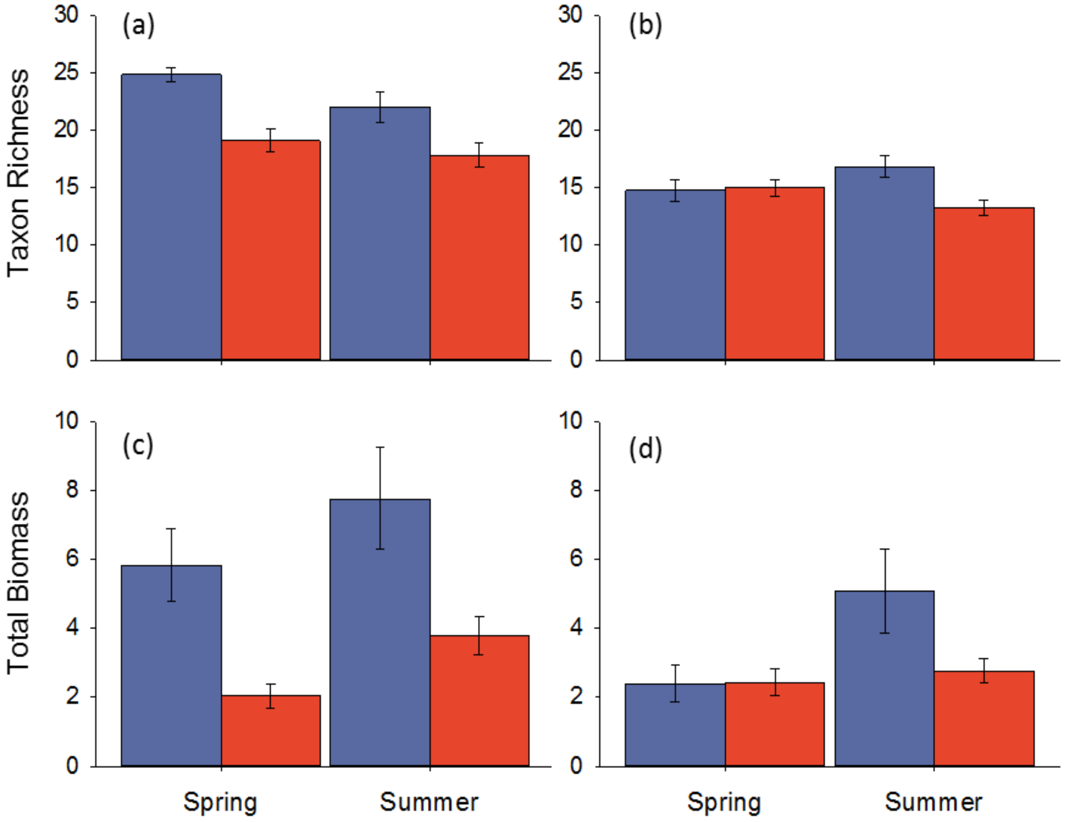


Fig 3.7 Univariate assemblage-level metrics for holdfast assemblages: (a) taxon richness at Mewstone, (b) taxon richness at Ramscliff Point, (c) total biomass at Mewstone, (d) total biomass at Ramscliff Point. Blue bars indicate *L. hyperborea*; red bars indicate *L. ochroleuca.* Values are means of 12 holdfasts per site/season/species (± S.E).

3.5. *Discussion*

Climate change is driving a global redistribution of species and consequent reconfigurations of communities and ecosystems (Scheffers *et al.*, 2016; Pecl *et al.*, 2017). In the marine realm, where species distributions are strongly influenced by temperature, warming has led to a general poleward shift in species' distributions as they track moving isotherms (Parmesan, 1996; Burrows *et al.*, 2011; Wernberg *et al.*, 2011b; Sunday *et al.*, 2012; Pinsky *et al.*, 2013; Poloczanska *et al.*, 2013). While the indirect effects of shifting distributions will vary between species, range shifts involving HFS may have significant consequences for associated communities and ecosystems given that they underpin core ecological processes (Sorte *et al.*, 2010; Smale & Wernberg, 2013; Wernberg *et al.*, 2016). Recent climate change has, either directly or indirectly, driven widespread losses of marine HFS, which in turn has invoked biodiversity declines and community reorganisation (Ling, 2008; Verges *et al.*, 2014a; Thomson *et al.*, 2015; Wernberg *et al.*, 2016). Previous research has focused primarily on the community-level effects of major structural changes, such as climate-driven loss of foundation species (e.g. Smale & Wernberg, 2013; Thomson *et al.*, 2015; Sorte *et al.*, 2017), and much less is known about the wider and perhaps more subtle consequences of replacements of seemingly-similar HFS. Our study, however, has unequivocally demonstrated that climate-driven substitutions of HFS can also result in depleted levels of biodiversity and significant structural changes in associated communities.

We observed striking differences in the structure of sessile assemblages associated with the stipes of *L. hyperborea* and *L. ochroleuca*, the direction and significance (but not magnitude) of which were consistent between sites and sampling events. Differences in holdfast assemblages were less pronounced but still evident. The particularly marked dissimilarity in the structure of stipe-associated assemblages was due to significantly greater richness and biomass values associated with *L. hyperborea* stipes compared with *L. ochroleuca*. While all stipe-associated taxa recorded in the study were found on *L. hyperborea*, only ~50% were found on *L. ochroleuca*, and ~55% of all *L. ochroleuca* stipes sampled were devoid of epibionts altogether. Additionally, the multivariate structure of stipe-associated assemblages differed markedly between host kelp species.

Such pronounced dissimilarity in stipe assemblages was likely driven by subtle differences in the structure of the HFS, including variability in surface roughness, and chemical and mechanical defences. First, the surface topography and texture of the stipe differs between species as *L. ochroleuca* is characterised by a uniformly smooth stipe, whereas the stipe of *L. hyperborea* is rough and pitted. Surface roughness has been shown to play a role in settlement and recruitment of microbial biofilms (Hutchinson *et al.*, 2006), sessile organisms (Köhler *et al.*, 1999) and macroalgae (Harlin & Lindbergh, 1977), to ultimately influence the composition of assemblages. Rough surfaces increase the amount of surface planes available for attachment of macroalgal spores, allow greater penetration by the rhizoids, and reduce the likelihood of removal by wave action, leading to more dense growth of macroalgae on these substrates (see Fletcher & Callow, 1992 and references therein). Sessile invertebrates have been demonstrated to settle ‘preferentially’ in concavities, and more densely on rough surfaces than smooth surfaces (e.g. barnacles; Hills & Thomason, 1996, 1998). Post-settlement mortality has also been shown to be lower for sessile invertebrates settling on rough substrates, where the surface features provide refugia (Walters & Wethey, 1996).

Second, kelps, among other algae, have long been recognised to produce compounds which inhibit the settlement and growth of epibionts (Hornsey & Hide, 1974; Hellio *et al.*, 2001; Goecke *et al.*, 2010). These chemicals function as anti-foulants, and are important in the regulation of biofouling assemblages (Al-Ogily & Knight-Jones, 1977). Exudates from *L. ochroleuca* may inhibit microalgal growth and the attachment and germination of macroalgal spores (Hellio *et al.*, 2000). In contrast, those produced by *L. hyperborea* exhibit few or none of these effects (Hornsey & Hide, 1974).

Third, and last, loss of epidermatic material has been shown as mechanism for the control of epiphytes in some algae (McArthur & Moss, 1977; Sieburth & Tootle, 1981; Moss, 1982), including some species of kelp (e.g. *Lessonia nigrescens*; Martínez & Correa, 1993). This sloughing of the surface of the epidermis in kelps seems to be most active in young, rapidly-growing tissue, and has been suggested as a possible driving factor in gradients of epiphyte growth in some *Laminaria* species (see Russell & Veltkamp, 1984 and references therein). While there is currently no evidence of this occurring in relation to *Laminaria ochroleuca*, it may be a possible cause of the stark differences observed between epibiont assemblages found on the stipes of these species, and requires further research.

Regardless of the underlying mechanisms driving the observed pattern, the marked differences in the biomass and richness of stipe-associated assemblages between the two HFS are likely to be ecologically significant (as shown in Fig 3.1). This is because epiphytic algae colonising kelp stipes represent an important component of temperate reef communities, forming secondary biogenic habitat and increasing overall living space and complexity (Christie *et al.*, 2007; Thomsen *et al.*, 2010). Indeed, epiphytic algae on kelp stipes can support very high abundances of mobile invertebrates such as gastropods, amphipods and polychaetes (Christie *et al.*, 2003; Teagle *et al.*, 2017), which utilise the habitat for both shelter and food (Christie *et al.*, 2007; Leclerc *et al.*, 2013) and are in turn important food sources for high trophic levels, such as fish and lobsters (Norderhaug *et al.*, 2005). In addition, stipe-associated algal assemblages can exhibit high levels of primary productivity in their own right, and may make a substantial contribution to total primary production within the kelp forest (Leclerc *et al.*, 2013), although the importance of this process can vary considerably between locations (e.g. see Pedersen *et al.*, 2014). As such, a net reduction in the amount of kelp-associated epibionts, caused by a decrease in the strength of an important habitat cascade (*sensu* Thomsen *et al.*, 2010), is likely to have significant impacts on wider ecological functioning. If the abundance of *L. ochroleuca* relative to *L. hyperborea* continues to increase at its poleward range edge in response to ocean warming, the strength and direction of both trophic and non-trophic species interactions within the kelp forests community will change, with likely shifts in structure and functioning as a result.

In contrast to stipe-associated assemblages, differences in holdfast assemblages between the HFS were less well defined. Both taxon richness and biomass varied between host kelp species and between sites, as greatest values were recorded for *L. hyperborea* populations at the Mewstone. About 78% of the total number of holdfast taxa recorded were found in association with *L. ochroleuca*, compared to ~91% in association with *L. hyperborea*. The structure, but not the variability, of holdfast assemblages differed between kelp species. The magnitude of variability between sampling events and sites, however, was greater, indicating the importance of both spatial and temporal environmental variability in structuring kelp holdfast assemblages (e.g. Christie *et al.*, 1998; Anderson *et al.*, 2005). The holdfasts of both species are morphologically and structurally very similar, and have similar surface textures, which may account for the similarities between the holdfast assemblages recorded. That said, many sessile taxa including red algae and bryozoans were more abundant on the holdfasts of *L. hyperborea*, providing further evidence of a breakdown of an important facilitative interaction with a climate-driven replacement of a cool-water HFS with a warm-water HFS. The majority of previous research into kelps as HFS has focussed solely on the holdfast structure (Teagle *et al.*, 2017). However, the differences between species observed in this study highlight the importance of considering the plant as a whole, as taking into account variability between microhabitats found within species allowed for more representative comparisons to be made across HFS.

The amount, complexity and structure of habitat provided by HFS influence the composition, abundance and richness of associated assemblages. For example, larger more complex holdfast structures have been shown to support more diverse and abundant invertebrate assemblages (Sheppard *et al.*, 1980). Similarly, larger stipes that provide a greater surface area for colonisation can support a higher biomass of epiphytic algae and, in turn, greater numbers of associated invertebrates (Whittick, 1983). Here, the habitat co-variate (i.e. stipe surface area or holdfast living space) was a consistently significant variable in explaining the observed variability in sessile assemblage structure. For the cool-water HFS*, L. hyperborea*, we observed a general pattern of increasing habitat size, for both stipes and holdfasts, corresponding to increased richness in epibiotic assemblages. However, this pattern was not observed for the warm-water HFS, *L. ochroleuca,* as relationships between habitat size and assemblage metrics were either much weaker (for holdfasts) or not recorded (for stipes). This demonstrates a fundamental breakdown in the facilitative relationship between habitat-former and associated organisms, and again points to inherent differences in the functioning of these kelp species as HFS.

Due to the substantial level of taxonomic work required, our study involved only two sites and events and, as a result, the sampling design and analytical approach did not allow for formal generalisations of the observed patterns across broader spatial or temporal scales. However, anecdotal evidence strongly suggests that the patterns described here are consistent throughout the range of these kelp species, and that replacement of the cool-water HFS by the warm-water HFS will alter local biodiversity patterns. *In situ* observations made by the authors at >10 sites across these species' overlapping distributions in the southwest UK confirm that *L. hyperborea* consistently supports abundant epiphytic assemblages, whereas *L. ochroleuca* is characteristically devoid of epibionts. Similar patterns have been described for each species independently from other locations across their geographical ranges (John, 1969; Christie *et al.*, 2003; Blight & Thompson, 2008; Norderhaug & Christie, 2011), providing further support and allowing for cautious generalisations to be made.

Within the context of biodiversity conservation, kelp forest communities are protected and managed in some parts of the world, as they provide a range of ecosystem services including habitat provision and high rates of primary productivity, as well as being harvested directly for food, alginate and other products (Smale *et al.*, 2013; Vega *et al.*, 2014; Blamey & Bolton, 2017). However, ocean warming is driving shifts in the distributions of many HFS of kelp, with knock-on effects for associated communities and habitat structure. When considering the wider impacts of species range shifts, indirect facilitative effects are often overlooked, despite being prevalent in marine ecosystems (Bruno *et al.*, 2003; Bennett & Wernberg, 2014). Here, the cool-water HFS facilitated the establishment of abundant and diverse sessile invertebrate and algal assemblages, which in turn will provide habitat for associated mobile invertebrates (e.g. Christie *et al.*, 2007; Christie *et al.*, 2009), yet the strength of the facilitative interaction was drastically reduced for the warm-water HFS. As such, the positive facilitative interactions that structure this temperate marine community are indirectly broken down by climate, as the relative abundance of *L. ochroleuca* to *L. hyperborea* has increased in response to ocean warming. Crucially, when considering how communities may change in response to predicted environmental change it is important not only to consider negative interactions, but also positive facilitative interactions, which are often overlooked but prominent in marine ecosystems (Thomsen *et al.*, 2010; Bulleri *et al.*, 2016). Recent rapid ocean warming has caused widespread mortality of marine HFS, including seagrasses (Thomson *et al.*, 2015), corals (Moore *et al.*, 2012) and macroalgae (Smale & Wernberg, 2013; Filbee-Dexter *et al.*, 2016), with consequent loss of biodiversity and shifts in community structure (Wernberg *et al.*, 2016). Climate change is, however, also causing species replacements; our study has shown that substitutions of HFS can also lead to a restructuring of communities and depletion of local biodiversity, despite the HFS seeming functionally similar.

Chapter 4. Climate-driven range expansion of a foundation species leads to the breakdown of a facilitation cascade and altered community structure

4.1. *Abstract*

Climate change can alter ecological communities both directly, by driving shifts in species distributions and abundances, and indirectly by influencing the strength and direction of species interactions. Within benthic marine ecosystems, foundation species often underpin important cascades of facilitative interactions. These include habitat cascades, whereby indirect positive effects on organisms are mediated by the successive formation or modification of biogenic habitat. This study examined the wider impacts of climate-driven shifts in the relative abundances of foundation species within a temperate reef system, with particular focus on an important habitat cascade (i.e. kelp to epiphytic algae to mobile invertebrates). Specifically, we tested whether the warm water kelp *Laminaria ochroleuca,* which has proliferated in line with recent warming trends, facilitates a secondary habitat-former (epiphytic algae) and associated mobile invertebrates, to the same degree as the cold water kelp *Laminaria hyperborea*. The facilitative interaction between kelp and epiphytic algae was dramatically weaker for the warm water kelp species, and resulted in significantly reduced secondary habitat and impoverished associated faunal assemblages. On average, the warm water kelp supported >250 times less epiphytic algae (by biomass) and >50 times fewer mobile invertebrates (by abundance) than the cold water kelp. Moreover, by comparing regions of pre and post range expansion by *L. ochroleuca*, we found that warming-impacted kelp forests supported around half the biomass of epiphytic algae and one-fifth of the abundance of mobile invertebrates, per unit area, compared with unimpacted forests. We also suggest that disruption to this habitat cascade has the potential to impact upon higher trophic levels, specifically kelp forest fishes, through lower prey availability. As climate change drives the redistribution of species and hence reshuffling of communities, shifts in the relative abundances of foundation species may indirectly lead to widespread ecosystem change, through major alteration of ecological interactions. This is, to our knowledge, the first documented example of climate driven disruption to a habitat cascade within a marine ecosystem.

4.2. *Introduction*

Anthropogenic climate change is impacting ecosystems throughout the biosphere. There is considerable evidence demonstrating the effects of climate change on community composition and population structure (Sala *et al*., 2000; Parmesan & Yole, 2003), but it may also induce less obvious changes to ecological processes such as species interactions. The strengths and directions of interactions are influenced by environmental change, given that they are mediated by the behaviour, phenology, physiology, and the relative abundances of multiple species (Tylianakis *et al*., 2008). Benthic marine communities are structured by a range of physical and biological processes, acting across multiple spatial and temporal scales (e.g. Osman, 1977; Richmond & Seed, 1991; Rosenberg *et al*., 1992; Perkol-Finkel & Benayahu, 2009; Bulleri & Chapman, 2010; Airoldi & Bulleri, 2011). Species interactions such as competition (e.g. Connell *et al*., 2004), grazing (e.g. Paine & Vadas, 1969; O'Connor & Crowe, 2005), predation (e.g. Griffin *et al*., 2008), and parasitism (e.g. Sousa & Gleason, 1989) can be of particular importance at local scales and play a key role in the maintenance of biodiversity (Bascompte *et al*., 2006), the mediation of ecosystem responses to global environmental change (Brooker, 2006; Moore *et al*., 2007; Suttle *et al*., 2007), and the stability of ecosystem services (Dobson *et al*., 2006). Historically, the overriding ecological view of the natural world was structured principally by negative species interactions, such as competition and predation (Bruno & Bertness, 2001; Bruno *et al*., 2003). Indeed, the majority of marine ecological research carried out over the last half-century has focused on the importance of competition and predation, as well as physical disturbance and physiological stress, in structuring populations and communities (Boucher, 1985; Bruno *et al*., 2003). More recently however, the influence of positive species interactions (i.e. ‘facilitation’) on population and community level variables have been shown to be at least as important as other factors (Burtness & Callaway, 1994; Burtness & Leonard, 1997; Bruno *et al*., 2003).

Facilitative interactions (first described by Connell & Slatyer, 1977 in the context of succession) are encounters between organisms that benefit at least one of the individuals involved, and harm neither (Stachowicz, 2001). If both species involved derive benefits from the interaction, they are considered ‘mutualisms’ (Stachowicz, 2001). The effects of facilitation on the fitness and performance of individuals, population dynamics, and on community composition and diversity have been shown experimentally (e.g. Callaway, 1995; Bertness & Leonard, 1997; Jones *et al*., 1997; Bruno & Bertness, 2001). Many of the positive interactions that are important in structuring communities relate to ‘habitat modification’ (Stachowicz, 2001), whereby the existence of an organism alters local environmental conditions and resource availability with direct positive effects on other species. For example, large canopy-forming macroalgae (e.g. kelps) form extensive subtidal forests and provide complex habitat for a vast array of associated species (e.g. kelp forests; Teagle *et al*., 2017). As such, foundation species that form or modify habitats (e.g. mussels, corals, kelps) have direct positive effects on associated organisms and are of significant ecological importance (Bruno & Bertness, 2001).

Foundation species can also have indirect positive effects on other organisms via cascading interactions (Thomsen *et al*., 2010). Facilitation cascades are defined as successive interactions in which the positive effects of a secondary facilitator are contingent on the provision or modification of habitat by a primary facilitating species (Altieri *et al*., 2007). Most previous research on positive interactions has focused on habitat formation, with foundation species underpinning a common type of facilitation cascade - the habitat cascade (sensu Thomsen *et al*., 2010) - whereby indirect positive effects on organisms are mediated by the successive formation or modification of biogenic habitat (Thomsen *et al*., 2010). Habitat cascades are prominent within in a wide array of biogeographical contexts and have been documented in a number of terrestrial (Stuntz *et al*., 1999; Ødegaard, 2000; Ellwood *et al*., 2002; Stuntz *et al*., 2002; Ellwood & Foster, 2004; Cruz-Angón & Greenberg, 2005; Cruz-Angón *et al*., 2009) and marine ecosystems globally (Hall & Bell, 1988; Edgar & Robertson, 1992; Martin-Smith, 1993; Bologna & Heck Jr, 1999; Norderhaug, 2004; Christie *et al*., 2007; Thomsen *et al*., 2010; Thomsen *et al*., 2016). Ocean warming associated with anthropogenic climate change is also driving a global redistribution of species as they occupy thermally-favourable habitats (Sunday *et al*., 2012; Poloczanska *et al*., 2013). Shifts in the distributions and relative abundances of foundation species would be expected to have cascading effects on associated species, with significant ramifications for wider biodiversity patterns and trophic linkages.

Kelps are foundation species which dominate subtidal rocky reefs in nearshore marine habitats throughout the worlds temperate and polar regions (Steneck *et al*., 2002). Kelps promote enhanced secondary productivity through the provision of three-dimensional habitat structure, which supports a vast array of marine life, including species of commercial and ecological importance (Teagle *et al*., 2017). As kelps are cool-water species, populations found towards trailing, equatorward range edges are particularly susceptible to seawater warming. As such, several accounts of climate-driven loss of kelp populations has been reported in the past decade (Fernandez, 2011; Verges *et al*., 2014b; Filbee-Dexter *et al*., 2016), with wider consequences for associated biodiversity and ecosystem functioning (Tuya *et al*., 2012; Voerman *et al*., 2013; Wernberg *et al*., 2013; Wernberg *et al*., 2016). In the northeast Atlantic specifically, a number of more northerly distributed kelp species (e.g. Laminaria digitata, *Laminaria hyperborea*, Alaria esculenta) have shown or been predicted to retract at their southern range edge in response to ocean warming (Hiscock *et al*., 2004; Müller *et al*., 2009; Raybaud *et al*., 2013), while more southerly distributed species have increased in abundance at their northern range edge (e.g. *Laminaria ochroleuca*; Smale *et al*., 2015). As different foundation species may support distinct assemblages, any changes in the relative abundances of kelp species may have consequences for associated biodiversity (Blight & Thompson, 2008), and potentially on higher trophic levels (Norderhaug *et al*., 2005). The implications of such shifts in habitat-forming species for ecosystem structure and functioning are almost entirely unknown in marine systems.

Laminaria hyperborea is a boreal species, distributed from northern Portugal to northern Norway, Iceland and the Russian Murmansk coast (Fig 4.1a); it is the dominant habitat-forming kelp on subtidal rocky reef habitat throughout much of the northeast Atlantic. *L. hyperborea* is a large stipitate kelp, which is known to provide extensive habitat to associated assemblages (Christie *et al*., 2003; Christie *et al*., 2009; Teagle *et al*., 2017). *L. hyperborea* also underpins an important habitat cascade (sensu Thomsen *et al*., 2010) by providing living space for an intermediate habitat former (i.e. epiphytic algae) on its stipe (see Whittick, 1983), which subsequently provides habitat space for a diverse array of associated fauna (e.g. gastropods, amphipods). Since the late 1940s, a morphologically similar warm-water species, *Laminaria ochroleuca*, has been increasing in abundance at the poleward limit of its range in the southwest of Britain (Parke, 1948b; John, 1969; Teagle & Smale, in press/Chapter 2), in line with recent ocean warming trends, which is predicted to continue in the future (Assis *et al*., 2017). Typically, moderately wave-exposed subtidal reef sites in this region now support mixed kelp stands of *L. ochroleuca* and the assemblage dominant *L. hyperborea* (Smale *et al*., 2015). *L. ochroleuca* is a Lusitanian species distributed from northern Africa to its northern range limit at the Isle of Lundy in north Devon (Fig 1 a,b). While morphologically similar to *L. hyperborea*, recent evidence suggests that it supports distinct, depauperate assemblages both within its holdfast and on its stipe (Teagle & Smale, in press/Chapter 3). Crucially, it lacks the characteristic intermediate habitat provided by the epiphytic algae attached to the stipes of *L. hyperborea* (Smale *et al*., 2015). This lack of a facilitative effect may lead to the breakdown of an important habitat cascade (Teagle & Smale, in press/Chapter 3), which may in turn influence local

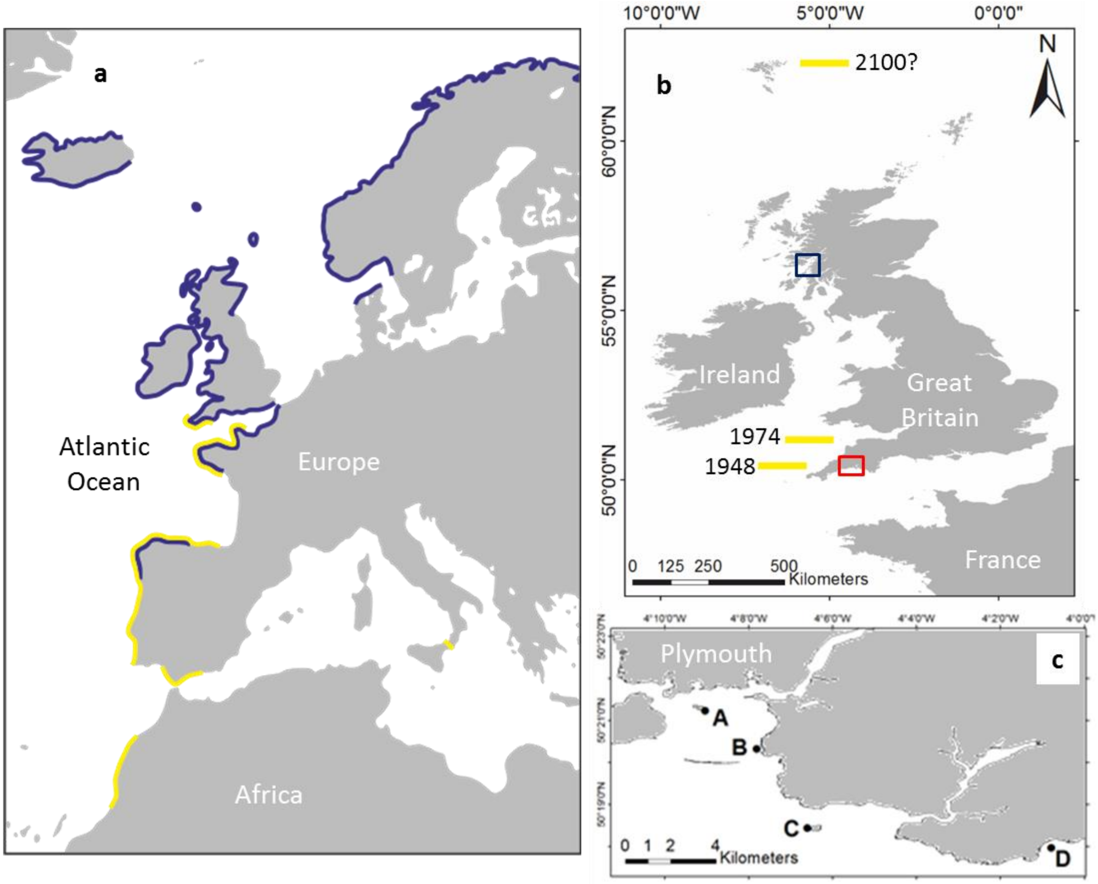


Fig 4.1 Maps indicating (a) the current distributions of *Laminaria hyperborea* (blue) and *Laminaria ochroleuca* (yellow), (b) the spread of *L. ochroleuca* after its first record in the UK in 1948 and the predicted poleward range edge of *L. ochroleuca* in 2100, and (c) the locations of the four study regions within Plymouth Sound, southwest UK: (A) Drakes Island, (B) Ramscliff Point, (C) the northwest Mewstone and (D) Stoke Point. Map (b) also shows the wider location of the study area in the southwest of England (red box), and the comparison region in west Scotland (blue box). The predicted future distribution of *L. ochroleuca* is taken from Assis *et al.* (2017).

biodiversity patterns and, potentially, impact upon higher trophic levels.

The strength of the influence of a climate-driven shift in the relative abundance of habitat-forming kelp species may be dependent on local environmental conditions. Wave exposure in particular has been demonstrated to have a profound effect on the morphology of a number of kelp species (Malloy & Bolton, 1996; Wernberg & Thompson, 2005; Fowler-Walker *et al*., 2006). Morphological changes in response to increased water motion often include strength-increasing adaptations, such as increased stipe length (Smale *et al*., 2016) and increased stipe thickness (Klinger *et al*., 2016). Water movement also increases algal growth by transporting nutrients over algal surfaces (Norderhaug *et al*., 2014), potentially increasing the biomass of epiphytic algae found growing on kelp stipes in exposed conditions. As faunal abundances generally increase with increasing habitat size, a relationship exists between local hydrodynamic conditions and the faunal diversity of communities found in association with kelps (Schultze *et al*., 1990; Christie *et al*., 1998; Christie *et al*., 2003; Anderson *et al*., 2005; Norderhaug *et al*., 2007; Norderhaug & Christie, 2011; Norderhaug *et al*., 2012; Norderhaug *et al*., 2014; Walls *et al*., 2016). As such increased water movement may increase the strength of the facilitative effect for both *L. hyperborea* and *L. ochroleuca*.

The wider consequences of climate-driven shifts in the relative abundances of foundation species were examined, with particular focus on the important epiphytic habitat cascade common within kelp forests. The overall aim was to assess whether climate-driven replacement of a cold-water foundation species with a warm-water congener could cause shifts in local biodiversity and trophic structure. I also looked to ascertain if local environmental conditions (i.e. wave exposure) played a role in the strength of these shifts, by selecting study sites which spanned a gradient of wave exposure. The following specific hypotheses were examined: (1) that the strength of the facilitative interaction between kelp and stipe-associated epiphytic algae is greater for *Laminaria hyperborea* than *Laminaria ochroleuca*, regardless of environmental context (i.e. wave exposure); (2) that decreased secondary habitat provision leads to impoverished, distinct mobile invertebrate assemblages associated with *Laminaria ochroleuca*; and (3) that shifts in the structure or abundance of mobile invertebrate assemblages has the potential to impact upon higher trophic levels (e.g. predatory fish).

4.3. *Methods*

i. Study area

The study was conducted in the southwest of the UK (near Plymouth, England). Here subtidal rocky reefs support mixed, well developed kelp stands comprising *L. hyperborea* and *L. ochroleuca,* which tend to dominate subtidal kelp forests on all but extremely sheltered or exposed coasts. Surveys and collections were conducted at four sites within and just outside of Plymouth Sound (Fig 1c); Drakes Island (site ‘A’), Ramscliff Point (B), northwest Mewstone (C), and Stoke Point (D). The sites spanned a wave exposure gradient from sheltered, within Plymouth Sound which is protected by Plymouth Breakwater, to exposed on open coastline. Site A was the most sheltered site and site D represented the most exposed site. All sites were characterised by extensive gently sloping subtidal rocky reef at depths of 0 to >5 m (below chart datum), characterised by dense kelp canopies.

ii. Kelp canopy structure

The density of the two kelp species was quantified through *in situ* surveys conducted by scuba divers. At each site, ten replicate 1 m^2 quadrats were haphazardly placed within dense kelp stands and the densities (no. m^{-2}) of mature, canopy-forming *Laminaria hyperborea* and *Laminaria ochroleuca* plants were recorded. Surveys were conducted in summer (June-August) 2015 and values obtained (see results) were comparable to previous, more-detailed surveys in the region (Smale & Vance, 2015; Smale *et al.*, 2016; Smale & Moore, 2017) being representative of wider habitat structure. Other canopy-forming macroalgae present included *Saccharina latissimia* and *Saccorhiza polyschides*, which were common but not dominant (Smale & Vance, 2015; Smale & Moore, 2017) and not the focus of the current study.

iii. Sample collection and processing

Five replicate stipe samples were collected from each species in early autumn (i.e. September/October) at each site (40 samples in total). Mature, canopy-forming plants were selected haphazardly from within well-established kelp stands at depths of 2-4 m (below chart datum). Divers removed the blade from selected kelp plants, before immediately enclosing the stipe, its epiphytic assemblage and any associated invertebrate fauna within a fine-mesh cotton bag. The stipe was then removed by cutting immediately above the holdfast and the bag sealed with a cable tie. Individual kelp plants were situated >2 m apart and the 2 species were intermixed. Samples were immediately processed on return to the laboratory. Stipes were carefully removed from the bag and rinsed thoroughly under freshwater to remove all associated mobile fauna, which was collected in a 1 mm sieve. All fauna was transferred to a 70% industrial methylated spirit (IMS) solution for preservation prior to identification. All epiphytic algae was then removed from the stipe (any additional fauna was removed and added to the sample), and weighed (wet weight) to quantify biomass. All mobile fauna was subsequently identified to species level where possible (~74% of taxa) and enumerated. The age of each kelp plant was estimated by counting the number of annual growth rings in the basal section of the stipe sample (Kain, 1963).

iv. Fish stomach contents

During the late summer of 2015, fish were sampled from within dense kelp forests (at sites C&D) using a combination of fyke nets (set by divers) and rod and line fishing. All sampled fish were identified to species, before immediately removing the stomach and digestive tract and transferring them to 70% IMS solution for preservation. Stomach contents were later analysed; the poor condition of many prey organisms allowed for identification only to a high taxonomic level (i.e. order or class) or to a morphological group. The wet weight and abundance of each group was then quantified (abundances of partly-digested prey items were estimated from shell fragments, number of antennae, gnathopods, jaws and other conspicuous remains).

v. Comparison between pre-and post-climate driven range expansion

To examine the likely impacts of continued range expansion of the warm-water kelp *L. ochroleuca* into kelp forests dominated by the cold-water *L. hyperborea*, a space-for-time substitution approach was used by comparing a region which has not yet experienced an incursion of the range expanding kelp ('pre-expanded') with the current study region ('post expanded'). The current northern distribution limit of *L. ochroleuca* is in north Devon in the southwest of the UK, but it is predicted to expand polewards to the north of Scotland by the end of the century (Assis et al 2017, Fig 1b). As such, the west of Scotland was selected as a 'pre-expanded' region in which to examine and compare facilitative interactions and assemblage structure within kelp forests. Subtidal kelp forests in west Scotland were characterised by similar conditions, reef topography and wave exposure to those in sampled near Plymouth (Smale *et al.*, 2016; Smale & Moore, 2017) . However, these kelp forests are yet to be influenced by the infiltration of *L. ochroleuca* and are completely dominated by *L. hyperborea*; they therefore offer an opportunity to compare 'present' with likely 'future' conditions. The overall density of kelps (*L. ochroleuca* and *L. hyperborea*, m^{-2}), the total biomass of stipe associated epiphytic algae (m^{-2}), and the total abundance of epiphyte associated mobile fauna (m^{-2}) were compared between both regions, using identical approaches. Two survey sites from within each region were selected for the comparison; all sites were comparable in wave exposure, substrate type, nutrients and light availability, and grazing pressure, but the regions differed in mean sea temperature (by ~2°C) and the presence of *L. ochroleuca*. Data from west Scotland were collected as part of a wider UK-focussed survey (see Smale & Moore, 2017 for more detail).

vi. Statistical analysis

All analysis was conducted using univariate/multivariate permutational analyses using the PERMANOVA add on (Anderson *et al.*, 2008) for Primer v7 software (Clarke & Gorley, 2015). Variability in assemblage structure was examined using multivariate PERMANOVA using a 2-factor design, with kelp 'Species' (2 levels) and 'Site' (4 levels, representing a gradient in wave exposure) as fixed factors. To examine correlations with habitat size, epiphyte biomass was included as a co-variable in the analysis. Permutations (4999 under a reduced model) were based on a Bray-Curtis similarity matrix constructed from square root transformed abundance data. Pair-wise tests were conducted between Species, within the Site factor, wherever significant interactions were observed ($p < 0.05$). Differences in multivariate dispersion between kelp species was carried out using the PERMDISP routine. Where significant differences in assemblage structure were detected, SIMPER analysis was performed to establish which taxa contributed most to the observed dissimilarity. Univariate metrics (i.e. taxon richness and total biomass) were examined using the same model but with permutations based on Euclidian distances of untransformed data. Univariate habitat metrics (i.e. epiphyte biomass and kelp age) were examined using the same model, but without the co-variable. Kelp density data were converted to the abundance of *Laminaria ochroleuca* relative to the kelp assemblage as a whole (i.e. *L. ochroleuca* + *L. hyperborea*), and was subsequently analysed using a 1-factor design with 'Site' (4 levels) as a fixed factor.

4.4. *Results*

i. Habitat structure

The densities of *L. ochroleuca* and *L. hyperborea* generally varied along the gradient in wave exposure, with *L. ochroleuca* becoming less abundant with increasing wave exposure, and *L. hyperborea* becoming more abundance with wave exposure (Fig 4.2a). The relative abundance of *L. ochroleuca* to *L. hyperborea* thus exhibited a clear trend with wave exposure (Fig 4.2b), being significantly different between sites (PERMANOVA; $F_{3,39} = 31.55$, $P < 0.001$; site B=C, all other sites differed significantly from one another).

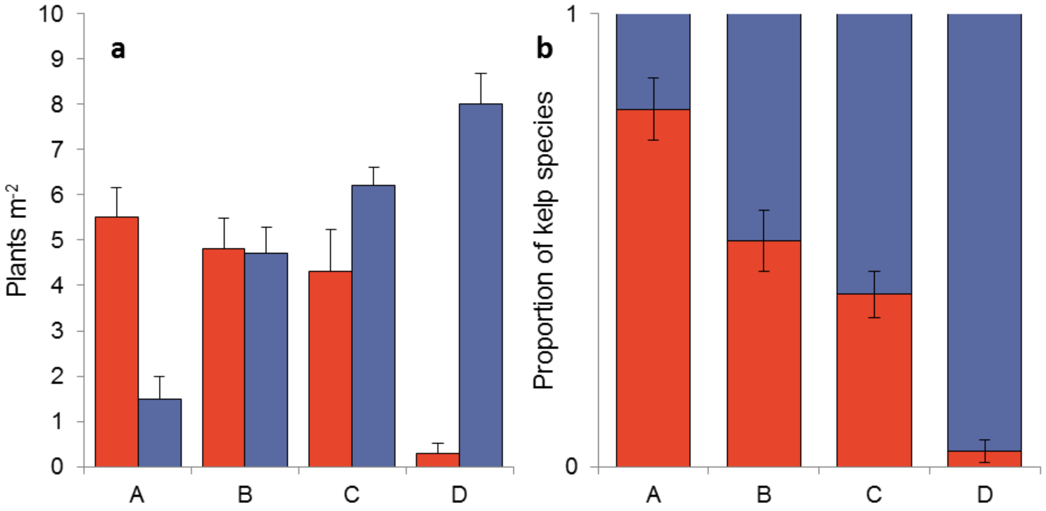


Fig 4.2 Habitat structure of mixed *Laminaria ochroleuca* (red bars) and *Laminaria hyperborea* (blue bars) kelp stands at each site. Density measurements are means derived from 15 x 10 m^2 replicate quadrats at each site. All shown ± SE.

The average age of each species was fairly consistent across sites (Fig 4.3a), although individual plants ranged from 10 (site B) to 4 years (site A) for *L. hyperborea*, and from 7 (site D) to 3 years (sites A & B) for *L. ochroleuca*. *L. hyperborea* plants were significantly older than *L. ochroleuca* plants (Table 4.1). The surface area of stipes was consistent between species, but differed across sites (Table 4.1); stipes of host kelps were generally larger in more wave exposed conditions (site A was statistically different to all others; Fig 4.3b). The total biomass of epiphytic algae differed greatly between kelp species (Fig 4.3c), as the average biomass of epiphytes associated with *L. hyperborea* was >50g per plant at all study sites. In stark contrast, *L. ochroleuca* was devoid of any epiphytes at all but the most exposed site. The epiphytic biomass associated with *L. hyperborea* was significantly greater, this pattern being consistent across sites (Table 4.1).

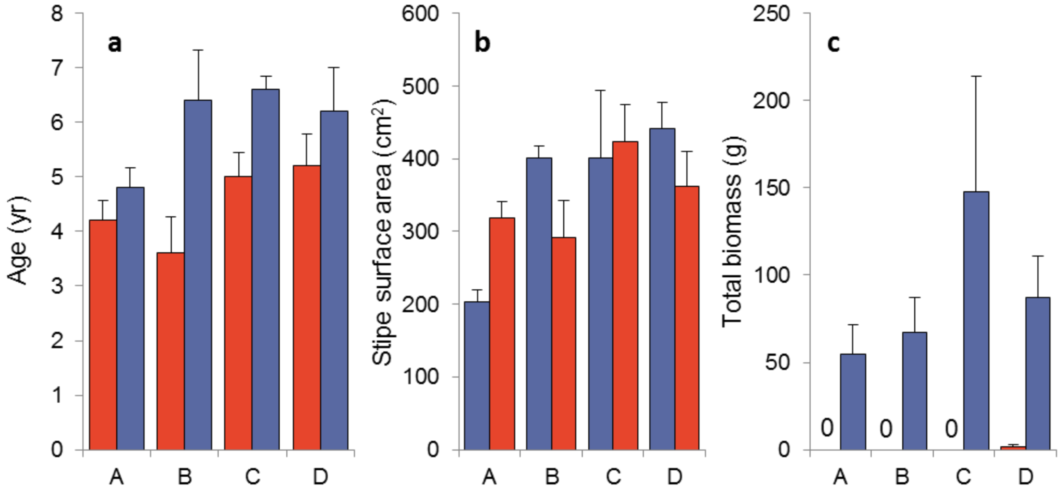


Fig 4.3 Habitat structure provided by *Laminaria ochroleuca* (red bars) and *L. hyperborea* (blue bars): (a) kelp age, (b) stipe surface area, and (d) total biomass of epiphytic algae**.** All values are means derived from 5 replicate stipes per species, per site. All are shown ± SE.

Table 4.1 Results of the univariate PERMANOVA to test for differences in assemblage-level univariate habitat metrics (a. kelp age, b. stipe surface area and c. epiphyte biomass). Permutations were based on a Euclidean distance similarity matrix generated from untransformed data. All tests used a maximum of 4999 permutations under a reduced model; significant effects (P<0.05) are shown in bold.

Source	**a. Kelp age**			
	df	MS	*F*	P
Site	3	3.7667	2.122	0.128
Species	1	22.5	12.68	**0.001**
Site x Species	3	2.3	1.296	0.309
Residual	32	1.775		
Total	39			
	b. Stipe surface area			
Site	3	48097	4.151	**0.013**
Species	1	1670.4	0.144	0.694
Site x Species	3	25846	2.231	0.109
Residual	32	11587		
Total	39			
	c. Epiphyte Biomass			
Site	3	4281.4	1.222	0.313
Species	1	78854	22.51	**0.001**
Site x Species	3	4289.5	1.2241	0.357
Residual	32	3504.1		
Total	39			

ii. Assemblage structure

In total, 2430 individuals representing 73 taxa from 6 phyla were recorded from the 40 stipe samples (20 per species; Appendix 2). Over 70% of taxa identified were recorded exclusively in association with *L. hyperborea*. In contrast, only ~2.5% of taxa were recorded exclusively in association with *L. ochroleuca*. The overall assemblage was dominated by amphipods (26 taxa), which made up >35% of the total fauna recorded. Polychaete worms (14 taxa) and gastropod molluscs (11 taxa) were also well represented. The remainder of the assemblage was made up of pycnogonids (5 taxa), decapods (4 taxa), isopods (4 taxa), chitons (2 taxa), brittlestars (2 taxa), mysids (1 taxa), bivalve molluscs (1 taxa), starfish (1 taxa), Platyhelminthes (1 taxa) and nemertea (1 taxa). Nearly 50% of *L. ochroleuca* stipes were devoid of all invertebrate fauna.

The total abundance of mobile invertebrates ranged from 19 to 375 per stipe and 0 to 25 per stipe for *L. hyperborea* and *L. ochroleuca*, respectively. Mean abundance values were consistently markedly higher for *L. hyperborea* assemblages compared with *L. ochroleuca* (Fig 4.4a). Univariate PERMANOVA detected a significant Site x Species interaction term (Table 4.2), as the magnitude of difference between the kelp species was lower at site D (but still significant). The main effect of species and the covariable (epiphyte biomass) were highly significant (Table 4.2). Taxon richness varied from 8 taxa to 29 taxa per stipe for *L. hyperborea* stipes, and from 0 taxa (9 stipes) to 9 taxa for *L. ochroleuca* stipes. Again,

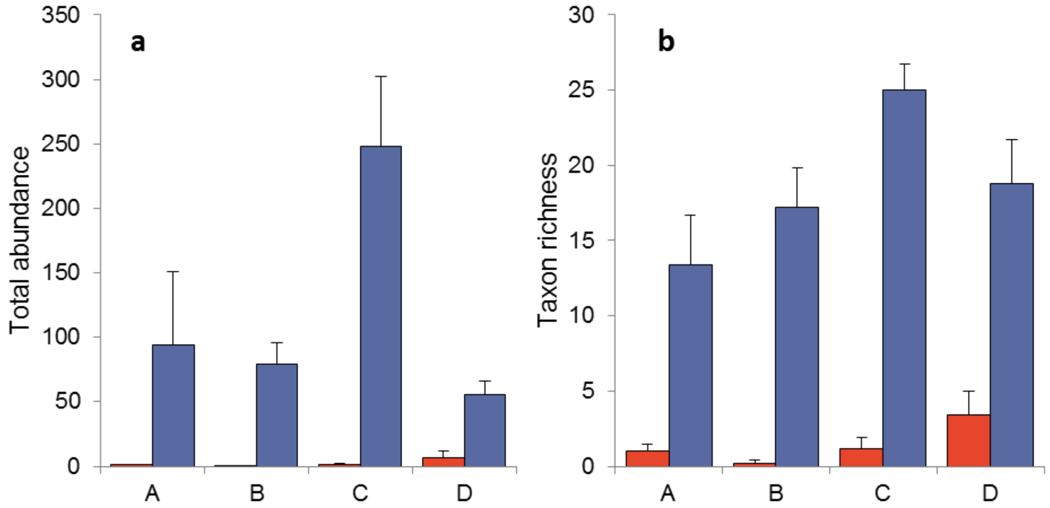


Fig 4.4. Univariate assemblage-level metrics for stipe assemblages: (a) total faunal abundance and (b) mean taxon richness. Red bars indicate *Laminaria ochroleuca*, blue bars indicate *Laminaria hyperborea*. Values are means of 5 replicate stipes per species, per site (±SE).

Table 4.2 Results of univariate PERMANOVA to test for differences in assemblage level univariate metrics in assemblage structure between sites (fixed) and kelp species (fixed); (a) total abundance and (b) taxon richness. Permutations for all univariate analysis were based on a Euclidean distance similarity matrix generated from untransformed diversity data. Results of multivariate PERMANOVA to test for differences in assemblage structure using the same model are also shown (c). Permutations for multivariate analysis were based on a Bray-Curtis similarity matrix generated from square-root transformed abundance data. Epiphyte biomass was included as a covariable in all analysis. All tests used a maximum of 4999 permutations under a reduced model; significant effects (P<0.05) are shown in bold.

Source	**a. Total Abundance**			
	df	MS	*F*	P
Epiphyte Biomass	1	191150	54.90	**0.001**
Site	3	7937	2.280	0.088
Species	1	23990	6.890	**0.013**
Site x Species	3	12263	3.521	**0.021**
Residual	31	3482.1		
Total	39			
	b. Taxon Richness			
Epiphyte Biomass	1	1901.7	96.74	**0.001**
Site	3	9.562	0.487	0.681
Species	1	1314.2	66.86	**0.001**
Site x Species	3	38.337	1.950	0.128
Residual	31	19.657		
Total	39			
	c. Assemblage Structure			
Epiphyte Biomass	1	22180	18.62	**0.001**
Site	3	4648.7	3.902	**0.001**
Species	1	31846	26.73	**0.001**
Site x Species	3	3281.4	2.754	**0.001**
Residual	31	1191.5		
Total	39			

mean taxon richness values were notably higher for *L. hyperborea* assemblages compared with *L. ochroleuca* (Fig 4.4b). At site D, for example, *L. hyperborea* supported ~5.5 times as many taxa as *L. ochroleuca*. Taxon richness associated with *L. hyperborea* was significantly higher than *L. ochroleuca*, which was consistent across the study (Table 4.2).

Principal component ordination (PCO) plots indicated clear partitioning in multivariate assemblage structure between host species, with some small degree of convergence only evident at the most exposed site (site D; Fig 4.5a). PCO also indicated partitioning between sites, with a gradient evident between the most sheltered and most exposed sites (Fig 4.5a). PERMANOVA detected a significant Site x Species interaction (Table 4.2), suggesting that magnitude of difference between species was not consistent between sites. Pairwise

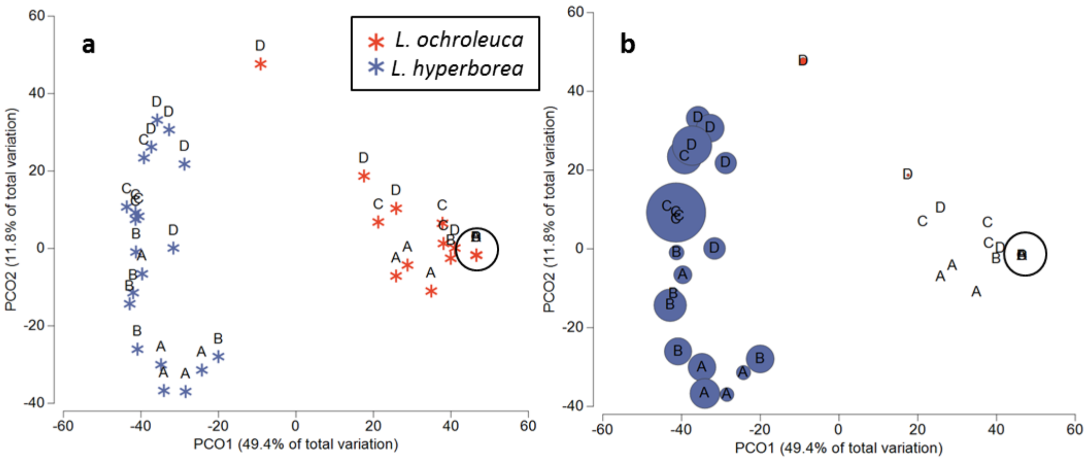


Fig 4.5 Principal component ordinations depicting the structure of stipe assemblages (a), and overlaid with bubbles representing epiphyte biomass (b). Red points indicate *Laminaria ochroleuca* assemblages, and blue points indicate *L. hyperborea* assemblages. Labels indicate site. Circles enclose samples devoid of any faunal assemblage.

tests within the interaction term showed that assemblages associated with *L. hyperborea* were statistically distinct from those associated with *L. ochroleuca* at all sites; but the magnitude of dissimilarity was lower at site D. The main effects of species and site were highly significant (Table 4.2). The co-variable, epiphyte biomass, was significantly correlated with assemblage structure (Table 4.2), and bubble plots overlaid onto the PCO plot showed how partitioning in assemblage structure was related to epiphytic biomass. PERMDISP showed no significant differences between sites in within-factor multivariate dispersion ($F_{3,36}$ = 0.76, P = 0.45). SIMPER analysis was used to identify which taxa were the principal contributors to the observed dissimilarity in assemblage structure between the kelp species. The dissimilarity in epiphytic assemblage between kelp species was consistently related to lower abundances of key taxa recorded on *L. ochroleuca* stipes compared with *L. hyperborea* stipes (Table 4.3).

iii. Fish stomach contents

From the 19 fish stomachs analysed, 10 higher taxonomic groups (class or order), and 6 morphological groups were identified (Table 4.4). Prey items were largely comparable across fish species. The exception was *Labrus bergylta* (Ballan wrasse), which fed more heavily on gastropods compared with the other species (Table 4.4). Generally, the groups

Table 4.3 Percentage contributions of individual taxa to observed differences in mobile stipe assemblages between species, as determined by SIMPER analysis. Letters following species names indicate higher taxonomic denominations (P = polychaete, N = nemertean, A = amphipod).

Species	Av. abund **L. ochroleuca**	Av. abund **L. hyperborea**	Av. diss	Diss/SD	Contrib%	Cum%
Eusyllis blomstrandi P	0.00	2.84	7.62	1.76	7.83	7.83
Platynereis dumerilii P	0.05	2.09	7.02	1.03	7.21	15.04
Nemertea spp. N	0.00	2.54	6.83	2.23	7.02	22.06
Odontosyllis spp. P	0.00	1.96	6.70	1.25	6.89	28.95
Jassa spp. A	0.05	2.79	6.44	1.43	6.62	35.57
Myrianida spp. P	0.00	1.88	4.99	1.07	5.13	40.70
Apherusa bispinosa A	0.00	1.65	4.34	1.08	4.46	45.16
Corophium acutum A	0.00	1.33	3.97	0.84	4.08	49.23

observed in the fish stomachs reflected the dominant taxa sampled in the stipe-associated assemblages, with high abundances of decapods, gastropods, gammerid and caprellid amphipods, and isopods observed in both instances.

iv. Comparison between regions, pre-and post-expansion of Laminaria ochroleuca

The density of kelp plants per square metre was comparable across regions (Plymouth: 10 plants m^{-2}; Scotland: 9 plants m^{-2}; Fig 4.6 a). *L. ochroleuca* comprised ~45% of the plants recorded across both sites in southwest England. The total biomass of stipe-associated epiphytes varied dramatically between regions, with almost twice the amount of epiphytic algae (per unit area) recorded in Scotland (Fig 4.6 b). Differences in the abundance of mobile faunal assemblages were even more pronounced, with total abundances (per unit

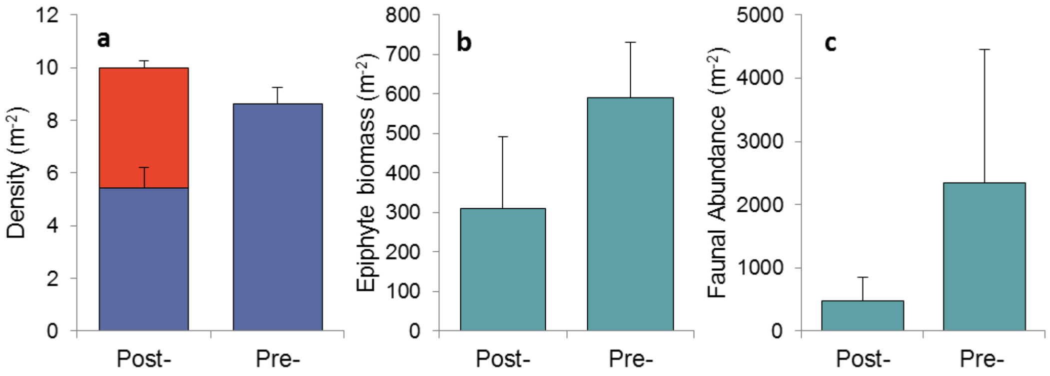


Fig 4.6 Comparison between regions post- and pre-expansion of *Laminaria ochroleuca* in the UK: (a) density of kelp plants, (b) epiphyte biomass, and (c) the abundance of mobile invertebrates per unit area within each region. Red bars indicate *Laminaria ochroleuca*, blue bars indicate *Laminaria hyperborea*, teal bars indicate combined values for the kelp stand (all shown ± SE).

Table 4.4 Results of fish gut analysis from fish caught at kelp dominated sites in Plymouth Sound. Figures represent biomass values (g); figures in parentheses represent abundance values.

Species	*Pollachius pollachius*(Pollock)						*Labrus bergylta* (Ballan Wrasse)							*Labrus mixtus* (Cuckoo Wrasse)				*Symphodus melops* (Corkwing Wrasse)	*Ctenolabrus rupestris* (Goldsinny Wrasse)
Fish #	1	2	3	4	5	6	1	2	3	4	5	6	7	1	2	3	4	1	1
Decapoda	<0.001 (1)	<0.001 (1)	1.818 (1)		0.809 (1)		0.216 (4)	2.175 (22)	0.289 (4)		0.141 (1)		3.921 (1)		1.650 (1)	1.166 (2)	0.293 (1)	<0.001 (1)	0.081 (1)
Gastropoda							1.359 (156)	0.655 (115)	0.062 (22)	0.018 (5)		0.334 (1)							
Bivalvia								0.011 (3)	<0.001 (1)										
Polychaetea				0.002 (1)		0.003 (1)	0.015 (2)	<0.001 (1)	0.011 (1)										0.029 (1)
Cephalopoda		1.786 (1)																	
Gammaridae	0.008 (4)	<0.001 (1)	0.004 (4)		0.047 (14)	0.019 (5)	0.016 (12)	0.017 (21)	0.009 (16)	0.049 (9)		0.002 (3)		0.041 (1)					
Caprellidae	<0.001 (1)				0.394 (113)														
Isopoda	0.007 (2)					0.219 (11)	0.008 (7)	0.002 (5)	0.017 (1)	0.001 (1)									
Caridea								0.004 (1)	0.007 (2)										
Mysida	0.106 (19)	0.008 (2)	0.066 (6)				0.004 (1)												
Decapod larvae	0.004 (1)		<0.001 (1)															<0.001 (1)	
Fish part				0.005 (1)															
Crustacean part					0.108 (1)	0.272 (1)				1.280 (3)									
Digested material			0.532				0.202	0.859	0.608								0.039		
Algae	0.003	0.002					0.066	0.091	0.016						0.006				
Detritus		1		0.217		0.289				0.637	0.411		1.003						0.0212
Unidentified				0.064 (1)															

area) in the pre-expansion region ~5 times greater than that in the post-expansion region (Fig 4.6 c).

4.5. Discussion

i. Consequences of climate-driven shifts for epiphytic assemblages

Climate-driven shifts in the distribution and abundance of habitat-forming macroalgae can significantly alter the structure and functioning of coastal marine ecosystems (Fernandez, 2011; Smale & Wernberg, 2013; Voerman *et al.*, 2013; Wernberg *et al.*, 2013; Wernberg *et al.*, 2016). The vast majority of evidence-to-date, however, has focussed on the loss of foundation species. This study has demonstrated how subtle shifts in the abundance of superficially similar species can have significant impacts on local biodiversity patterns, through weakening of a facilitative interaction, with potential ramifications for higher trophic levels. A recent increase in the abundance of *Laminaria ochroleuca* relative to *Laminaria hyperborea*, which aligns with recent warming trends, has disrupted an important habitat cascade associated with the stipe-epiphyte complex, leading to significantly reduced secondary habitat and impoverished faunal assemblages (Fig 4.7). Reductions in faunal abundances may limit the quantity of available prey items, with potential impacts on kelp forest fishes (Fig 4.7).

Kelp forests support high biodiversity in coastal marine ecosystems (Teagle *et al.*, 2017). A number of recent studies have compared habitat provision by different species, and have shown that different species host distinct assemblages (e.g. Blight & Thompson, 2008; Tuya *et al.*, 2011; Teagle & Smale, in press/Chapter 3). Our results corroborate previous observations. The mobile macro-invertebrate assemblages associated with *L. hyperborea* and *L. ochroleuca* stipes differed dramatically: of the 2430 individual fauna recorded throughout the study, over 98% were found in association with *L. hyperborea*. On average, each *L. hyperborea* stipe hosted ~120 individuals representing ~17 taxa, whereas *L. ochroleuca* hosted just over 2 individuals representing ~1.5 taxa per plant. We recorded a study-wide richness value of 73 taxa, comparable to the richness of mobile fauna found in holdfasts in the same region (Teagle et al., in press/Chapter 2). This was generally lower than the values reported for *L. hyperborea* stipe/epiphyte associated mobile fauna in Norway (Christie *et al.*, 2003; Jorgensen & Christie, 2003), and with other macrophyte habitats (e.g. seagrass meadows; Edgar & Robertson, 1992; Como *et al.*, 2008).

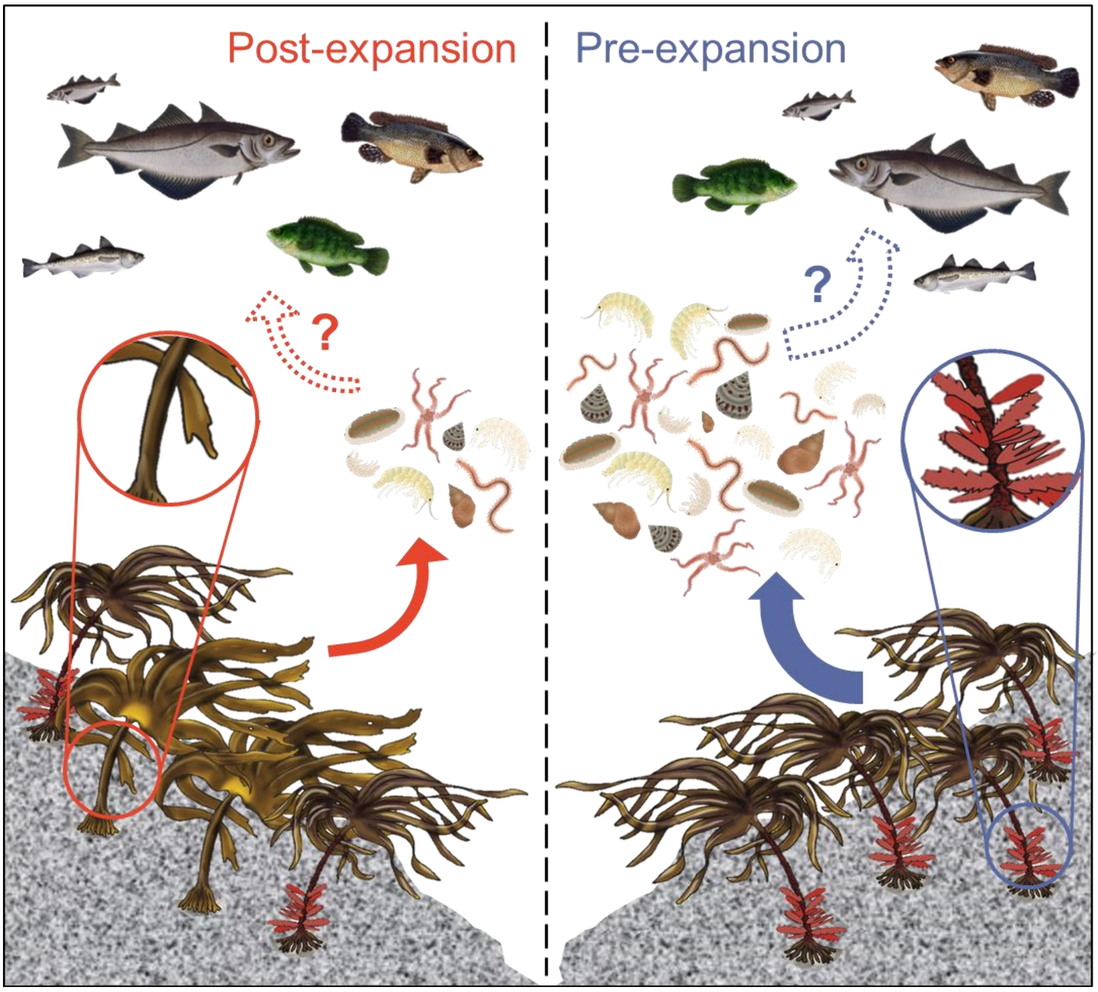


Fig 4.7 Habitat cascades in kelp forests in the northeast Atlantic, post- and pre-expansion of the warm water kelp *Laminaria ochroleuca*. An increase in the abundance of *L. ochroleuca* relative to *L. hyperborea* is likely to reduce the extent of secondary epiphytic habitat available for colonisation, and therefore reduce the abundance of faunal assemblages. Higher trophic levels, such as predatory fish, may be subsequently affected. Macrofaunal symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/). Kelp symbols courtesy of Jack Sewell.

The secondary habitat provided by epiphytic algae on kelp stipes has been shown to facilitate the development of highly diverse and abundant faunal assemblages (Christie, 1995; Christie *et al.*, 2003). Epiphyte biomass varied dramatically between species and 90% of *L. ochroleuca* stipes were devoid of any epiphytic material. The study-wide total abundance of epiphytes found in association with *L. hyperborea* was 1783 g, over 250 times greater than those observed on *L. ochroleuca* (which, study-wide, hosted just 7 g). The magnitude of dissimilarity observed here is greater than that of previous preliminary comparisons between these species (e.g. Smale *et al.*, 2015). The marked difference in epiphyte biomass observed between these kelp species is likely to underpin the observed variation in associated invertebrate assemblage structure, and in particular the depauperate assemblage associated with *L. ochroleuca*.

ii. Environmental context

Ecological interactions are mediated by the environmental context in which they occur (Sanford, 1999; Harley *et al.*, 2012). In the current study, the strength of the facilitative interaction between kelps and stipe-associated epiphytic algae differed between sites along the wave exposure gradient. With regards to *L. hyperborea*, the biomass of epiphytes and the taxon richness (and to a lesser extent, the total abundance) of associated assemblages all followed a similar pattern, with the highest values recorded in the intermediately exposed site (site C), and the lowest values found in the most sheltered site (site A). In contrast, only at the most exposed site did *L. ochroleuca* host low epiphytic biomass; being devoid of epiphytic material at all sites of less exposure. The structure of assemblages associated with *L. ochroleuca* seem to reflected this, with the highest taxon richness and total abundance of mobile faunal assemblages for *L. ochroleuca* found at the most exposed site (site D).

Although formal generalisations are difficult due to a lack of replication across levels of wave exposure, it was likely an important driver of epiphytic algal assemblages and, consequently, stipe associated mobile invertebrate assemblages, aligning with previous work (Christie *et al.*, 2003; Andersen, 2007; Norderhaug & Christie, 2011). An increase in the biomass of epiphytic algae with increasing wave exposure may be due to elevated resource availability because: (i) light penetration through the overlying canopy is enhanced by water movement (e.g. in *Macrocystis pyrifera* forests; Wing *et al.*, 1993); (ii) transport of nutrients across algal surfaces is facilitated by water motion, leading to increased growth rates (Norderhaug *et al.*, 2014); and (iii) biogenic habitat space may be enhanced due to morphological responses of the kelps themselves to increased wave exposure (Pedersen *et al.*, 2014; Smale *et al.*, 2016). Moreover, while the export of mobile fauna from kelp forests can be high (Waage-Nielsen *et al.*, 2003), epiphytic algae can provide shelter from wave action (Fincham, 1974; Fenwick, 1976). Epiphyte associated invertebrate assemblages are relatively resilient to wave action, with amphipod populations (making up a third of the total assemblage recorded here) able to cope with a loss of 1 – 2% of total abundance without experiencing a sustained reduction in population size (Christie & Kraufvelin, 2004). As such, an increase in faunal abundance along a wave exposure gradient suggests that such loss of fauna is offset by other factors linked to habitat availability and faunal fitness (Norderhaug & Christie, 2011). It is clear, however, that despite the environmentally-driven variation in epiphyte biomass and faunal assemblage within both species, the facilitative interaction between kelp and epiphytic algae is consistently stronger for *L. hyperborea* compared to *L. ochroleuca,* regardless of environmental context.

iii. Trophic consequences

It has long been recognised that kelp forests provide critically-important habitat for a number of coastal fish species, which utilise these habitats as nursery and feeding areas and as refugia from predation (Bodkin, 1988; Norderhaug *et al.*, 2005; Reisewitz *et al.*, 2006). Kelp forest extent and condition have been positively linked with local fisheries production (Bertocci *et al.*, 2015). There is strong evidence to suggest that fish in kelp forests feed heavily on kelp associated fauna (Fredriksen, 2003; Norderhaug *et al.*, 2005). Stable isotope analysis has shown that fish, despite their high mobility, feed extensively within kelp forests (Norderhaug *et al.*, 2005; Leclerc *et al.*, 2013). Despite the low taxonomic resolution of the fish gut contents presented in this study, the main groups recorded aligned closely with those found associated with the stipe-epiphyte complex (primarily of *L. hyperborea*), and a number of well represented species are known to constitute a high proportion of the diets of kelp forest fish (e.g. *Jassa* spp., *Ampithoe* spp., Caprellid amphipods, and *Rissoa* spp. gastropods; Norderhaug *et al.*, 2005). It is reasonable therefore to suggest that the fish gut content data collected in this study support the assertion that the fish were probably feeding within the kelp forests they were sampled from. Likewise, the accessible, exposed nature of the stipe-epiphyte assemblage to predatory fish, in contrast to holdfast or epilithic algal assemblages, and the high abundance of fauna within these assemblages would suggest that they enhance prey availability for kelp forest fish. Stable isotope analysis has demonstrated that both kelp forest macro-invertebrates and fish are dependent on kelp-derived carbon (Fredriksen, 2003), suggesting that the habitat cascade underpinned by *L. hyperborea* provides a key pathway for kelp forest production from kelp, through associated macro-invertebrates to higher trophic levels (Norderhaug *et al.*, 2005). However, further experimental work is required to reveal trophic pathways within these systems and to determine the magnitude of impacts caused by the disruption of this important habitat cascade.

iv. Future patterns

Shifts in the structure and functioning of kelp forests in the northeast Atlantic are predicted to occur throughout the coming century in response to ocean warming (Brodie *et al.*, 2014; Assis *et al.*, 2017). By comparing the current state of kelp forests in regions where *L. ochroleuca* has proliferated with those in regions where it does not yet occur, we can gain some insight into potential impacts of this species substitution at a broader scale. While the total densities of kelp plants were similar between both study regions, almost half of the assemblage recorded in the post-expanded region comprised *L. ochroleuca*. The lower relative abundance of the cold-adapted *L. hyperborea* led to a per unit area reduction in the biomass of epiphytic algae of ~50%. This, when scaled up to the total areal extent of these forests (up to 16,000 km^2 in the UK alone, see Yesson *et al.*, 2015), would represent a significant loss of secondary habitat. The reduction in epiphytic algal biomass also had a considerable impact on mobile invertebrate abundances and the structure of faunal assemblages, with those in post-expanded regions supporting 5 times fewer mobile invertebrates per unit area than those in pre-expanded regions. The magnified effect of a reduction in the quantity of secondary habitat underlines the importance of indirect positive effects to the habitat provision by kelps in temperate marine ecosystems. With further range extensions expected for *L. ochroleuca* populations (Assis *et al.*, 2017), and contrasting range retractions predicted for *L. hyperborea* (Assis *et al.*, 2016; Assis *et al.*, 2017), the weakening of these facilitative interactions and the subsequent impacts to local biodiversity patterns and trophic linkages are likely only to be exacerbated in the near future. Crucially, the structural role of kelp forests in supporting biodiversity, and the trophic functional benefits for fish species, may both be diminished following continued climate-driven reshuffling of kelp habitat composition.

v. Concluding remarks

Kelps are key foundation species in temperate marine ecosystems, playing a major role in the structuring and regulation of local biodiversity patterns (see Teagle *et al.*, 2017 and references therein). As the distribution of kelp species is ultimately constrained by temperature at geographic scales, climate change is likely to play an important role in the structure and functioning of these habitats by driving shifts in the geographic ranges of kelp species (Fernandez, 2011; Verges *et al.*, 2014b; Filbee-Dexter *et al.*, 2016). Our study highlights how the indirect effects of climate-driven shifts in kelp forest composition may manifest as disruption to an important habitat cascade, as kelp forests become less dominated by *L. hyperborea*. Overall, kelp forests once dominated by *L. hyperborea* and now within the potential range of expansion of *L. ochroleuca* host a depauperate associated faunal assemblage compared with those still dominated by *L. hyperborea*; thus hypotheses 1 and 2 can be accepted. Such major shifts in local biodiversity patterns will likely have ramifications for higher tropic levels supporting hypothesis 3. More focused research is required, however, to understand the magnitude of this effect, by pinning down the feeding behaviour and prey preference of fish within these kelp forests. Our study also underlines the importance of positive, facilitative interactions when investigating the impact of apparently minor shifts in community structure of species providing biogenic structure and secondary habitat.

Chapter 5. Climate-driven extinction scenario reveals how loss of marine foundation species leads to altered community structure and biomass dynamics on temperate rocky shores

5.1. *Abstract*

Kelps represent ecologically important foundation species and play a critical role in structuring nearshore temperate habitats. They provide extensive substrata for colonising organisms, generate three-dimensional habitat for a vast array of marine organisms, and ameliorate environmental conditions for understorey assemblages. *Laminaria digitata* is the dominant intertidal kelp species throughout much of the north Atlantic, where it exhibits a predominantly northerly, cold water distribution. Observations and predictions indicate that marginal populations of *L. digitata* along the coastline of Western Europe are on the verge of local extinction due to increasing sea water temperatures associated with climate change. The ecological consequences of the loss of this foundation species on temperate rocky shores are, however, unknown. Here we conducted a 2.5 year-long manipulative field experiment to test whether a loss, or reduction, in the density of *L. digitata* at its equatorward range edge drives significant changes in the structure of intertidal algal assemblages. We observed a shift in dominance to the annual pseudo-kelp *Saccorhiza polyschides* on a wave exposed shore, while on a more wave sheltered shore the impact was mitigated by the presence of the perennial kelp, *Saccharina latissima*. Critically, the overall standing stock of algal assemblages on intertidal rocky shores was significantly diminished with the removal of *L. digitata*, regardless of environmental context (~47% on the exposed shore, 56% on the sheltered shore). Shifts in the dominant canopy forming species in these areas, from perennial to annual, will likely have significant knock-on effects on habitat provision, and may have wider implications to overall production and detrital processes in nearshore environments.

5.2. *Introduction*

Intertidal habitats sit at the interface between marine and terrestrial realms and are therefore subjected to a wide range of environmental conditions and abiotic stressors (Helmuth *et al.*, 2006). It has been suggested that intertidal systems are at particular risk from anthropogenically driven changes in climate, and perhaps serve as useful 'early-warning' systems for the impacts of climate change (Southward *et al.*, 1995; Hawkins *et al.*, 2003; Harley *et al.*, 2006; Mieszkowska *et al.*, 2006; Hawkins *et al.*, 2009). Rocky shores in temperate, sub-polar and Arctic regions are generally characterised by dense stands of large, canopy forming seaweeds, typically kelps or fucoids (Steneck *et al.*, 2002; Harley *et al.*, 2012). Canopy forming seaweeds underpin highly productive and diverse habitats (Mann, 1973; Brady-Campbell *et al.*, 1984; Reed *et al.*, 2008), and make a significant contribution to primary production in coastal environments (Mann, 1973; Krumhansl & Scheibling, 2012). Kelps, in particular, exert significant influence over the rocky shore communities in which they persist (Hawkins & Harkin, 1985; Jenkins *et al.*, 1999; Teagle *et al.*, 2017), as they support a vast array of species through the provision of three-dimensional habitat and as a food source, both directly for grazers and indirectly as detritus (Steneck *et al.*, 2002; Blight & Thompson, 2008; Arnold *et al.*, 2016). The canopy itself also alters local environmental conditions for a diverse understorey algal community (Norton *et al.*, 1977; Maggs, 1986), and provides shelter from heat and desiccation during low tides (Kendall *et al.*, 2004). Moreover, some species such as *Laminaria digitata* can, exert local disturbance through kelp 'whiplash', leading to impoverished understorey assemblages dominated by crustose algae and sponges (Velimirov & Griffiths, 1979; Hawkins & Harkin, 1985).

Kelps, like all macroalgae, compete for light, space and nutrients, and their relative success at accruing these resources is dependent on relative resource availability, and on environmental variables (Harley *et al.*, 2012). Human activities have influenced the global climate and core processes acting across the land-sea interface and, in doing so, have altered both the availability of some resources (e.g. nutrients; Smith *et al.*, 1999), and the severity of environmental stressors (e.g. temperature and wave exposure; Wolf & Woolf, 2006; Lima & Wethey, 2012; Wang *et al.*, 2014; Oliver *et al.*, 2018). Changes in resource availability and environmental context will, in turn, influence the strength and direction of biological interactions such as competition and grazing on rocky shores (Harley *et al.*, 2012). Removal of competitively dominant species by environmental extremes (e.g. heat-wave or storm events) will allow for the proliferation of subdominant species, and potentially facilitate the ingress of non-native species (e.g. the Japanese kelp, *Undaria pinnatifida*; Valentine & Johnson, 2003, 2004). The sub-lethal consequences of such environmental factors will also play a role in determining the outcome of competitive interactions (Davison & Pearson, 1996), and thus influence the composition of macroalgal assemblages prior to the local extirpation of a species.

Kelps are generally cool water species, and as such can become physiologically stressed if exposed to high temperatures (Steneck *et al.*, 2002). As a result, the distribution of kelps is strongly linked to temperature, and populations found at trailing equatorward range edges are particularly susceptible to seawater warming (Straub *et al.*, 2016). Indeed, increased temperature has been linked with changes in the geographical distributions of kelps, and a number of species have undergone poleward range contractions in response to recent warming trends (Fernandez, 2011; Wernberg *et al.*, 2011b; Voerman *et al.*, 2013; Filbee-Dexter *et al.*, 2016). Within habitats where canopy-forming species are lost, major changes to ecological structure and functioning may ensue (Smale & Wernberg, 2013; Wernberg *et al.*, 2016), especially where replacement by functionally-similar species does not occur. In addition to the contraction of cold water species, some kelp species are better adapted to warmer conditions and may proliferate with warming, which in turn may impact upon competitive interactions and the composition of native canopies and associated communities (e.g. *Laminaria ochroleuca*; Smale *et al.*, 2015). Further range shifts of canopy-forming seaweeds have been predicted to occur in the near future in response to continued warming (Hiscock *et al.*, 2004; Müller *et al.*, 2009; Raybaud *et al.*, 2013; Assis *et al.*, 2017).

Wave exposure has long been known to play a pivotal role in structuring marine benthic communities (Ballantine, 1961; Denny, 1987; Gaylord, 1999). Across kelp-dominated habitats, variability in wave exposure can alter the morphology and size of kelp plants, and impact the age structure and overall biomass of kelp forests (Sjøtun & Fredriksen, 1995; Wernberg & Thomsen, 2005; Fowler-Walker *et al.*, 2006; Pedersen *et al.*, 2012; Bekkby *et al.*, 2014). Intense episodes of extreme wave action can also impact kelp population structure, as the hydrodynamic forces generated by storm events are capable of causing high mortality of kelps through damage and dislodgement (Krumhansl & Scheibling, 2011b; Filbee-Dexter & Scheibling, 2012). Large waves, characteristic of winter storm events, can cause thinning of the kelp canopy due to dislodgement of entire kelp plants, and in extreme cases lead to complete defoliation of reef habitats (Thomsen *et al.*, 2004; Saunders & Metaxas, 2008; Reed *et al.*, 2011; Smale & Vance, 2015). Such extreme disturbance events, coupled with temperature-related changes to competitive and facilitative interactions on rocky shores, may alter kelp species identity and abundance, with consequences for wider ecological structure and functioning on temperate rocky reefs (Smale *et al.*, 2013).

Across much of the northeast Atlantic, wave exposed rocky reefs are dominated by the kelp *Laminaria digitata*, where it can form dense continuous stands in low intertidal and shallow subtidal zones. In more wave-sheltered areas, *L. digitata* is often found as a conspicuous member of a mixed seaweed canopy alongside other species of kelp (e.g. *Saccharina latissima* and *Saccorhiza polyschides*), as well as canopy-forming fucoids (e.g. *Fucus* *serratus* and *Himanthalia elongata*). *L. digitata* is also found across the north and northwest Atlantic, where it can penetrate into deeper waters on subtidal reefs (Lüning, 1979). *L. digitata* is characterised by a highly flexible stipe, well suited to the high energy environment of the intertidal rocky shore, which scours the substratum and may exert physical disturbance upon associated understorey assemblages. *L. digitata* is perennial, reaches maturity in 1 – 2 years, persists for up to 6 years, and attains a maximum length of 3 m in wave-exposed areas (Kain, 1979). *L. digitata* represents an important food source, both directly through grazing (e.g. by the blue rayed limpet, *Patella pellucida*; Graham & Fretter, 1947; Warburton, 1976), and indirectly as detritus following microbially-driven degradation and nitrogen enrichment (Schaal *et al.*, 2010). A wide array of organisms utilise *L. digitata* as habitat, especially within the holdfast which can support high levels of biodiversity (Schultze *et al.*, 1990; Blight & Thompson, 2008; Schaal *et al.*, 2012; Walls *et al.*, 2016), and within diverse understorey assemblages, which in turn support abundant invertebrate communities (Schaal *et al.*, 2016). As kelp canopies alter water motion, attenuate waves and reduce the degree of wave breaking (e.g. *Laminaria hyperborea*; Løvås & Tørum, 2001), it is likely that *L. digitata* plays an important role in the hydrodynamics of the surf zone. Finally, *L. digitata* as a living resource has significant economic value for various industries (e.g. food, paint, fabric and cosmetics) as a source of alginate, a gel-forming polysaccharide (Billot *et al.*, 2003), food for human consumption (Mabeau & Fleurence, 1993; Kolb *et al.*, 2004) and, increasingly, as a base component in the production of biofuels (Adams *et al.*, 2011b; Adams *et al.*, 2011a; Jung *et al.*, 2013).

L. digitata is a northerly distributed cold-water species, and its geographical range is strongly constrained by temperature, particularly at the warm water trailing range edge. Unlike the majority of *Laminaria* species, *L. digitata* is a summer fertile kelp and, as such, its reproduction is subject to comparatively high water temperatures (Bartsch *et al.*, 2013). At sea temperatures above 18°C, *L. digitata* is no longer able to reproduce (Lüning, 1980; Bolton & Lüning, 1982), while sporogenesis has a relatively narrow thermal tolerance between 5 and 10°C (Bartsch *et al.*, 2013). Moreover, mature sporophytes are adversely affected by high temperatures. For example, the physiological performance of kelp plants is reduced following prolonged exposure to sea temperatures ≥18°C (Hargrave *et al.*, 2017) and ecologically realistic short, consecutive exposures to air temperatures ≥24°C can lead to stress and eventual mortality (King *et al.*, 2018). As such, the southern limit of *L. digitata* - currently in northern France - is likely to be largely determined by maximum summer temperatures (Southward *et al.*, 1995). Given that air and sea temperatures in the wider northeast Atlantic region have increased significantly over recent decades (L'Hévéder *et al.*, 2016; Hughes *et al.*, 2017), it is somewhat unsurprising that marginal populations towards the trailing range edge have been adversely affected by warming. Declines in the density, cover and spatial extent of *L. digitata* have been recorded around Ireland (Simkanin *et al.*, 2005), the English Channel (Gevaert *et al.*, 2008) and northern France (Cosson, 1999; Davoult *et al.*, 2011), and further reductions are predicted in the near future (Raybaud *et al.*, 2013). Indeed, a number of populations may already be at or near to their thermal limit of reproduction, especially in warm shallow bays (e.g. Helgoland; Bartsch *et al.*, 2013), despite the persistence of populations further south. Populations of *L. digitata* in the southwest UK are currently close to the trailing range edge and as such at risk of significant reductions, and eventual local extirpation as early as the first half of the 21st century (Raybaud *et al.*, 2013). Local loss or reduction will likely drive changes in canopy composition as competitively inferior species colonise space previously held by *L. digitata*. On wave exposed shores the main competitor of *L. digitata* is *Saccorhiza polyschides*, an annual which grows faster than *L. digitata* and is often a mid-successional species in disturbed canopies (Engelen *et al.*, 2011). In more sheltered areas, *Saccharina latissima* is the principal competitor, and in very sheltered environments may serve as the assemblage dominant (Parke, 1948a; Kain, 1979). The invasive kelp *Undaria pinnatifida* also co-occurs with *L. digitata* in the southwest UK, and is more abundant in areas of disturbance and/or with reduced cover of *Laminaria* spp. (De Leji *et al.*, 2017; Epstein & Smale, 2017). Further loss of *L. digitata* may lead to further ingress of opportunistic invasive and fast growing annual species, leading to a shift in habitat structure from a stable, perennial dominated system to an annual dominated system characterised by 'boom-bust' cycles, with knock-on effects on biodiversity and productivity (Smale *et al.*, 2013).

The aim of the current study was to experimentally examine the impact of a reduction or loss of *L. digitata*, following a simulated disturbance event and sustained reduction in density, on the structure of associated communities at two locations with differing degrees of wave exposure. Specific hypotheses tested were: 1) reduced density or total loss of *L. digitata* canopy will lead to changes in seaweed canopy composition because of altered competitive interactions; 2) understorey assemblage structure will change in response to altered canopy cover and composition; and 3) responses in both canopy and understory assemblages will differ between the exposed and sheltered rocky shores examined. To test these hypotheses, I conducted a long-term (~2.5 years) manipulative field experiment whereby realistic climate-related local extirpation scenarios were maintained.

5.3. *Methods*

i. Study sites

Two sites were selected for experimental work, the wave exposed Crownhill Bay (CHB), and the wave sheltered Firestone Bay (FSB), near Plymouth, southwest UK (Fig 5.1a). Sites were selected based on wave exposure (determined by the fetch model presented in Burrows *et al.*, (2008), and observed differences in seaweed canopy composition. Both sites are characterised by extensive low shore rocky reef, with appropriate areas of relatively smooth, topographically simple reef suitable for establishing and maintaining experimental plots. CHB is dominated by extensive mono-specific *Laminaria digitata*

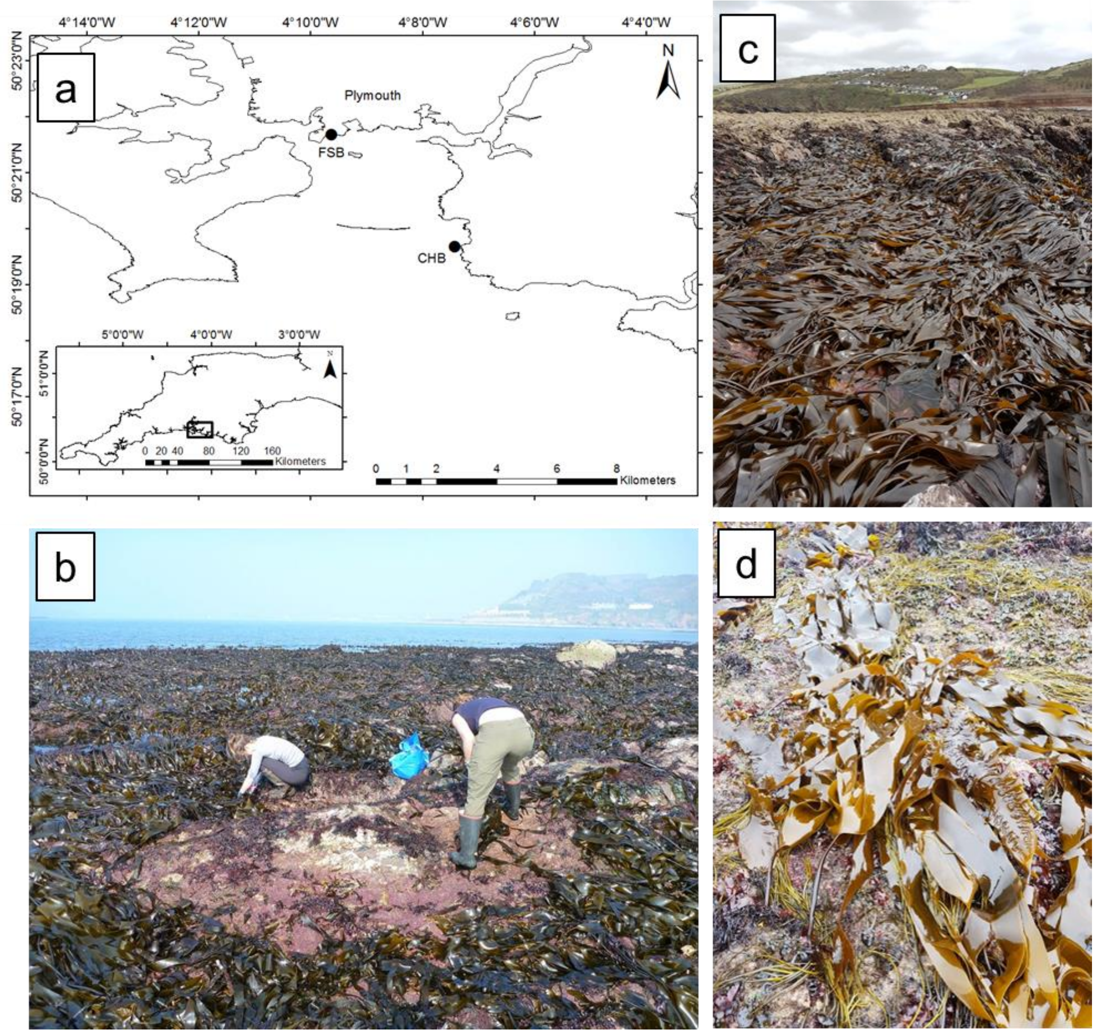


Fig 5.1 (a) Map indicating the locations of the two study sites in Plymouth, southwest UK, (b) an example of a treatment plot after initial clearance at Crownhill Bay in March 2015, and examples of typical canopy composition at (c) Crownhill Bay and (d) Firestone Bay.

canopies (Fig 5.1c), whereas FSB is characterised by more mixed canopies comprising *L. digitata*, *Saccharina latissima*, *Himanthalia elongata*, and to a lesser extent *Saccorhiza polyschides* and the invasive kelp *Undaria pinnatifida* (Fig 5.1d). These sites were chosen to assess the impact of a reduction or loss of *L. digitata* canopy in 1) an area dominated by *L. digitata*, and 2) an area in which *L. digitata* persists within a mixed canopy.

ii. Experimental reduction and loss of a canopy-former at the range edge

In March 2015, 9 plots were selected towards the middle of the vertical distribution of *L. digitata* stands at each site (~0.4 -0.6 m above chart datum). Plots were positioned in areas of relatively smooth, gently sloping reef, avoiding rock pools or other topographic irregularities (e.g. overhangs, crevices). Plots were established in parallel to the shore, and were widely distributed across each site with replicate plots separated by >4 m. Within each plot, a central hole was drilled into the rock using an electric hammer action drill. Metal shield anchor eyebolts were then secured to the reef and a circular plot of 4 m diameter was established using the bolt as a centre point. The bolts were marked with fluorescent cable ties and identifying markers. Prior to establishing and maintaining treatments (see below), all canopy-forming macroalgae (but not understorey algae) were removed (using secateurs, a knife and wire brush) in order to simulate intense physical disturbance (i.e. a storm event) and to initiate the experimental period. The area of each plot was ~12.6 m^2.

Manipulations focussed specifically on *L. digitata*, to examine the effects of climate-driven reduction or loss of a foundation species during post-disturbance succession. Three experimental treatments were established: (1) a 0% removal of *L. digitata*, whereby assemblages were left un-manipulated and allowed to recover with *L. digitata* individuals; (2) a 100% removal treatment, whereby all *L. digitata* plants were selectively removed as they recruited; and (3) a 50% removal treatment, whereby *L. digitata* recruits were weeded to yield densities of ~50% relative to 'background' populations within control plots (see below). At each site, each treatment was pseudo-randomly assigned to 3 replicate plots (to ensure relatively even dispersion of treatments). Plots were maintained whenever spring tides were low enough to access the experimental area (typically monthly through spring and autumn and bimonthly through summer and winter). Macroalgal recruits could be confidently identified in the field to species-level once they had attained ~5 cm in length; only *L. digitata* were removed and all other species were left unmanipulated in all plots. Three reference plots (i.e. un-cleared, un-manipulated, 'background' assemblages) were established in gaps between existing plots in March 2016, taking care to select areas of reef with similar attributes (physical and ecological) to manipulated plots, in order to establish if and when treatments returned to a pre-disturbed state.

iii. Data collection

Plots were sampled on low spring tides, at approximately 6 monthly intervals, in spring and autumn. To quantify assemblages, a 0.5 x 0.5 m (i.e. 0.25 m^2) quadrat was haphazardly placed within each plot. Three replicate quadrats (i.e. subsamples) were collected from each plot, pseudo-randomly placed to ensure no overlap and even distribution across the plot. Data were not collected from the outer 50 cm and from the area immediately surrounding the marker bolts, to avoid edge effects and any influence of the metal bolts respectively. The density and percentage cover of each canopy-forming macroalgal species (i.e. kelps, fucoids, Tilopteridales), and all understorey algae was recorded *in situ*. Understorey algae were split into broad taxonomic groups (e.g. red algae, green algae) to enable the entire sampling process to be achieved within the short window at low tide.

After 2.5 years of post-disturbance recovery, plots were sampled destructively in October 2017. All macroalgae was harvested from three 0.5 x 0.5 m quadrats within each plot and immediately returned to the laboratory for analysis. All canopy-forming species were counted to quantify density and weighed to establish biomass (fresh weight). *H. elongata* was considered a canopy-forming species, but due to difficulties in estimating abundance due to presence of 'buttons' as well as plants with well-developed thalli, only biomass of this species was used in analysis. All understorey algae were sorted into coarse functional groups (sensu Phillips *et al.*, 1997; see Table 5.1), and each group was weighed to establish biomass (fresh weight).

iv. Statistical analysis

All analysis was conducted using univariate and multivariate permutational analysis of variance (PERMANOVA), with the PERMANOVA add on (Anderson *et al.*, 2008) for Primer v7 software (Clarke & Gorley, 2015). Multivariate permutations (4999 under a reduced model) were based on Bray-Curtis similarity matrices constructed from square root transformed density or biomass data, where appropriate. Univariate permutations (4999 under a reduced model) were based on Euclidean distance similarity matrices, constructed using untransformed data. Percent cover was averaged, while abundance data was summed, both from three subsamples of 0.5 m^2 quadrats per treatment plot. The

Table 5.1 Functional groups of algae. Adapted from Phillips *et al.* (1997)

Functional Group	Morphological Characteristics	Example
FG2 – Filamentous Algae	Uniseriate, multiseriate or lightly corticated; filamentous; filaments attached by holdfasts; soft texture	*Ceramium* spp.
FG3 – Foliose Algae	Thin sheet and tubular; uncorticated; one to several cells thick; soft texture	*Ulva* spp.
FG3.5 – Corticated Foliose Algae	Sheet-like; corticated; several cells thick; soft-fleshy texture	*Palmaria palmata*
FG4 – Corticated Terete Algae	Coarsely branched; upright; terete; morphologically complex; thalli differentiated into outer cortex and inner medulla; fleshy-wiry or tough texture	*Mastocarpus stellatus*
FG5 – Leathery Macrophytes	Thick blades and branches; more heavily corticated than FG4; thick-walled cells; morphologically most complex; includes non-calcified crusts; leathery-rubbery texture	*Fucus serratus*
FG6 – Articulated Calcareous Algae	Articulated; calcareous; upright; calcified segments connected by flexible joints; stony texture	*Corallina officinalis*

assemblage data were condensed to broad taxonomic groups (i.e. Laminariales, Tilopteridales, Fucoids, red algae and green algae) prior to analysis.

The effect of treatment on *L. digitata* and its most abundant competitor (*S. polyschides* at CHB, and *S. latissima* at FSB) was tested using univariate PERMANOVA using a 2-factor design, with treatment (3 levels) and month post-disturbance (6 levels) as fixed factors, to ensure treatments had functioned as intended and to examine the effects of competitive release, respectively. Multivariate PERMANOVA was then carried out on percent cover data for the complete assemblage (minus *L. digitata*, but including all understorey algae) using the same model design. Prior to analysis of the complete dataset, 0% treatments (i.e. 0% of *L. digitata* removed) and Control treatments were analysed separately. As no significant difference was found between 0% and Control treatments for either site (CHB: P = 0.718, FSB: P = 0.317), Control treatments were removed from further analysis. Full analysis was then carried out on the remaining data set. Pair-wise tests were carried out within factors wherever a significant effect of that treatment was detected (P < 0.05). Where significant differences in assemblage structure between treatments were detected, SIMPER analysis was performed to determine which taxa contributed most to the observed dissimilarity. Multivariate data derived from destructive sampling events were analysed using a single factor design (treatment, fixed), with Bray-Curtis similarity matrices derived from square-root transformed data, on abundance (canopy forming algae only) and biomass (canopy forming algae and understorey algae) data. Canopy forming and understorey assemblages were analysed separately. *L. digitata* was excluded from all analyses. *H. elongata* was considered as a canopy-forming species, but as only biomass measurements were recorded, this species was not included in any analysis associated with density data. Differences in multivariate dispersion were tested for using the PERMDISP routine, based on Euclidean distance derived resemblance matrices derived from canopy abundance and biomass data independently. Differences in the total biomass of all algae (canopy and understorey) present in each treatment following destructive sampling were investigated using a single factor design (Treatment, 4 levels) based on Euclidean distance resemblance matrices constructed from untransformed biomass data.

5.4. *Results*

i. Laminaria digitata versus main competitor

Density and percentage cover of *L. digitata* were shown to differ significantly between treatments at both sites (Table 5.2 a,b; Table 5.3 a,b), with *L. digitata* density and cover in 50% treatments generally tracking those in 0% treatments at expected levels and with 0% treatments reaching reference density and cover at both sites by autumn 2017 (i.e. 2.5 years post clearance), indicating the treatments had functioned as intended (Fig 5.2 a,b; Fig 5.3 a,b). Time was also shown to have a significant impact on the abundance and percent cover of *L. digitata* at both sites (Table 5.2 a,b; Table 5.3 a,b). Significant interaction terms were observed for percent cover of *L. digitata* at CHB, and for both metrics at FSB, likely

Table 5.2 Results of univariate PERMANOVA to test for differences in the (a) abundance and (b) percent cover of *L. digitata*, and the abundance (c) and percent cover (d) of *S. polyschides* at CHB. Permutations were based on a Euclidean distance similarity matrix generated from untransformed abundance/biomass data. All tests used a maximum of 4999 permutations under a reduced model; significant effects (P<0.05) are shown in bold.

	a. *L. digitata* abundance				b. *L. digitata* percent cover			
Source	*df*	MS	Pseudo-F	P	*df*	MS	Pseudo-F	P
Treatment	2	14714	41.54	**0.001**	2	3631.4	68.73	**0.001**
Time	5	1398.5	3.948	**0.012**	5	258.41	4.891	**0.001**
TreatmentxTiime	10	546.88	1.544	0.182	10	120.43	2.279	**0.036**
Residual	34	354.21			34	52.832		
Total	51				51			
	c. *S. polyschides* abundance				d. *S. polyschides* percent cover			
Treatment	2	372.07	18.21	**0.001**	2	1729.7	13.16	**0.001**
Time	5	60.575	2.965	**0.019**	5	515.73	3.924	**0.01**
TreatmentxTime	10	43.273	2.118	0.052	10	251.2	1.911	0.07
Residual	34	20.431			34	131.43		
Total	51				51			

Table 5.3 Results of univariate PERMANOVA to test for differences in the (a) abundance and (b) percent cover of *L. digitata*, and the abundance (c) and percent cover (d) of *S. latissima* at FSB. Permutations were based on a Euclidean distance similarity matrix generated from untransformed abundance/biomass data. All tests used a maximum of 4999 permutations under a reduced model; significant effects (P<0.05) are shown in bold.

	a. *L. digitata* abundance				b. *L. digitata* percent cover			
Source	*df*	MS	Pseudo-F	P	*df*	MS	Pseudo-F	P
Treatment	2	207.35	29.70	**0.001**	2	450.97	30.67	**0.001**
Time	5	40.819	5.867	**0.002**	5	183.65	12.32	**0.001**
TreatmentxTime	10	24.352	3.488	**0.001**	10	99.821	6.699	**0.001**
Residual	36	6.9815			36	14.899		
Total	53				53			
	c. *S. latissima* abundance				d. *S. latissima* percent cover			
Treatment	2	79.185	1.835	0.189	2	10.543	0.387	0.699
Time	5	214.15	4.963	**0.003**	5	200.99	7.372	**0.001**
TreatmentxTime	10	40.963	0.949	0.493	10	41.657	1.528	0.185
Residual	36	43.148			36	27.265		
Total	53				53			

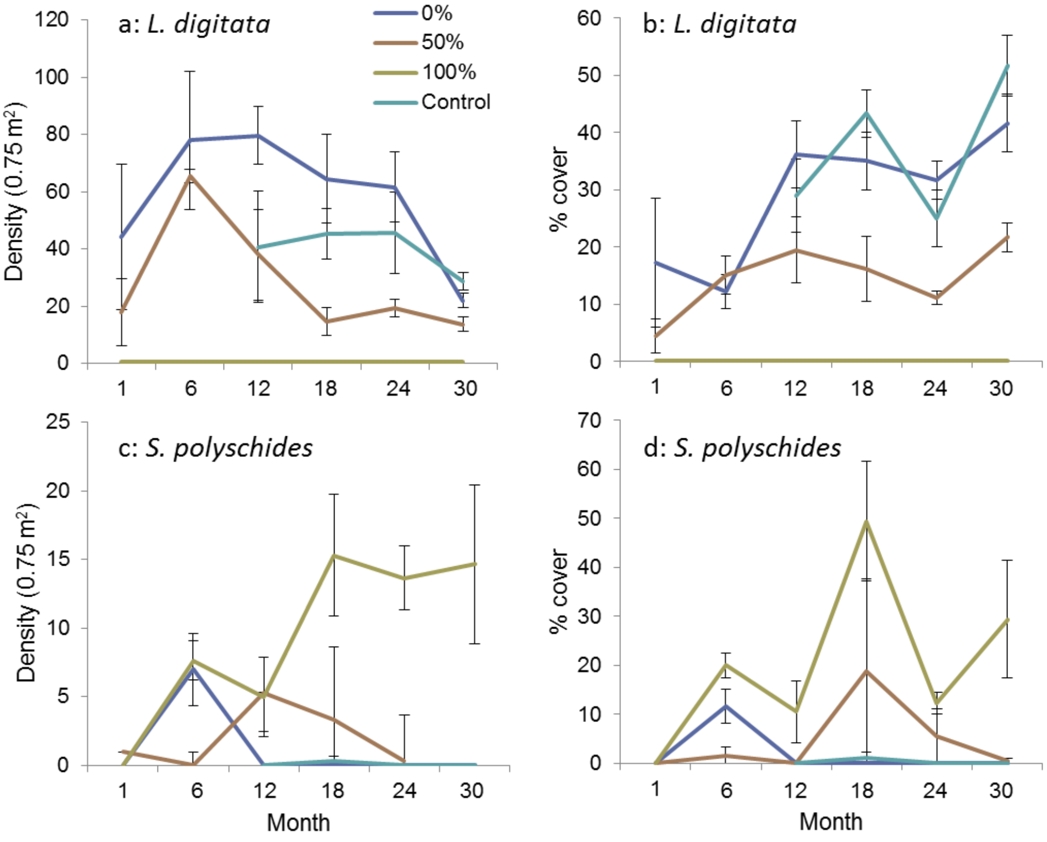


Fig 5.2 Change in abundance (a) and percent cover (b) of *L. digitata* and its main competitor *S. polyschides* (c) and (d) at CHB following initial canopy clearance for all treatments (± SE). Abundance data is pooled quadrat data and represents density per 0.75 m^2. X axis shows months post-disturbance.

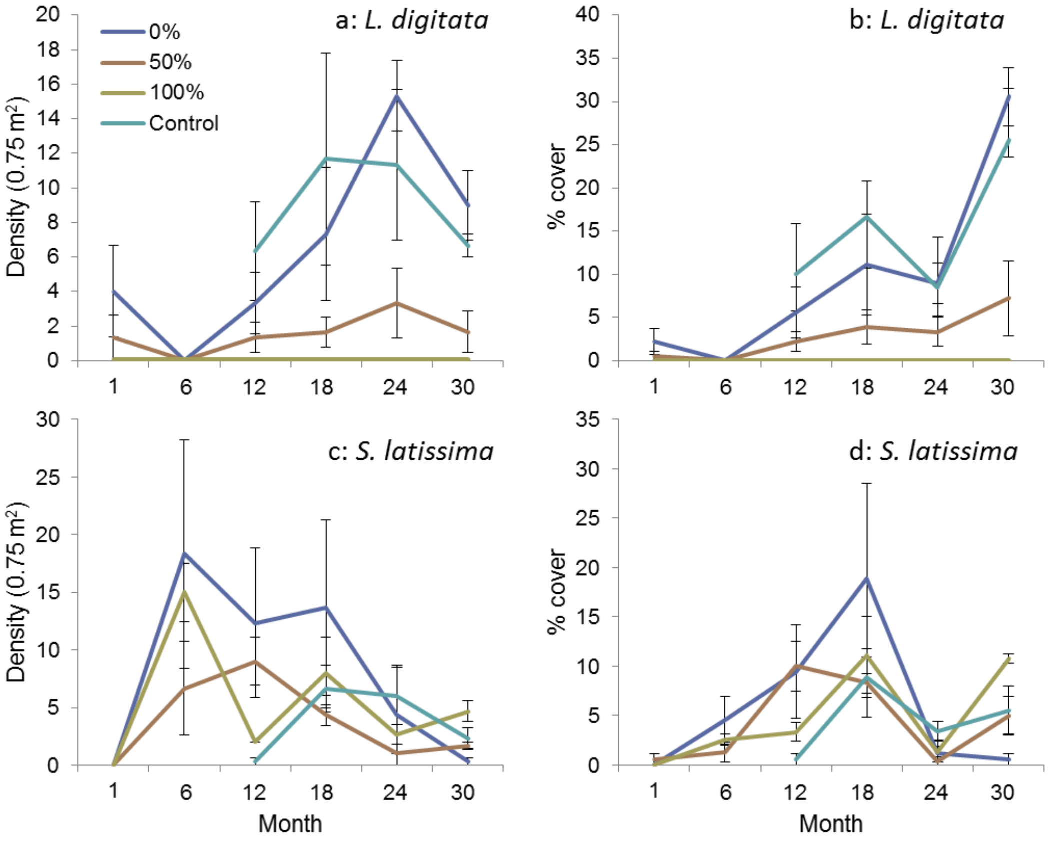


Fig 5.3 Change in abundance (a) and percent cover (b) of *L. digitata* and its main competitor *S. latissima* (c) and (d) at FSB following initial canopy clearance for all treatments (± SE). Abundance data is pooled quadrat data and represents density per 0.75 m^2. X axis shows months post-disturbance.

caused by changes in the magnitude of difference between treatments through time, particularly as 0% treatments were colonised by *L. digitata* plants and 100% were not (Fig 5.2 a,b; Fig 5.3 a,b).

CHB was characterised by fast recolonization by *L. digitata* recruits, with 40 – 50 identifiable *L. digitata* juveniles present in 0% plots within 1 month of clearance. Recruitment persisted until autumn of 2015, where density plateaued and gradually dropped as plants became established, and plant density thinned, presumably due to intra-specific competition between plants. This trend was generally echoed in 50% treatments. Percent cover values of *L. digitata* at CHB continued to rise independently from density right up until autumn 2017, suggesting that the plants present were continuing to mature. A similar pattern in *L. digitata* recruitment, density and cover was observed at FSB, albeit with a pronounced lag in the recruitment of *L. digitata* to all treatments compared with the more exposed site. No *L. digitata* was recorded at FSB in any treatment in autumn 2015. Densities of *L. digitata* were significantly higher at CHB, the more exposed site.

Convergence of 0% treatments and control plots was reached in autumn 2016 in CHB, and no difference was observed between controls and 0% treatments in FSB (after the controls were initiated in spring 2016).

At CHB, the more exposed site, the main competitor of *L. digitata* was observed to be *S. polyschides*, particularly in areas of disturbance and on the fringes of established *L. digitata* canopy (Fig 5.2 c,d). The density and percentage cover of *S. polyschides* was greatest in 100% treatments, less in 50% treatments and after an initial pulse of recruitment between spring and autumn 2015, was mostly absent from 0% and control treatments. PERMANOVA identified significant differences in *S. polyschides* density and percentage cover between treatments and time points (Table 5.2 c,d). No significant Treatment x Time interaction was observed for either measure. Further investigation using pair-wise tests showed that for both measures of *S. polyschides* abundance (i.e. density and percent cover), differences were found between 100% treatments and all others; but no difference was observed between 0% and 50% treatments. At FSB, the main competitor of *L. digitata* was observed to be *S. latissima* (Fig 5.3). No significant difference was observed in the density or percentage cover for *S. latissima* between treatments, but a significant effect of time was observed for both measures (Table 5.3 c,d).

ii. Multivariate assemblage

As the manipulation after initial clearance was concerned solely with the density of *L. digitata*, this species was removed from the multivariate analysis. At CHB, metric MDS (mMDS) plots showed some partitioning between treatments, and to some extent, time

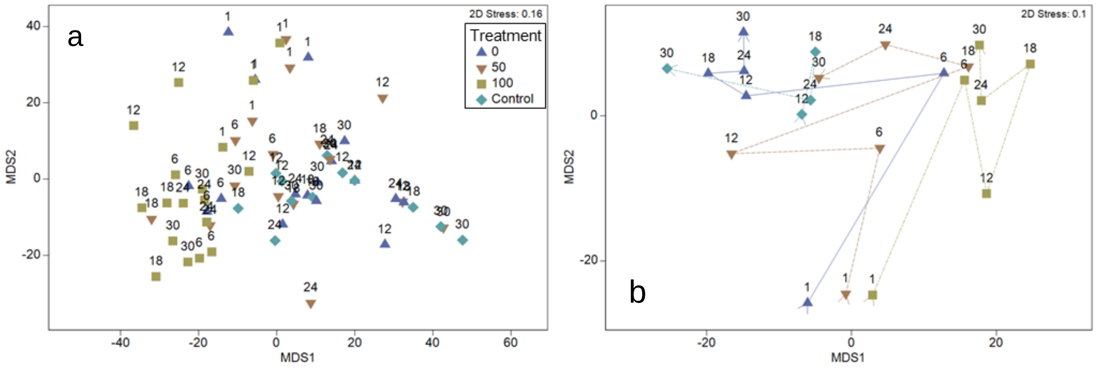


Fig 5.4 Metric MDS plots depicting community structure of algal assemblages at CHB over three years during manipulation, for all treatments. Centroids represent treatment plots (a) and treatments (b), labels in all instances represent months post-disturbance. An overlay representing the trajectory of change is present in (b).

Table 5.4 Results of multivariate PERMANOVA to test for differences in algal assemblage structure at (a) CHB and (b) FSB during manipulation. Permutations were based on a Bray-Curtis similarity matrix generated from square-root transformed percent cover data. All tests used a maximum of 4999 permutations under a reduced model; significant effects (P<0.05) are shown in bold =.

	a. CHB			
Source	*df*	MS	Pseudo-F	P
Treatment	2	4104.6	8.578	**0.001**
Time	5	2083.8	4.355	**0.001**
TreatmentxTime	10	545.3	1.139	0.296
Residual	34	478.5		
Total	51			
	b. FSB			
Treatment	2	788.17	2.808	**0.014**
Time	5	1833	6.529	**0.001**
TreatmentxTime	10	292.55	1.042	0.425
Residual	36	280.72		
Total	53			

points (Fig 5.4a). mMDS plots with a trajectory overlay demonstrated that treatments reacted similarly over time, with 0% treatments tracking control treatments by time point 3 onwards, while 100% treatments were separate and 50% treatments falling somewhere between (Fig 5.4b). PERMANOVA identified significant differences in assemblage structure between treatments and time points, but no significant interaction was observed (Table 5.4). Within the Treatment factor, significant differences were observed between 100% treatments and all others, but no difference was observed between 0% and 50% treatments. SIMPER analysis demonstrated that the observed differences were driven principally by high percent cover of *S. polyschides* in 100% treatments, and to a lesser

Table 5.5 Percentage contributions of individual taxonomic groups to observed differences in algae community composition (minus *L. digitata*) between treatments at CHB, as determined by SIMPER analysis.

Group	Av. abund	Av. abund	Av. diss	Diss/SD	Contrib%	Cum%
	0%	**50%**				
Red algae	5.23	5.72	10.49	1.26	30.70	30.70
Fucoids	1.20	1.29	8.57	1.18	25.06	55.76
Green algae	0.99	0.90	8.46	0.71	24.76	80.52
	0%	**100%**				
Tilopteridales	0.59	3.76	16.36	1.40	39.74	39.74
Red algae	5.23	6.31	8.41	1.24	20.43	60.17
Fucoids	1.20	2.20	7.82	1.37	18.99	79.17
	50%	**100%**				
Tilopteridales	0.87	3.76	16.18	1.45	39.88	39.88
Red algae	5.72	6.31	9.06	1.21	22.32	62.20
Fucoids	1.29	2.20	7.56	1.33	18.63	80.83

extent an increase in fucoids and understorey red algae from 0% to 50% to 100% treatments (Table 5.5).

In regards to FSB assemblages, mMDS plots display limited separation between treatments and time points (Fig 5.5a). Trajectory overlays are again, not as clear as those resulting from CHB data, but follow a similar pattern, with 0% treatments tracking controls and 50% and 100% treatments more distinct (Fig 5.5b). The ‘zig-zag’ pattern apparent here is likely due to seasonal effects on algal cover, particularly in relation to those annual species that make up the assemblage at this site (i.e. *S. polyschides* and *U. pinnatifida*), supported by a similar pattern observed in control plots. PERMANOVA again detected significant differences in assemblage structure between treatments and time points, but no significant interaction was observed (Table 5.4). Within the factor Treatment, no difference was observed between 50% and 100% treatments, but significant differences were observed between the 0% and the other treatments. SIMPER analysis demonstrated that the differences observed between treatments were driven by higher cover of *S. polyschides* and other Laminariales (excluding *L. digitata*) in the 50% treatments, with less in the 100% and less again in the 0% treatments (Table 5.6). There was also evidence of increased cover of fucoids in 100% removals, and similarly to CHB, an increase in understorey red algae from 0% to 50% to 100% treatments (Table 5.6).

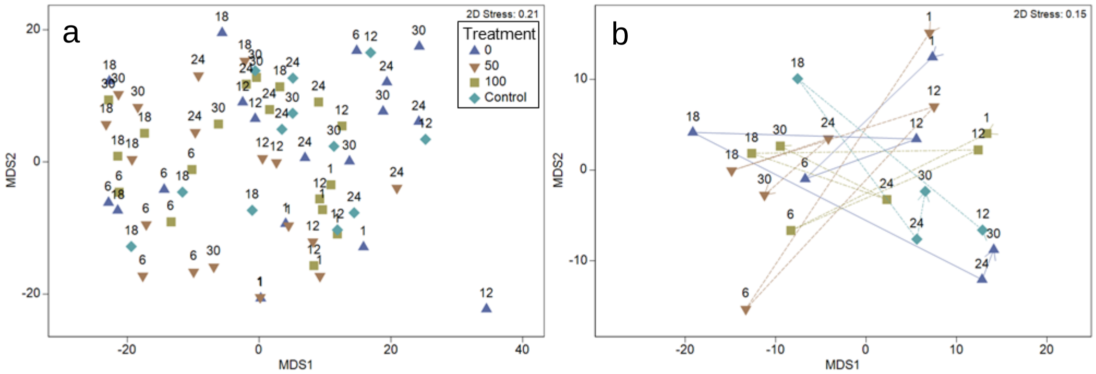


Fig 5.5 Metric MDS plots depicting community structure of algal assemblages at FSB over 2.5 years during manipulation, for all treatments. Centroids represent treatment plots (a) and treatments (b), labels in all instances represent months post-disturbance. An overlay representing the trajectory of change is present in (b).

iii. Destructive sampling

1. Canopy-forming algae

At CHB, alongside *L. digitata*, *S. polyschides*, *L. hyperborea* and *H. elongata* were found as components of the canopy after three years of maintaining all treatments (i.e. 0, 50 and 100%). mMDS plots displayed significant partitioning between treatments, principally between 100% treatments and all others for both measures (i.e. density and biomass; Fig 5.6 a,b). PERMANOVA detected significant differences in both measures between treatments (Table 5.7), with pair-wise tests showing that 100% treatments differed significantly from all other treatments and controls. SIMPER analysis for density data identified *S. polyschides* as the primary driver of this dissimilarity, being recorded exclusively in 100% treatments (Table 5.8). *H. elongata* followed the same pattern and was another key driver of dissimilarity in the biomass data. Species were then considered in isolation to determine the effect of treatment on individual members of the canopy. Neither the density nor the biomass of *Laminaria hyperborea* was shown to differ between treatments. However, the density and biomass of *S. polyschides* were shown to differ between treatments, with pair-wise tests showing significantly higher values for 100% treatments compared to all others. Likewise, the biomass of *H. elongata* differed between treatments, with 100% treatments being significantly greater than the others. Specimens of both *S. polyschides* and *H. elongata* were found solely in 100% removal treatments, and were absent from other treatments and controls (Fig 5.6 c,d). Significant differences in multivariate dispersion were observed for both canopy abundance, and canopy biomass

Table 5.6 Percentage contributions of individual taxonomic groups to observed differences in algae community composition (minus *L. digitata*) between treatments at FSB, as determined by SIMPER analysis.

Group	Av. abund **0%**	Av. abund **50%**	Av. diss	Diss/SD	Contrib%	Cum%
Laminariales	2.09	2.77	8.15	1.41	26.92	26.92
Tilopteridales	0.78	1.94	7.85	1.13	25.94	52.85
Red algae	4.25	4.68	4.91	1.16	16.22	69.08
	0%	**100%**				
Laminariales	2.09	2.42	7.42	1.54	25.52	25.52
Tilopteridales	0.78	1.35	6.31	0.93	21.69	47.22
Red algae	4.25	4.81	5.43	1.39	18.69	65.91
	50%	**100%**				
Tilopteridales	1.94	1.35	7.48	1.20	28.85	28.85
Laminariales	2.77	2.42	5.22	1.51	20.12	48.97
Fucoids	3.00	3.67	4.88	1.36	18.81	67.78

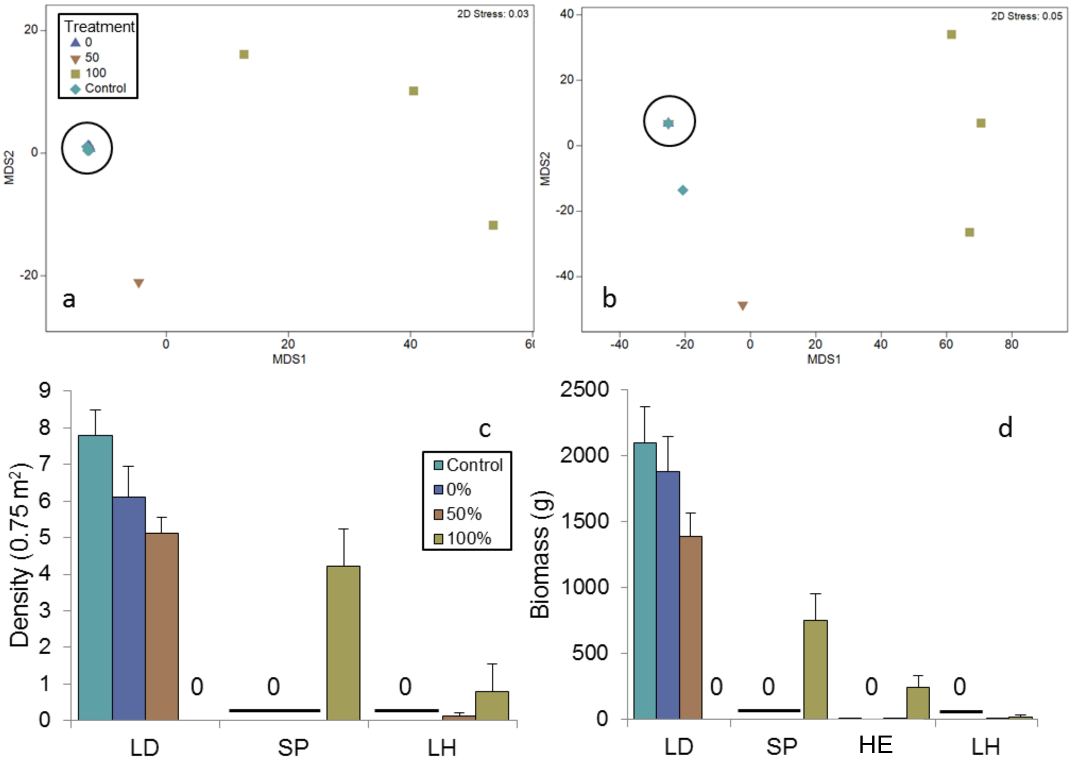


Fig 5.6 Metric MDS plots depicting the abundance (a) and biomass (b) of canopy forming species after destructive sampling at CHB after three years of manipulation in October 2017. Bars show abundance (c) and biomass (d) of individual canopy forming species (± SE). Circles enclose those samples which comprise solely *L. digitata*.

Table 5.7 Results of multivariate PERMANOVA to test for differences in (a) canopy forming algal abundance and (b) biomass, and (c) understorey algae biomass at CHB following destructive sampling after 2.5 years of manipulation. Permutations were based on a Bray-Curtis similarity matrix generated from square-root transformed biomass data. All tests used a maximum of 999 permutations under a reduced model; significant effects (P<0.05) are shown in bold.

a. Canopy abundance				
Source	*df*	MS	Pseudo-F	P
Treatment	3	3916.8	18.40	**0.001**
Residual	32	212.84		
Total	35			
b. Canopy biomass				
Treatment	2	15744	26.67	**0.001**
Residual	32	590.28		
Total	35			
c. Understorey biomass				
Treatment	3	2589.8	1.533	0.151
Residual	32	1689.2		
Total	35			

Table 5.8 Percentage contributions of individual species to observed differences in canopy community composition (minus *L. digitata*) between treatments at CHB after destructive sampling, as determined by SIMPER analysis. 0% and Control groups are not included as they were populated solely by *L. digitata*.

Group	Av. abund	Av. abund	Av. diss	Diss/SD	Contrib%	Cum%
	0%	**50%**				
L. hyperborea	0.00	0.11	100	N/A	100	100
	0%	**100%**				
S. polyschides	0.00	1.78	93.31	5.64	93.31	93.31
	50%	**100%**				
S. polyschides	0.00	1.78	87.34	3.66	87.75	87.75
	50%	**Control**				
L. hyperborea	0.11	0.00	100	N/A	100	100
	100%	**Control**				
S. polyschides	1.78	0.00	93.31	5.64	93.31	93.31

(Table 5.9). In both instances 100% treatments were most variable and 0% treatments were least variable (Table 5.9).

At FSB the canopy was comprised of *S. latissima*, *H. elongata*, *S. polyschides*, *U. pinnatifida* and *L. ochroleuca*, alongside *L. digitata*. Some partitioning between treatments was observed in mMDS plots displaying canopy biomass, but less so for canopy plant density (Fig 5.7 a,b). Overall PERMANOVA detected a significant effect of treatment on the structure of the complete assemblage (minus *L. digitata*; Table 5.10). Pair-wise tests showed significant differences between 0% and 50%, and control and 50% treatments for canopy density, and also between the 100% treatment and treatments 0% and 50% for

Table 5.9 Results of PERMDISP to test for differences in multivariate dispersion between treatments, for each site. Figures in bold represent significant P-values resulting from analysis. Other figures represent the order in magnitude of the variability between treatments, from greatest to lowest.

Site	Abundance	Biomass
CHB	**0.001**	**0.001**
	100>50>Con>0	100>50>Con>0
FSB	**0.021**	**0.04**
	50>100>Con>0	50>100>Con>0

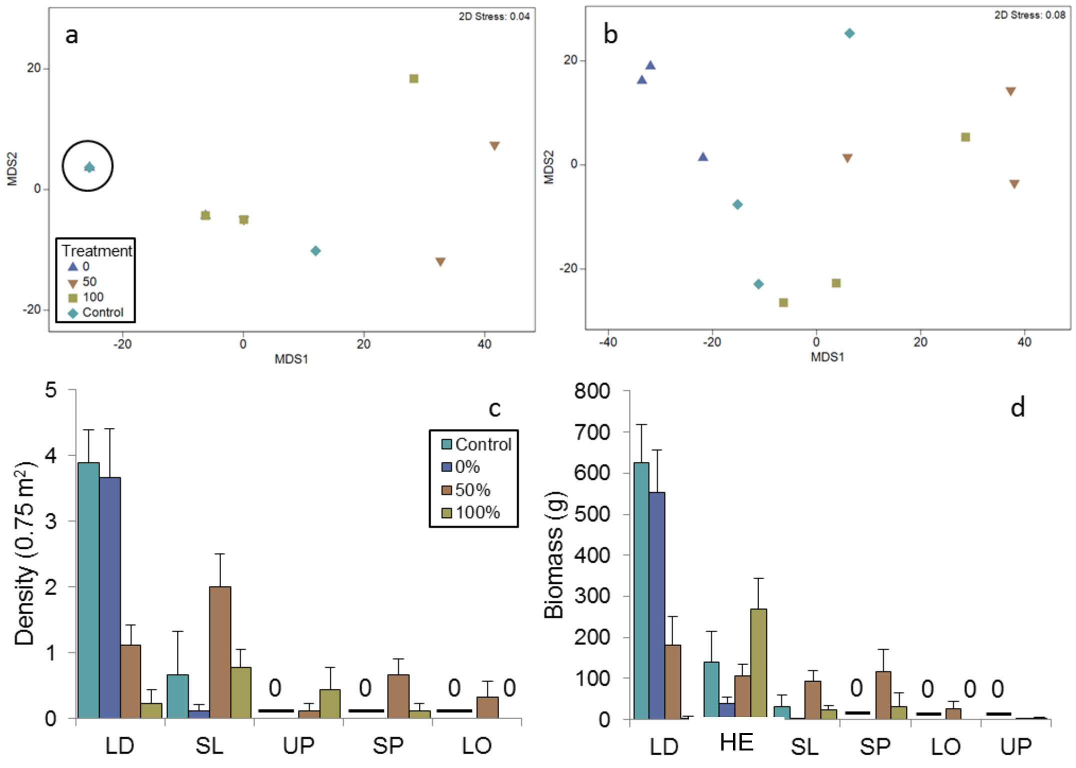


Fig 5.7 Metric MDS plots depicting the abundance (a) and biomass (b) of canopy forming species after destructive sampling at FSB after 2.5 years of manipulation in October 2017. Bars show abundance (c) and biomass (d) of individual canopy forming species (± SE). Circles enclose those samples comprising solely *L. digitata*.

Table 5.10 Results of multivariate PERMANOVA to test for differences in (a) canopy forming algal abundance and (b) biomass, and (c) understorey algae biomass at FSB following destructive sampling after three years of manipulation. Permutations were based on a Bray-Curtis similarity matrix generated from square-root transformed biomass data. All tests used a maximum of 999 permutations under a reduced model; significant effects (P<0.05) are shown in bold.

a. Canopy abundance				
Source	*df*	MS	Pseudo-F	P
Treatment	3	3467.1	7.437	**0.001**
Residual	32	466.21		
Total	35			
b. Canopy biomass				
Treatment	2	6458.5	5.935	**0.001**
Residual	32	1088.1		
Total	35			
c. Understorey biomass				
Treatment	3	1603.8	1.164	0.313
Residual	32	1378.4		
Total	35			

canopy biomass. SIMPER analysis identified the main drivers of the observed dissimilarity in density as *S. latissima* and *S. polyschides*, which were both most abundant in 50% treatments and lowest in 0% treatments and controls. Dissimilarities in biomass followed a similar pattern, but in contrast with density data featured *H. elongata*, which was least abundant in 0% and most abundant in 100% treatments (Table 5.11). Individual members of the canopy were then considered in isolation. The density and biomass of *S. latissima* was observed to differ significantly between treatments. Generally, higher densities and biomass of *S. latissima* was recorded in 50% treatments, and pairwise tests revealed that these treatments differed significantly from both 0% and control treatments (Fig 5.7 c,d). In terms of biomass, 50% treatments also differed from 100% treatments for the same reason (Fig 5.7 c,d). Similarly, the density and biomass of *S. polyschides* plants also differed significantly between treatments, with pairwise tests showing that significantly greater densities and biomass were found in 50% treatments compared to all others, which did not differ significantly (Fig 5.7 c,d). There was an overall effect of treatment on *H. elongata* biomass, but pair-wise tests demonstrated that only the 0% and 100% differed significantly, with much higher biomass found in 100% treatments (Fig 5.7 c,d). Treatment was observed to have no effect on the density or biomass of *U. pinnatifida* and *L. ochroleuca*, which were found only sparsely during this sampling event. Similarly to CHB, significant differences in multivariate dispersion were observed for both canopy abundance and biomass (Table 5.9). Unlike CHB however, at FSB 50% treatments displayed most within treatment variability (Table 5.9).

Table 5.11 Percentage contributions of individual species to observed differences in canopy community composition (minus *L. digitata*) between treatments at FSB after destructive sampling, as determined by SIMPER analysis.

Group	Av. abund	Av. abund	Av. diss	Diss/SD	Contrib%	Cum%
	0%	**50%**				
S. latissima	0.11	1.27	61.79	1.88	66.37	66.37
S. polyschides	0.00	0.60	20.30	1.19	21.81	88.18
	0%	**100%**				
S. latissima	0.11	0.65	72.69	2.09	79.10	79.10
	50%	**100%**				
S. latissima	1.27	0.65	38.50	1.06	55.95	55.95
S. polyschides	0.60	0.11	16.15	1.06	23.47	79.42
	0%	**Control**				
S. latissima	0.11	0.27	96.59	6.87	100	100
	50%	**Control**				
S. latissima	1.27	0.27	62.90	2.01	67.26	67.26
S. polyschides	0.60	0.00	19.85	1.17	21.22	88.48
	100%	**Control**				
S. latissima	0.65	0.27	75.60	2.54	80.10	80.10

2. *Understorey assemblage*

The understorey assemblage at CHB was composed of functional groups FG2, FG4, FG5 and FG6, with FG4 the most abundant group overall, with little biomass of FG2 and FG4 recorded (Fig 5.8a; Table 5.1). mMDS plots showed little partitioning between treatments (Fig 5.8b). PERMANOVA detected no significant differences in assemblage structure between treatments (Table 5.7).

At FSB, the understorey assemblage was more diverse, with all functional groups recorded (Fig 5.9a). FG3.5 and FG4 (Table 5.1) were found to dominate the assemblage in all treatments, but in general the biomass of algae was lower than at CBH. Again, mMDS plots

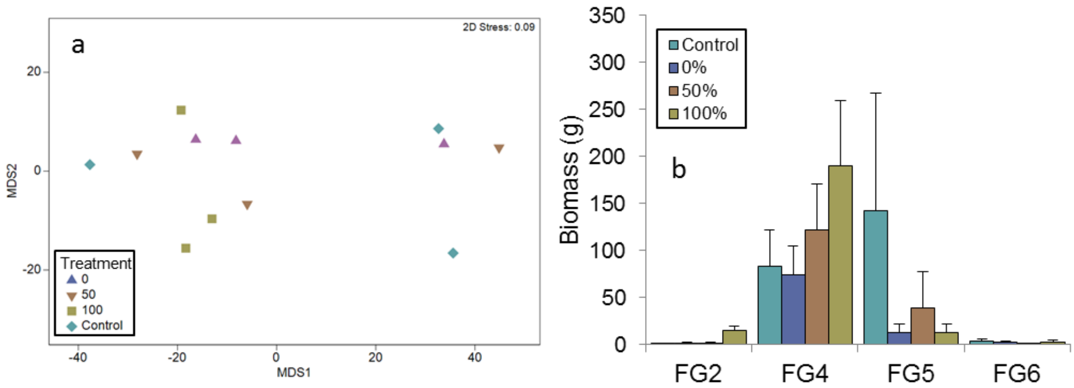


Fig 5.8 Metric MDS plots depicting the biomass (a) of understorey species after destructive sampling at CHB after three years of manipulation in October 2017. Bars show biomass (c) of individual understorey functional groups (± SE).

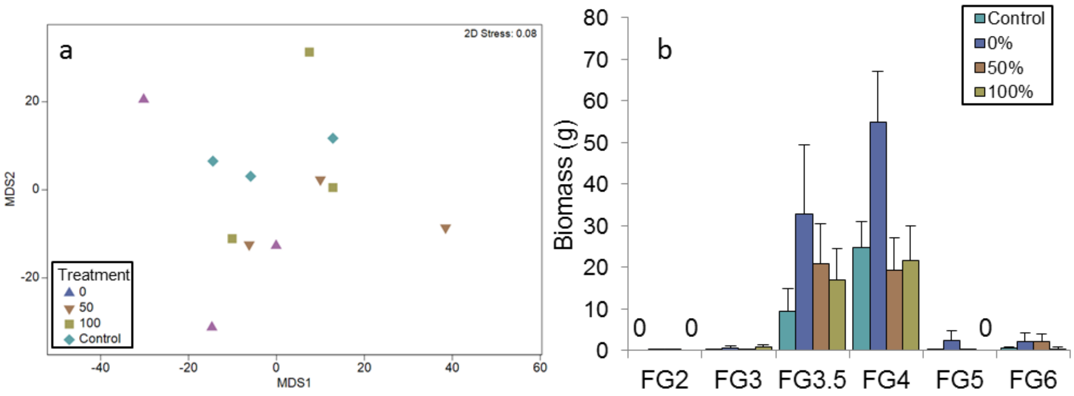


Fig 5.9 Metric MDS plots depicting the biomass (a) of understorey species after destructive sampling at FSB after three years of manipulation in October 2017. Bars show biomass (c) of individual understorey functional groups (± SE).

showed little partitioning between treatments (Fig 5.9b). PERMANOVA detected no significant effect of treatment on assemblage structure (Table 5.10).

3. Total assemblage biomass

Overall the total biomass of algal assemblages (canopy and understorey) found in all treatments at FSB was considerably lower than at CHB. At both sites, benthic standing stock was greatest when *L. digitata* was present (i.e. control and 0% treatments), and was lowest when *L. digitata* was removed (i.e. 100% treatments). Statistically, the total biomass of the complete algal assemblage was shown to differ between treatments for both sites (CHB: $F_{1,35} = 4.179$, $P = 0.02$, FSB: $F_{1,35} = 4.033$, $P = 0.013$). Further investigation was undertaken using pair-wise tests. At CHB, the total biomass of the algal assemblage in 100% treatments was lower than all other treatments, with the exception of 50% treatments (Fig 5.10 a). At FSB, 100% treatments had lower total biomass values than all other treatments (Fig 5.10 b). Reduction in density of *L. digitata*, on both shores, resulted in significant reductions in total biomass of macroalgal assemblages after 2.5 years of manipulation. These reductions were greater on the sheltered shore (FSB; ~56% reduction) compared with the exposed shore (CHB; ~47% reduction) despite the lower initial algal biomass in these areas (Fig 5.10).

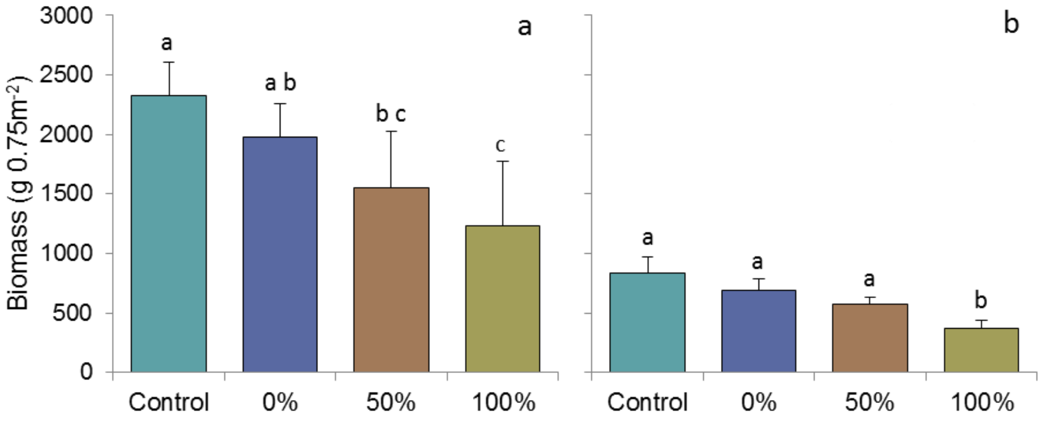


Fig 5.10 Mean total biomass per 0.75 m^2 of all algae (canopy and understorey) at (a) CHB and (b) FSB for each treatment following destructive sampling in Autumn 2017 (± SE). Letters depict results of pairwise tests.

5.5. *Discussion*

i. Effects of L. digitata manipulation at the exposed site

The ecological effects of loss of marginal populations of *Laminaria digitata* at Crownhill Bay (CHB), on a wave exposed coast was largely related to the response of a single species: *Saccorhiza polyschides*. *S. polyschides* is a fast-growing, pseudo-annual species which is common through the UK, often found growing at the margins of dense *Laminaria* forests on exposed coasts (Norton, 1969; Smale & Moore, 2017). It is typically present in low abundances at CHB, often growing in pools and gullies where cover of *L. digitata* is naturally low (H. Teagle pers. Obs.), but was found in only very low abundances of small plants in control plots (i.e. within *L. digitata* canopy) in autumn. It appears that competition with *L. digitata* is an important factor affecting the distribution and abundance of *S. polyschides* at this site. *S. polyschides* is an opportunistic species which readily colonises vacant space available in the infralittoral zone. Its disadvantage however, lies in the fact that it is an annual plant and therefore must establish itself each year, while *L. digitata* is perennial and once established will persist for a number of years (Norton & Burrows, 1969; Lapointe *et al.*, 1981). In instances of reduced *L. digitata* canopy (i.e. 50% treatments) *S. polyschides* populations suffer once mature *L. digitata* plants become established. When *L. digitata* canopies are entirely lost however, *S. polyschides* dominates, as it does on southern European shores where *L. digitata* is not present (Hawkins & Harkin, 1985). The lack of any other competitors on exposed temperate rocky shores suggests that the loss of *L. digitata* canopies may result in a dramatic phase shift to *S. polyschides* dominated shores, with significant implications for kelp forest structure and functioning (Smale *et al.*, 2013).

A shift from *L. digitata* to *S. polyschides* represents a shift from a stable habitat, to one dominated by boom-bust cycles as *S. polyschides* grows rapidly in the spring and summer and senesces in autumn, before the holdfast and remaining thallus is dislodged by winter storms (Norton, 1970). The loss of material in autumn represents a significant loss of habitat for associated organisms, habitat which would otherwise remain mostly intact in perennial dominated systems. A single plant of *S. polyschides*, similarly to Laminarian kelps, forms a complex habitat, and can support up to 50 species of algae and 100 species of animals (Norton & Burrows, 1969; Norton, 1971). These levels of diversity are comparable to those recorded for *L. digitata* (Lippert *et al.*, 2001; Blight & Thompson, 2008; Włodarska-Kowalczuk *et al.*, 2009; Walls *et al.*, 2016), and the habitat provision of *S.*

polyschides has been directly compared to that of *L. hyperborea* in Portugal, with similar levels of diversity and abundance observed (Tuya *et al.*, 2011). However, the seasonal disappearance of *S. polyschides* could have dramatic effects; loss of the thallus directly removes potential habitat, and will result in loss of three-dimensional vertical habitat structure, reducing shelter for associated organisms. The majority of diversity associated with *S. polyschides* is found within the complex, bulb-like holdfast (Norton, 1969), the low profile of which likely reduce their exposure to wave action, and can result in their persistence late into winter once the remainder of the thallus has been lost, potentially acting as a form of refuge for holdfast associated organisms.

As the dominant primary producer may influence the turnover, fate and associated nutrients within an ecosystem (Cebrián *et al.*, 1998), the observed shift in kelp species densities may also have impacts over a broader spatial scale. Annual species generally grow faster, are more susceptible to grazing loss, and decompose faster than perennial species (Littler & Littler, 1980; Cebrián & Duarte, 1994; Duarte, 1995; Banta *et al.*, 2004). Thus the production of *S. polyschides* may be transferred to heterotrophs faster, through increased grazing and decomposition of detrital material, when compared to *L. digitata* (Duarte, 1995). High abundances of numerous grazers have been observed on the lamina of *S. polyschides* (e.g. Norton, 1971), whereas the only herbivore commonly found on the lamina of *L. digitata* is the blue-rayed limpet, *Patella pellucida* (McGrath, 2001; McGrath & Foley, 2005). Kelp detritus forms an important food source, which can be consumed locally (Duggins *et al.*, 1989; Norderhaug *et al.*, 2003) or transported to adjacent (Tallis, 2009) or distant habitats (Vanderklift & Wernberg, 2008). Kelp derived detritus can represent an important spatial energy subsidy to other systems (Bedford & Moore, 1984; Bustamante & Branch, 1996; Wernberg *et al.*, 2006; Vanderklift & Wernberg, 2008; Tallis, 2009). It is likely that such a significant shift in canopy composition will result in considerable seasonal loss of habitat as well as altered detrital pathways, timings, and turnover rates of organic matter.

ii. Effects of L. digitata manipulation at the sheltered site

Successional sequences at the more wave sheltered site, Firestone Bay (FSB), were considerably different to that observed at CHB. The reduction or removal of *L. digitata* canopy did not lead to the dominance of a single species, and therefore the changes observed at FSB were more subtle. An initial increase in the density of *S. latissima* was observed after removal of the canopy in all treatments. *S. latissima* is a perennial species, but tends to have a shorter life span than *L. digitata* (~4 years and ~6 years respectively; Smale *et al.*, 2013). *S. latissima* grows throughout the winter and in early spring , whereas *L. digitata* grows from spring, though summer and the growth rate in September is only 50% of the optimum (Lüning, 1979). As initial clearance was undertaken in early spring, it would appear that *S. latissima* was able to fill free space more quickly than *L. digitata*. Clearly *S. latissima* can function as an early successional species under moderate wave exposure conditions (e.g. Leinaas & Christie, 1996). Large, mature individuals dominated 100% treatments 3 years after the initial clearance, but were almost absent from 0% treatments. Interestingly the density and biomass of *S. latissima* recorded during destructive sampling after 3 years was highest in 50% treatments, where it grew alongside *L. digitata*, suggesting a facilitative effect of *L. digitata* canopies on the recruitment and growth of *S. latissima*. A number of other kelp species were recorded at FSB. *S. polyschides* was present in low densities in comparison to CHB, and the invasive kelp *Undaria pinnatifida* was also present in low abundances. After three years, both these species were only found in treatments in which recovery of the canopy of *L. digitata* had been manipulated (i.e. 50% and 100% treatments). *U. pinnatifida* is a fast growing annual species, and is well known to quickly colonise areas of disturbance and quickly reach high abundances in the absence of native canopy-formers (Valentine & Johnson, 2003; South *et al.*, 2015). That low abundances were recorded after 3 years of manipulation, suggest that after removal of *L. digitata* canopies, *U. pinnatifida* is able to compete against the remaining canopy, in this case primarily *S. latissima*. Previous research has suggested that competition for light, rather than space is important in determining *U. pinnatifida* abundance (Valentine & Johnson, 2003; De Leji *et al.*, 2017). As *L. digitata* forms a dense, often monospecific canopy, its large thick laminae are likely to significantly restrict the light reaching the substratum. In contrast *S. latissima* exhibits a shorter, more flexible stipe, a prostrate growth form and forms much more sparse canopies, therefore allowing more light to reach young *U. pinnatifida* sporophytes and thus exerts less competitive pressure than *L. digitata* (De Leji *et al.*, 2017). The same factors may be important in the establishment of *S. polyschides* populations. As *S. polyschides* and *U. pinnatifida* are both annual species they are unlikely to compete for resources until late summer when both species have reached maximum size. In more sheltered areas, a reduction or loss of *L. digitata* may lead to an overall decrease in extent of temporally stable canopy due to the patchy, sparse nature of *S. latissima* growth at these sites, as was observed at FSB. This in turn may lead to an increase in annual species abundance, both of which may hinder the ability of such habitats to resist invasion by non-native algae in the future. Canopy composition has been shown to influence biotic resistance to invasion of macroalgal beds in Australia (Valentine & Johnson, 2004) and New Zealand (Thompson & Schiel, 2012; South & Thomsen, 2016).

Himanthalia elongata density increased following removal of *L. digitata*, with the highest abundances after three years found in 100% treatments at both sites. *H. elongata* can form dense monospecific stands on temperate rocky shores (Creed, 1995), and this was observed at both sites in manipulated treatments. The increase of *H. elongata* has the potential to help limit the dominance of *S. polyschides* at more exposed sites, and *S. polyschides* and *U. pinnatifida* at more sheltered sites, simply through acquisition of space in areas absent from *L. digitata* canopy.

iii. Effects of L. digitata manipulation on understorey algal assemblages

The influence of canopy algae on understorey assemblages is well known; the structure, abundance and diversity of epilithic understorey assemblages is regulated by shading (Kain & Jones, 1975; Foster, 1982; Reed & Foster, 1984; Kennelly, 1987; Arkema *et al.*, 2009), alterations to water movement caused by the canopy (Eckman, 1983) and by physical disturbance by the kelps themselves (Hawkins & Harkin, 1985; Irving & Connell, 2006). The majority of understorey algae have been shown to be tolerant to low light conditions (Boney & Corner, 1963; Norton *et al.*, 1977), and suffer mortality at higher irradiances (Jones & Dent, 1971). However, following the total loss of canopy, understorey algae increased at both study sites. This effect persisted until 2.5 years post clearance in manipulated plots, with the highest densities of understorey red algae found in 100% treatments. *L. digitata* has a long, flexible stipe so that the lamina scours the immediate substratum under the influence of wave action. The scour of kelps has been shown to have significant impacts on understorey algae communities (e.g. Irving & Connell, 2006), and the removal of this physical disturbance may allow understorey algal communities to proliferate in the absence of *L. digitata*. Increased abundance of understorey algae may help to limit the proliferation of annual kelps and invasive species, in a similar fashion to *H. elongata*.

iv. Influence of L. digitata manipulation on other Laminaria spp.

At both sites there was some evidence of movement of other *Laminaria* spp. up the shore after removal or reduction of *L. digitata* canopies; *L. hyperborea* in exposed conditions, and

L. ochroleuca in more sheltered conditions. The upper limit of both these species would appear to be set by competition with *L. digitata* (also see Hawkins & Hartnoll, 1985; Jenkins *et al.*, 1999; Jenkins *et al.*, 2005 for examples of upper limits being set by biological interactions), the removal of which releases these species to recruit to areas previously inhabited by *L. digitata*. Recent research, however, has suggested that cumulative desiccation stress, resulting from exposure to high summer temperatures during successive low tides may limit the movement of *L. ochroleuca* up the shore (King *et al.*, 2018). *L. ochroleuca* may have partial success filling the niche of *L. digitata* by moving into low shore tidal pools (King *et al.*, 2018). These species are both relatively long lived perennial species, although *L. hyperborea* populations are typically older (Chapter 3). The presence of these species in the low intertidal may limit the impact of the increase in annual species at these sites.

v. Impacts of L. digitata manipulation on standing stock of macroalgae

At both sites, a decrease in the density of *L. digitata* canopy was associated with an overall loss of biomass of the entire algal communities after 2.5 years of manipulation. While the reduction in algal biomass suggests an overall decrease in habitat available for colonisation by organisms, it may also play an important role in carbon cycling. The fact that vegetated marine environments support significant burial of organic carbon has led to the development of various climate mitigation strategies hinged on conservation and restoration of these environments (Krause-Jensen & Duarte, 2016). These so called blue carbon strategies have been developed for a range of marine habitats (e.g. seagrass beds, salt marshes and mangrove forests), but have generally disregarded macroalgae dominated habitats which develop on rocky reefs, where burial of such material is unlikely (Nellemann *et al.*, 2009; Mcleod *et al.*, 2011; Duarte *et al.*, 2013). Recently however, a number of mechanisms for the transport and delivery of macroalgal derived carbon to marine sediments, both coastal and deep sea, have been identified (see Krause-Jensen & Duarte, 2016). Estimates of the amount of carbon sequestering by macroalgae are globally ecologically significant. Given the high productivity of these systems, any loss in total biomass of algae represents a significant loss in primary production and organic carbon. The climate driven reduction in standing stock of macroalgae on the temperate rocky shores observed in this study is significant (~47% on the exposed shore, ~56% on the sheltered shore), and could have implications for carbon sequestration by macroalgae at regional scales.

vi. Conclusions

It is clear that a reduction or loss of *L. digitata* canopies had significant impacts on the rocky shore algal communities on both the exposed and sheltered shores examined in this study. Generally, in exposed areas *S. polyschides* has the potential to fill the spatial niche once occupied by *L. digitata*, and lead to a shift from a stable perennial-dominated system to one characterised by rapid changes in habitat structure and biomass, and is likely to cause changes to production, grazing and detrital regimes, potentially with wide reaching consequences. In more sheltered areas, the presence of *S. latissima* may temper this response, but may also leave room for an increase in the abundance of annual species in the future, with potential impacts on the biotic resistance of these communities to future invasion. On both shores, there was some evidence for the movement of other perennial *Laminaria* spp. up the shore, which over a longer timescale may have the potential to limit the impact of these annual species. Critically, the loss of *L. digitata* due to climate change has the potential to result in significant reductions in standing stock of macroalgae regardless of exposure, and will likely have significant implications on the structure and functioning of low intertidal rocky shores in the UK in the near future.

Chapter 6. General Discussion

6.1. *Main conclusions*

The main aim of this thesis was to investigate the impacts of climate change on habitat provision by kelp species and the wider consequences for kelp forest biodiversity in the UK. The UK represents an ideal study region to examine the impacts of ocean warming on benthic species in general (Forbes, 1858; Hiscock *et al.*, 2004), and on kelp-associated habitat provision in particular, in a range of ways. The coastline of the UK represents a latitudinal gradient of temperature which includes a ~9° latitude portion in the range of the dominant habitat forming kelp in the region. The UK also sits at an important biogeographic transition zone (Lewis, 1964; Hiscock *et al.*, 2004; Hawkins *et al.*, 2008; Hawkins *et al.*, 2009) with a number of species at the equatorward (trailing) and poleward (leading) edge of their ranges (Smale *et al.*, 2013). Moreover, the seas surrounding the UK have warmed significantly in recent decades, at rates around or above the global average (Smyth *et al.*, 2010; Hughes *et al.*, 2017). Prior to my study, our understanding of spatiotemporal variability in kelp-associated assemblages, and the key environmental drivers of variability patterns was limited. Also, there has been a paucity of research on the impacts of subtle changes in the relative abundance of habitat-forming species, and on the subsequent implications for local biodiversity patterns. This thesis also presents the first evidence of climate driven disruption of an important habitat cascade in marine systems. The key findings of each chapter are outlined below.

The holdfast assemblages associated with *Laminaria hyperborea* in the UK described in Chapter 2 are characteristically diverse and abundant, and are comparable in terms of richness to other kelp-dominated systems globally, and to other vegetated marine habitats (i.e. seagrass beds), which are widely recognised for their high biodiversity value. This chapter also found that the spatial variability of both mobile and sessile assemblages was high at all spatial scales considered: between regions, between sites within regions, and between holdfasts within sites. The key environmental factors driving this variability differed between mobile and sessile assemblages. Mobile assemblages were more closely linked to temperature variability than sessile assemblage structure, which appeared principally to be structured by variability in wave exposure.

In Chapter 3, I documented that the abundance of *Laminaria ochroleuca* has increased relative to that of *L. hyperborea* at key monitoring sites in the southwest UK since the 1980s. I recorded significant differences in stipe and holdfast assemblages associated with these host species. Most strikingly, assemblages associated with the stipe of *L. hyperborea* were, on average, >12 times more diverse and >3600 times more abundance (in terms of biomass) compared with those associated with the stipe of *L. ochroleuca*. Overall, assemblages associated with *L. ochroleuca* were markedly impoverished and comprised far fewer rare or unique taxa.

In Chapter 4, the facultative interaction between kelp and stipe-associated epiphytic algae was observed to be weaker for *L. ochroleuca* than for *L. hyperborea*: the biomass of epiphytic algae present on *L. hyperborea* stipes was >250 times greater than that observed on *L. ochroleuca* stipes. This reduced epiphytic material led to a significantly impoverished macro-invertebrate assemblage associated with *L. ochroleuca* stipes. The comparable loss of secondary habitat and subsequent mobile macro-invertebrate assemblages associated with *L. ochroleuca* represents disruption to an important habitat cascade present in *L. hyperborea* dominated kelp forests in the UK. Overall, a reduction in faunal abundance in regions which currently fall within the range of *L. ochroleuca* compared to areas pre-expansion may have significant impacts on kelp forest fishes by removing an important source of prey items.

In Chapter 5, the loss of *Laminaria digitata*, the dominant canopy former on a moderately exposed rocky shore in the UK, was observed to result in a phase shift to a system dominated by the annual pseudo-kelp *Saccorhiza polyschides*. On a more sheltered shore, the reduction in density or loss of *L. digitata* had a more subtle impact, likely tempered by the presence of another perennial kelp species, *Saccharina latissima*. In a sheltered area, persistent removal of some or all of *L. digitata* canopies also led to an increase in the abundance of annual species, namely *S. polyschides* and the invasive kelp *Undaria pinnatifida*. Canopy thinning or removal also had impacts on understorey algal assemblages. Crucially, the total standing stock of macroalgae was significantly reduced following a reduction in density, or loss of *L. digitata*, by up to ~56% on a sheltered shore.

6.2. *Ecological significance of current findings*

There is considerable evidence presented within this thesis that the dominant habitat-forming subtidal kelp in the UK, *Laminaria hyperborea* supports significant biodiversity. Study wide, 261 taxa and 122 taxa were found in association with *L. hyperborea* holdfasts and stipes, respectively, throughout more or less the entire range of this species in the UK (Appendix 2). Single *L. hyperborea* plants and associated epiphytic algae regularly supported in excess of 1000 individual mobile taxa. The average taxon richness of *L. hyperborea* holdfasts sampled throughout the study region was ~40 taxa, a figure comparable to, but in many instances notably higher than, previous reports of kelp holdfast richness (see Teagle *et al.*, 2017 and references therein). These figures also compare to those reported for other marine vegetated habitats known for their high biodiversity values, such as seagrass beds (e.g. in Western Australia; Edgar, 1990a; and the Mediterranean; Como *et al.*, 2008). Faunal abundance is highly variable between regions and within sites, and between kelps at small spatial scales. However, the majority of the species recorded throughout this study are highly mobile and have been observed to move freely throughout the kelp forest and to quickly colonise new available habitat, so that exchanges between kelp plants are thought to occur frequently (Norderhaug *et al.*, 2002; Waage-Nielsen *et al.*, 2003). By combining average faunal abundances of holdfast (Chapter 2) and stipe-epiphyte assemblages (Chapter 4) associated with *L. hyperborea* throughout the UK, it is possible to scale up to determine the average abundance of mobile macro-invertebrate fauna in a typical m^2 of UK kelp forest: ~6000 individuals per m^2. It is difficult to make overarching comparisons between the mean faunal density associated with kelp forests in the UK and with those in other regions globally for a number of reasons. Firstly, the majority of studies concerning kelp as biogenic habitat focus on one of the three distinct micro-habitats (i.e. the holdfast, the stipe, and the blade) exhibited by kelps; typically the holdfast, making inferences into whole kelp levels of biodiversity impossible. Secondly, a great deal of studies report only pooled study wide species lists or taxon richness values, making direct comparison between individual 'average' kelps difficult. Lastly, the sampling method used to sample kelps for these studies varies dramatically between studies, making direct comparison between kelp species and geographical region challenging. Regardless, as *L. hyperborea* populations in the UK are predicted to inhabit an area in the region of 8,100 (Smale *et al.*, 2016) to 16,000 km^2 (Yesson *et al.*, 2015), it is clear that these systems currently underpin a significant component of biodiversity in UK coastal waters.

Our understanding of spatiotemporal variability in kelp-associated assemblages and the key environmental drivers of variability patterns was, prior to this thesis, fairly limited. Despite previous research reporting consistent, predictable patterns in holdfast assemblage structure along gradients of latitude (e.g. Anderson *et al.*, 2005), the evidence presented in Chapter 2 suggests that these patterns are not so clear in the UK. Although a high degree of variation was found in the structure of holdfast associated assemblages between regions, these patterns did not vary predictably with along a gradient spanning ~9° latitude. Generally, differences between regions did not correspond with sequential shifts in latitude, or in temperature, suggesting that complex processes operating over multiple spatial scales are important drivers of assemblage structure. Local, regional-scale environmental factors in particular are likely to be of great importance in the development and subsequent structure of holdfast assemblages. For instance, regional-scale differences in turbidity, rates of deposition of organic matter and, critically, wave exposure were all determinants of the local structure of holdfast associated assemblages. Interestingly, the sessile and mobile components of these assemblages exhibited different patterns and may be influenced by environmental drivers, particularly temperature and wave exposure, to differing degrees due to divergence in life history or growth strategy. Recent work by Jurgens and Gaylord (2017) demonstrated the potential for the physical effects of habitat-forming species to disrupt latitudinal, temperature driven patterns in assemblage structure, by altering conditions for focal organisms and reducing thermal stress. While this work focused on intertidal habitats and such trends are likely to be weaker in subtidal habitats, it highlights the extent to which habitat-forming species can buffer the effects of temperature on associated communities (Moore *et al.*, 2007; Pocklington *et al.*, 2017). Such effects are also likely to affect sessile and mobile organisms differently, depending on the strength of their association with the holdfast structure and the degree of its ameliorating influence. This highlights the importance of considering the entire assemblage when investigating structural patterns in faunal assemblage in kelp forests, and other similar systems dominated by habitat-forming species, over large spatial scales. High variability across both small and large spatial scales hints at the potential of these assemblages to enhance our understanding into the sources and functions of marine biodiversity globally (Anderson *et al.*, 2005).

Much of the focus of my thesis lies on the differences in habitat provision potential between host kelp species, and on the drivers and subsequent impacts of shifts in the relative abundance of these species due to climate change. Kelp identity has been demonstrated to be important in the formation and structuring of associated assemblages through comparative studies (e.g. McKenzie & Moore, 1981; Blight & Thompson, 2008; Raffo *et al.*, 2009; Tuya *et al.*, 2011; Arnold *et al.*, 2016). The majority of these studies, however, consider kelp species which differ considerably in morphology (e.g. *Saccorhiza polyschides* and *Laminaria hyperborea*; McKenzie & Moore, 1981; Tuya *et al.*, 2011), scale (e.g. *Macrocystis pyrifera* and *Undaria pinnatifida*; Raffo *et al.*, 2009) or habitat (e.g. the intertidal *Laminaria digitata* and the typically subtidal *Laminaria ochroleuca*; Blight & Thompson, 2008). Chapter 3, however, compares the habitat provision of two closely related, morphologically similar kelp species which occupy very similar subtidal environments. This coupled with the climate-linked nature of the expansion of *L. ochroleuca* makes the results of these chapters of particular relevance to current and predicted real world scenarios. One of the major findings of this thesis is the stark difference in habitat provision between these species, with *L. ochroleuca* hosting an impoverished and depauperate assemblage compared to *L. hyperborea*. While holdfast assemblages are broadly comparable between species (Chapter 3), the major difference between host kelps lies in the interaction between epiphytic algae and the stipe of these species (Chapter 4). Of all the *L. ochroleuca* plants sampled throughout the course of this study over 70% of them were completely devoid of epiphytic material (Chapters 3 and 4). In Chapter 4, the biomass of algae removed from the stipes of *L. hyperborea* stipes was over 250 times greater than that removed from the stipes of *L. ochroleuca* plants. While the exact mechanisms behind the differences in formation of the stipe-epiphyte complex remain poorly understood, and unfortunately falls outside the scope of this thesis, it is clear that the strength of the facilitative interactions between *L. hyperborea* and the epiphytic algae which makes up the characteristic algal assemblage present on its stipe, are far greater than those for *L. ochroleuca*. This climate driven disruption of a habitat cascade (*sensu* Thomsen *et al.*, 2010) is, to my knowledge, the first of its kind recorded in a marine environment.

The increase in abundance of *L. ochroleuca* relative to *L. hyperborea* is likely to have ecologically significant consequences at broad spatial scales. The epiphytic algae colonising kelp stipes represent an important component of temperate rocky reef communities, forming extensive secondary habitat and increasing the quantity and complexity of available habitat (Christie *et al.*, 2007; Thomsen *et al.*, 2010). The stipe-epiphyte complex often supports high abundances of mobile macro-invertebrates such as gastropods, amphipods and polychaete worms (Christie *et al.*, 2003; Teagle *et al.*, 2017), which utilise this habitat for shelter and food (Christie *et al.*, 2007; Leclerc *et al.*, 2013), and subsequently act as an important food source for higher trophic levels (Norderhaug *et al.*, 2005). The observed difference in mobile invertebrate abundance associated with the stipe-epiphyte complex of *L. ochroleuca* and *L. hyperborea* was stark, with over 98% of all fauna sampled found in association with *L. hyperborea* (Chapter 4). This difference is likely driven solely by the comparative weakness of the facilitative interactions between the stipe of *L. ochroleuca* and potential epiphytic algae. In this way, the positive interactions which play significant roles in structuring this temperate marine community are indirectly broken down by climate, as the relative abundance of *L. ochroleuca* to *L. hyperborea* has increased in response to ocean warming. The broad scale impacts of this are best understood when comparing 'present' kelp forests in the UK, to those of the 'future' (using a space-for-time approach). In Plymouth Sound, in the southwest UK, *L. ochroleuca* now makes up ~45% of the population of kelp forests on the moderately exposed subtidal reefs sampled during the course of this investigation. The occurrence of this species alongside *L. hyperborea* reduces the biomass of epiphytic algae in the wider kelp forest by around 50% compared to reefs further north, currently unaffected by the range expansion of *L. ochroleuca.* The loss of this secondary habitat will drastically impact associated mobile invertebrates, a reduction in average faunal abundance of around 80% in areas within the range of *L. ochroleuca* (Chapter 4). The impacts of a reduction in faunal abundance on this scale are likely to have significant impacts on higher trophic levels. Kelp forest fish are known to feed extensively within kelp forests (Norderhaug *et al.*, 2005; Leclerc *et al.*, 2013) and to prey heavily on kelp associated fauna (Fredriksen, 2003; Norderhaug *et al.*, 2005). While the taxonomic resolution of the fish stomach content data presented in Chapter 4 is low, links can be made between the main groups found in fish guts and those found associated with the stipe-epiphyte complex of *L. hyperborea*.

While much of my work has been concerned with the impacts of climate driven substitutions of kelp species, those areas at which dominant habitat-forming kelp species reach the trailing edge of their range are at risk from climate driven loss of key foundation species. The loss of *L. digitata*, the dominant canopy-forming kelp along much of the wave exposed, intertidal rocky reefs in the northeast Atlantic, was experimentally shown to have significant impacts on algal communities in both sheltered and exposed shores (Chapter 5). Generally, loss or reduction of *L. digitata* caused an increase in the density of annual species, particularly of *Saccorhiza polyschides* which formed monospecific stands where *L. digitata* was experimentally removed on exposed shores. Such drastic shifts in canopy composition have obvious ramifications on the structure and longevity of habitat provided by kelps on rocky shores in the future. While there is evidence to suggest that *S. polyschides* can support similar levels of faunal abundance and diversity as *L. digitata* (Norton & Burrows, 1969; Norton, 1971; Lippert *et al.*, 2001; Blight & Thompson, 2008; Włodarska-Kowalczuk *et al.*, 2009), due to substantial differences to the structure of these habitats, it is likely that the identity of the taxa found associated with each species will differ considerably (Arnold *et al.*, 2016). Further, the majority of the studies on the assemblages associated with *S. polyschides* were carried out on subtidal populations (e.g.

Norton, 1971; McKenzie & Moore, 1981; Tuya *et al.*, 2011), and are not directly comparable to populations found in intertidal environments. Regardless of habitat provision, the seasonal loss of annual species will have drastic impacts on associated assemblage, simply through loss of extensive habitat space and three-dimensional habitat structure, and may result in assemblages dominated by quick growing, opportunistic species. In addition, as the dominant primary producer may influence the turnover, fate and associated nutrients within an ecosystem (Cebrián *et al.*, 1998), observed shifts from perennial to annual species may have effects over a broad spatial scale. As annual species grow faster, are generally more susceptible to grazing, and decompose faster than perennial species (Littler & Littler, 1980; Cebrián & Duarte, 1994; Duarte, 1995; Banta *et al.*, 2004), such a shift on rocky shores may lead to shifts in the timing and rate of growth and detrital output, altered detrital pathways, and increased turnover rates of organic matter. In more sheltered areas, the loss of *L. digitata* may lead to a decrease in the biotic resistance to invasion by non-native species, through increased space available for colonisation and alterations to competitive interactions. Critically, the loss of *L. digitata* on intertidal rocky shores leads to a reduction in the standing stock of algae, regardless of exposure.

6.3. *Implications for Conservation and Management*

The variability in the structure of assemblages associated with the holdfast of *Laminaria hyperborea* has been shown to be highly variable throughout the UK, which makes up the central portion of its European range from northern Portugal to northern Norway and the Murmansk coast in Russia. The ~2.7°C change in temperature experienced by these assemblages from Plymouth in the southwest to Orkney in the north was not identified as the primary driver of regional patterns in assemblage structure. While the growth and morphology of kelps is strongly linked to temperature (Steneck *et al.*, 2002; Harley *et al.*, 2012), patterns in the structure of biogenic habitat (i.e. the overall size of holdfasts and the amount of free space for colonisation found within) provided by *L. hyperborea* throughout this range did not vary predictably with latitude. In the UK, local scale environmental variability appears to be more important in structuring kelp-associated assemblages than latitudinal-scale variation in sea temperature. Generally sessile holdfast assemblages are much more consistent at large spatial scales than their mobile counterparts, but both displayed local-scale variation in response to measurable changes in local environmental conditions. Such local scale variation has been observed in response to a range of anthropogenic stressors including pollution from sewage outfall effluent (Smith & Simpson, 1992) and oil spills (Smith & Simpson, 1998).

Clearly, anthropogenic stressors are of key importance to the quality and quantity of biogenic habitat provided by kelp, so that land-use, run-off, and increases levels of nutrients and sediments in the water column will have significant impacts on the assemblages associated with kelps in the UK. Such evidence has raised the question of whether kelp holdfasts can be used as self-contained units of biodiversity suitable for environmental monitoring (Sheppard *et al.*, 1980; Smith & Simpson, 1992; Anderson *et al.*, 2005). While processing and identification of holdfast fauna is time-consuming and requires a degree of taxonomic expertise, there is evidence to suggest that even at coarser taxonomic levels (Anderson *et al.*, 2005), studies of environmental impacts using holdfast fauna have successfully detected evidence of stress (Smith & Simpson, 1998). While further work is required in the UK, the lack of latitudinal patterns in kelp assemblage structure may allow for direct comparison between regions, and potentially assist in the use of holdfast assemblages as effective indicators of environmental change in the future.

Sea water temperatures have increased significantly around the UK in the recent decades (Southward *et al.*, 1995; Hawkins *et al.*, 2008; Belkin, 2009; Hawkins *et al.*, 2009) and are expected to continue to rise throughout the next century (Philippart *et al.*, 2011). Despite evidence that latitudinal-scale variation in temperature is less important in driving patterns in the structure of kelp-associated assemblages than local-scale environmental factors, temperature is likely to play more of a role in the near future. Areas in the southern UK are already experiencing temperatures high enough to have measurable impacts on the ecophysiology of kelps in the UK (e.g. *L. hyperborea*; Müller *et al.*, 2009) during anomalous warming events (e.g. Joint & Smale, 2017). Such sea water temperatures are predicted to become more common in the near future (Philippart *et al.*, 2011). In the UK and globally, range shifts of foundation species are already having significant effects on ecosystem structure and function. Shifts in the distribution of kelps in the UK have already begun (e.g. *Laminaria ochroleuca*; Parke, 1948b in response to warming up to the 1950's; Smale *et al.*, 2015 and to more recent rapid climate change), and more are predicted in the near future (e.g. *L. digitata*; Raybaud *et al.*, 2013; and *L. hyperborea*; Assis *et al.*, 2016; see Fig 6.1). Any climate-driven reduction in the biomass, density, spatial extent or longevity of dominant habitat-forming kelps will result in the reduction of habitat available for colonisation, and will have knock-on impacts on associated faunal assemblages. Shifts in

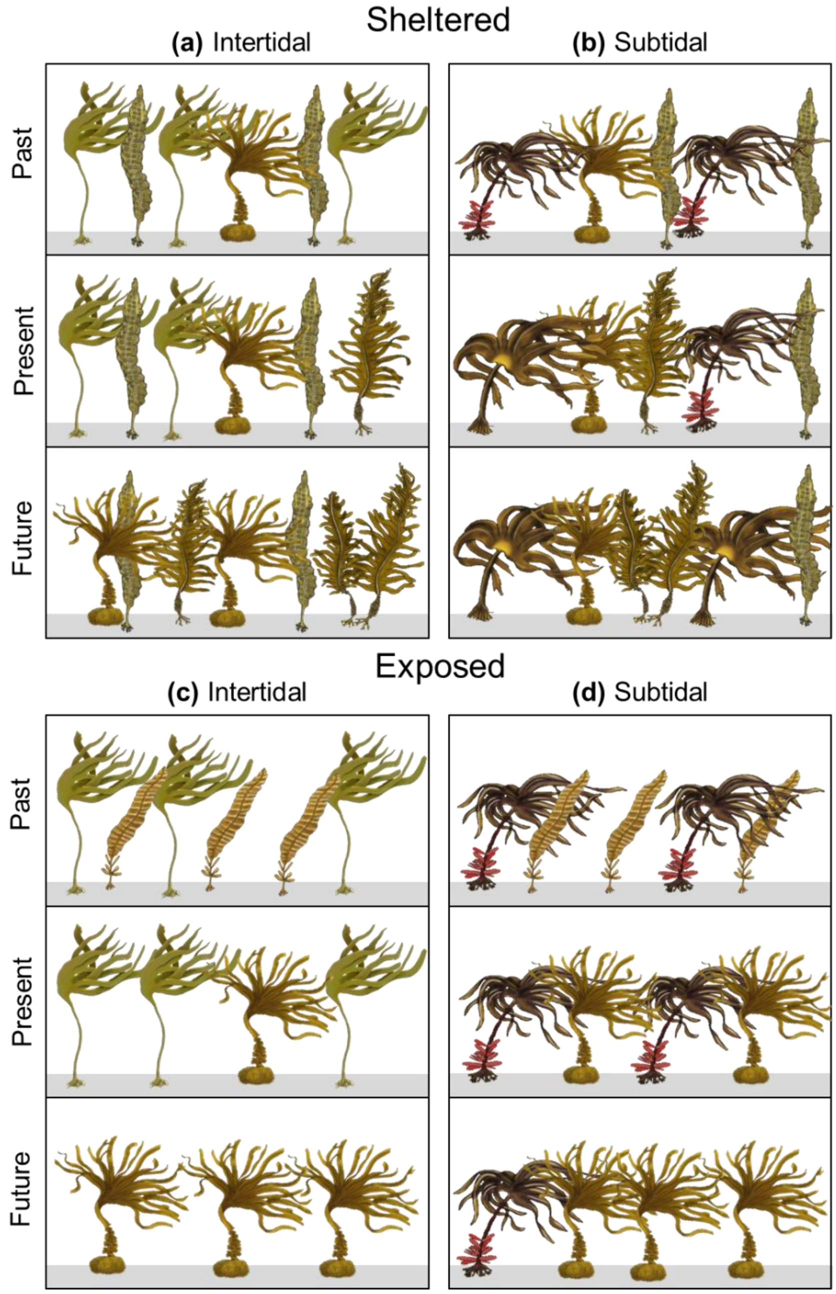


Fig 6.1 Past and present kelp forest structure and predicted future change in the southwest British Isles due to increasing seawater temperatures. (a) sheltered intertidal shores characterised by a mixed assemblage comprising *Laminaria digitata*, *Saccharina latissima* and *Saccorhiza polyschides*. Many of these shores have been invaded by the Japanese kelp, *Undaria pinnatifida*. Due to increasing seawater temperature, *L. digitata* is likely to be lost from these shores, resulting in an increase in annual species such as *U. pinnatifida* and the pseudo-kelp *S. polyschides.* (b) Subtidal rocky reef in sheltered environments characterised by mixed assemblages composed of *Laminaria hyperborea*, *S. polyschides* and *S. latissima*. Abundances of the warm-water kelp *Laminaria ochroleuca* have increased in this region since the late 1940s, potentially replacing the cold-water dominant *L. hyperborea* in more sheltered areas. These areas have also been invaded by *U. pinnatifida*. These trends are likely to continue into the future. (c) Exposed intertidal reefs were once characterised by mixed stands of *L. digitata* and *Alaria esculenta.* However, the range of *A. esculenta* retracted during the warm period of the 1940s and 1950s, and most populations have not recovered. Marginal populations of *L. digitata* are predicted to disappear from these shores in a similar manner to those in more sheltered areas, probably causing a shift in dominance to the annual pseudo-kelp *S. polyschides*. (d) Subtidal populations of *A. esculenta* responded in a similar way to the warm period of the 1940s and 1950s, and have been lost from many areas of the southwest British Isles. The abundance of *S. polyschides* has increased over the last few decades and it now forms mixed stands with the assemblage dominant *L. hyperborea* on many wave exposed subtidal reefs. Abundances of *L. hyperborea* are likely to be negatively impacted by increasing seawater temperatures in the near future. Kelp images courtesy of Jack Sewell.

the relative abundance of species will also alter the strength of species interactions, both positive and negative, with the potential to drastically alter habitat structure, longevity and abundance.

For instance, *L. digitata* is an intertidal kelp species which dominates wave exposed rocky reefs throughout much of the northeast Atlantic, represents an important source of three-dimensional habitat (Lewis, 1964; Schultze *et al.*, 1990; Blight & Thompson, 2008; Schaal *et al.*, 2012; Schaal *et al.*, 2016) and food in these systems (Schaal *et al.*, 2010). Populations of *L. digitata* in the UK are now marginal, occurring at the trailing range edge, with the southern limit of the range currently in northern France. Due to increasing air and sea water temperatures in the region over recent decades (L'Hévéder *et al.*, 2016; Hughes *et al.*, 2017), such populations have been adversely affected, with declines reported around Ireland (Simkanin *et al.*, 2005), the English Channel (Gevaert *et al.*, 2008), and northern France (Cosson, 1999; Davoult *et al.*, 2011). The experimental removal of this species on exposed shores in the southwest UK has resulted in an overall reduction in biomass of algae present, caused shifts in dominance to the annual pseudo-kelp *Saccorhiza polyschides*, and may reduce the biotic resistance to invasion of these shores by the invasive kelp *Undaria pinnatifida*. However, *L. digitata* also holds significant economic value as a source of alginate, a gel-forming polysaccharide used in numerous industries (e.g. paint, food, fabric and cosmetics; Billot *et al.*, 2003), as well as food for human consumption (Mabeau & Fleurence, 1993; Kolb *et al.*, 2004), and increasingly, as a base component in the production of biofuels (Adams *et al.*, 2011b; Adams *et al.*, 2011a; Jung *et al.*, 2013). The yield of such harvests can be high, with an average annual production of ~54,000 tons of *L. digitata* in France alone (Alban *et al.*, 2011). The importance of this species both ecologically and economically, and the drastic impacts of its loss on rocky shores in this region raises questions about the on-going sustainability of such exploitation. Marginal populations are at particular risk from the effects of harvesting, as genetic diversity in populations at the southern range edge are already significantly reduced, likely caused by local demographic effects of reducing population size (Valero *et al.*, 2011). Connectivity between populations of kelps is generally low (Santelices, 1990), due to the limited dispersal distances of these species (e.g. Sundene, 1962; Anderson & North, 1966; Dayton, 1973), particularly in intertidal species where spore or gamete dispersal is limited along the shore at low tide (Valero *et al.*, 2011). This highlights the importance of preservation of isolated populations located at the trailing edge (see Valero *et al.*, 2011). Clearly, such harvesting in the UK, particularly in the southwest where populations are most at risk from the effects of increasing sea water temperatures, should be closely regulated to avoid long-lasting detrimental effects, and ultimately the extirpation of marginal populations.

There is increasing evidence that vegetated marine habitats support ecologically and globally significant rates of organic carbon burial (Duarte *et al.*, 2005). Macroalgae dominated habitats however, have been large excluded from discussion regarding marine carbon sinks (Krause-Jensen & Duarte, 2016) as macroalgal assemblages typically grow on hard substrata (e.g. rocky reefs) where capture of carbon by burial is unlikely. Nonetheless, recently pathways for the export and sequestration of macroalgae derived carbon in coastal and deep sea sediments have been identified (Krause-Jensen & Duarte, 2016). Kelps in particular represent some of the productive habitats on Earth (Mann, 1973; Brady-Campbell *et al.*, 1984; Reed *et al.*, 2008). Through constant loss of old lamina material, and dislodgment of entire plants due to wave action, kelps underpin a continuous export of material to adjacent systems. As kelps dominate intertidal and subtidal rocky reefs throughout the coastline of the UK, and that the dominant subtidal kelp *Laminaria hyperborea* alone inhabits an area in the region of 8,000 (Smale *et al.*, 2016) to 16,000 km^2 (Yesson *et al.*, 2015), it is likely that kelp forests in the UK represent a globally relevant carbon sink. Climate-driven reductions in the local density of dominant canopy forming kelp species has been shown to reduce the total biomass of macroalgae present on temperate rocky shores by up to 57%, which will likely lead to significant changes in the production and detrital regimes of these systems and potential affect rates of carbon sequestration. Carbon sequestration should be taken into account when managing these systems in the UK and any changes in the sequestration of macroalgal derived carbon should be closely monitored. Restoration of degraded kelp forest should also be included in strategies to mitigate climate change.

With growing recognition of the importance of kelp dominated habitats, there are recent examples of conservation and management strategies specifically targeted at kelp species. In Australia, *Macrocystis pyrifera* forests were classified as ‘endangered’ under the Environmental Protection and Biodiversity Convention Act in 2012 (see Bennett *et al.*, 2016) following significant declines in these habitats since the 1980s (Johnson *et al.*, 2011). Two species of kelp from the Mediterranean (*Laminaria ochroleuca and Laminaria rodriguezii*) are listed in Annex 1 of the Bern Convention (Airoldi & Beck, 2007). There have also been calls to list *L. rodrigeuzii*, which now persists solely around a small off-shore island in the Adriatic, presumably as a result of bottom trawling, as ‘endangered’ under the IUCN Red List (Žuljević *et al.*, 2016). In Europe more generally, ‘Reefs’ are listed under Annex 1 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 & Beck, 2007). Protection of these kelp forest habitats has been shown to facilitate restoration of degraded reef (Shears & Babcock, 2002), as well as increase the abundance of commercially important finfish and shellfish compared to adjacent exploited areas (Babcock *et al.*, 1999; Paddack & Estes, 2000). It has been suggested that networks of smaller areas would be more effective in conserving kelp species than a single large-scale protected area (Valero *et al.*, 2011). Some of these smaller areas would subsequently require specific conservation measures, dependent on the kelp species involved, human impacts and uses within the area, and local environmental conditions. Indeed, the species of the kelps present in these areas is likely to inform the level of management required. The continued increase in abundance of the warm-water kelp *L. ochroleuca* in the southwest UK is having significant negative impacts on kelp forest associated biodiversity, and potentially on commercially important species of fish. While the abundance of *L. ochroleuca* is used as an indicator of climate change, it may also reduce the value of such areas compared to areas dominated by *L. hyperborea*, with subsequent implications for small-scale management. As these species differ in their tolerance to wave exposure, it may be as simple as requiring higher levels of regulation in more exposed areas, which may act as refugia for future *L. hyperborea* populations (Smale *et al.*, 2015).

Fundamentally, the main threat to kelp forests in general is on-going anthropogenic climate change driven by increasing carbon emissions. The fate of kelp forests in the UK, and more broadly in the northeast Atlantic as a whole, is dependent on the rate of this change. In a recent study by Assis *et al.* (2016), the loss of suitable habitats for *L. hyperborea* ranged from 8.4% to 39.5% depending on the emission scenarios used in the models. Recent evidence suggests, however, that even the highest emission scenarios set out by the IPCC may underestimate the extent of global climate warming (Brown & Caldeira, 2017). The implications of climate change on the persistence and future health of this, and other kelp species in the UK, is closely linked to the response of humankind, by changing economies, policy and technology (Moss *et al.*, 2010). The absence of change will likely result in negative effects for kelp forests globally.

6.4. *Limitations and Future Research*

This thesis was largely successful in that it addressed the broad questions set out in the introduction. The work has shown that climate change is having significant effects on the provision of habitat by kelp forests in the UK, by driving a redistribution of species and reshuffling of communities as biogeographic ranges respond to shifting isotherms. However, there are areas which require further research in the near future in order to fully understand the impacts of some of the results presented in this thesis, as well as other broader concerns which should be rectified. Firstly, further research is required into the impacts of an increase in the abundance of *L. ochroleuca* relative to *L. hyperborea* on higher trophic levels. While Chapter 4 presents data from fish stomach analyses, there is yet to be explicit evidence of the link between kelp-epiphyte associated macro-invertebrates and fishes in UK kelp forests. It is important to fill the missing gap in these results, in order to confirm the source of the prey fed on by kelp forest fish. The experiments required to generate this data, while simple in scope, can be logistically challenging, expensive, and time consuming, and unfortunately fell outside the scope of this thesis.

While the difference between habitat provision by *L. ochroleuca* and *L. hyperborea* is now well established, the mechanisms behind these differences are yet to be fully explored. The difference in the strength of facilitative interactions between the stipe of these species and epiphytic algae is likely caused by differences in surface topography and texture in the stipe, the production of antifouling compounds, or the loss of epidermatic material by *L. ochroleuca*, or likely a combination of the three (Chapter 3). Experimental manipulation of these parameters through the use of high resolution plastic mimics could begin to shed some light on the mechanisms driven the differences observed between species. Advances in 3D modelling and printing could also 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.

The wider impacts resulting from an increase in the abundance of *L. ochroleuca* relative to *L. hyperborea* on algal and macrofaunal assemblages found within kelp forests, but not directly associated with kelps are also yet to be investigated. Subtle differences in morphology, such as stipe length and the colouration of the lamina, between species (e.g. Smale *et al.*, 2015) may have impacts on epilithic understorey algal assemblages, with potential implications for associated assemblages. Longer stipes may cause *L. ochroleuca* to break the typically dense canopy associated with *L. hyperborea* forests, altering the light environment beneath, causing structural changes to understorey algal assemblages. As these assemblages host significant diversity (Leclerc *et al.*, 2015) and the structure of host algae is of great important to the diversity and abundance of associated assemblages (e.g. Christie *et al.*, 2007), subtle alterations to the composition and density of epilithic algal assemblages may have significant implications for wider biodiversity patterns.

The impacts associated with the loss of *L. digitata* on exposed rocky shores were a major finding of this research. However, the wider impact of replacement of this species with the annual *Saccorhiza polyschides* has yet to be investigated. Comparisons in the habitat provision by both of these species, specifically in the intertidal, would allow further insight into the results of seasonal habitat loss and alterations in three-dimensional habitat structure on kelp associated assemblages in these environments. Additionally, further investigation in to changes in total standing stock of algae and biomass dynamics on these shores, as well as subsequent impacts on detrital pathways, timings, transport and consumption, and potential differences in grazing resistance and thallus palatability between species will also allow broader predictions to be made into the wider effects of the loss of this dominant habitat-forming species on future intertidal rocky shores.

Finally, steps must be taken to form an accurate picture of habitat provision and associated biodiversity patterns for representative number of kelps globally; 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 different sampling methods, survey designs, habitat metrics (e.g. total habitat volume versus habitable space; see Introduction) and ecological response variables used and presented between studies. 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 assemblages 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.

6.5. Concluding remarks

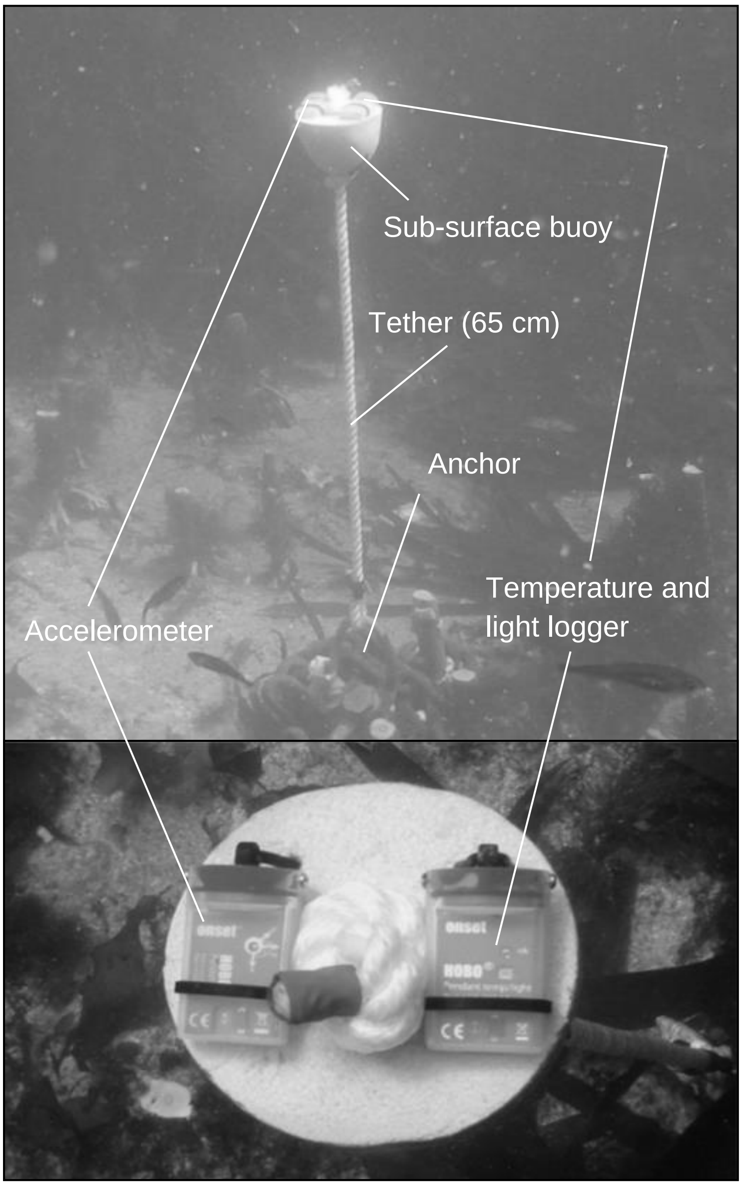
It is clear that kelp forests in the UK support significant biodiversity, even at the scale of a single plant. On-going increases in sea water temperature associated with climate change are driving changes in kelp forest structure, through the addition and subtraction of species as biogeographical ranges respond to shifting isotherms. Such changes are altering species interactions, and subsequently driving change in local and regional biodiversity patterns, likely with wide ranging impacts to trophic interactions.

The loss or degradation of similar biogenic habitat in other systems (e.g. coral reefs, seagrass beds) has received considerable media attention, and generates considerable international funding to assist in critical research. Kelp forests however, are not subject to the global awareness, both political and public, of similar, perhaps more charismatic systems, despite the importance of kelp forests to the millions of people globally who interact with these habitats, many of whom depend on the ecosystem services supported by these systems. Efforts must be made to engage with the public and with policy makers, to help to rid kelp of its unfortunate, and frankly, undeserved image problem, in order to allow for continued, collaborative research, management, and protection of these critical near-shore habitats.

Appendices

Appendix 1.

Fig. A1. Environmental sensors deployed during data collection for *Chapter 2* and *Chapter 3*. Water motion was recorded with an accelerometer (HOBO® Pendant G Logger), attached to a subsurface pellet buoy which was tethered to the seabed by a 0.65 m rope and clump weight, to measure water movement in three axes every 5 minutes (Figurski *et al.*, 2011). An additional sensor (HOBO® Temperature/Light Weatherproof Pendant Data Logger 8k) was attached to the buoy, facing upwards, and collected and logged temperature and light intensity data every 20 minutes.



Appendix 2.

Table A1. Complete list of taxa identified, including higher taxonomic groups. Crosses denote in which chapter(s) examples of each taxa were recorded. Sessile assemblage precedes mobile assemblage. HFG = higher taxonomic group.

HTG	Species	2	3	4	5
Phaeophyta	*Himanthalia elongata*				X
Phaeophyta	*Laminaria digitata*				X
Phaeophyta	*Laminaria hyperborea*	X	X	X	X
Phaeophyta	*Laminaria ochroleuca*		X	X	X
Phaeophyta	*Saccharina latissima*				X
Phaeophyta	*Saccorhiza polyschides*				X
Phaeophyta	*Undaria pinnatifida*				X
Rhodophyta	*Callophyllis lacinata*		X		
Rhodophyta	*Cryptopleura ramosa*		X		
Rhodophyta	Encrusting coralline		X		
Rhodophyta	Haraldiophyllum bonnemaisonii		X		
Rhodophyta	*Heterosiphonia plumose*		X		
Rhodophyta	*Lomentaria articulata*		X		
Rhodophyta	*Membranoptera alata*		X		
Rhodophyta	*Palmaria palmata*		X		
Rhodophyta	*Phycodrus rubens*		X		
Rhodophyta	*Polysiphonia* sp.		X		
Rhodophyta	*Rhodymenia holmessii*		X		
Rhodophyta	*Rhodymenia pseudopalmata*		X		
Anthozoa	*Actiniidae spp.*	X			
Ascidiacea	*Ascidan spp.*	X			
Ascidiacea	*Botryllus schlosseri*		X		
Ascidiacea	*Dendrodoa grossularia*		X		
Ascidiacea	*Didemnidae* spp.	X	X		
Ascidiacea	*Mogula* spp.		X		
Ascidiacea	*Phallusia mammillata*		X		
Ascidiacea	*Polycarpa fibrosa*		X		
Ascidiacea	*Polycarpa pomaria*		X		
Ascidiacea	*Pyura tessellata*		X		
Ascidiacea	*Stolidobranchia* spp.		X		
Ascidiacea	*Styela clava*		X		
Ascidiacea	*Styela coriacea*		X		
Bivalvia	*Anomia ephippium*	X	X		
Bivalvia	*Hiatella arctica*	X	X		
Bivalvia	*Kellia suborbicularis*	X	X		
Bivalvia	*Mediolula phaseolina*	X	X		
Bivalvia	*Mimachlamys varia*	X			
Bivalvia	*Musculus subpictus*	X	X		
Bivalvia	*Musculus* spp.		X		
Bivalvia	*Mytilus spp.*	X	X	X	
Bivalvia	*Parvicardium minimum*		X		
Bivalvia	*Parvicardium pinnulatum*		X		

Bivalvia	***Parvicardium spp.***	**X**	
Bivalvia	*Pectinidae spp.*	X	
Bivalvia	*Polititapes rhomboides*	X	X
Bivalvia	*Timoclea ovata*	X	
Bivalvia	*Turtonia minuta*	X	
Bivalvia	*Venerupis corrugata*	X	X
Bryozoa	*Aetea anguina*	X	
Bryozoa	*Amathia lendigera*	X	X
Bryozoa	*Amphiblestrum flemingii*	X	
Bryozoa	*Bicellariella ciliata*	X	
Bryozoa	*?Bugulina fulva*	X	
Bryozoa	*Callopora lineata*	X	X
Bryozoa	*Callopora rylandi*	X	
Bryozoa	*Cellepora pumicosa*	X	X
Bryozoa	*Celleporella hyalina*	X	X
Bryozoa	*Celleporina hassallii*	X	X
Bryozoa	*Cradoscrupocellaria reptans*	X	X
Bryozoa	*Crisia aculeata*	X	X
Bryozoa	*Crisia denticulata*	X	X
Bryozoa	*Crisia eburnea*	X	X
Bryozoa	*Crisida cornuta*	X	X
Bryozoa	*Disporella spp.*	X	X
Bryozoa	*Electra pilsoa*	X	X
Bryozoa	*?Escharella labisoa*	X	X
Bryozoa	*Escharoides coccinea*	X	X
Bryozoa	*Fenestrulina malusii*	X	
Bryozoa	*Filicrisia geniculata*	X	X
Bryozoa	*Haplota clavata*		X
Bryozoa	*Membranipora membranacea*	X	X
Bryozoa	*Membraniporella nitida*	X	
Bryozoa	*Microporella ciliata*	X	X
Bryozoa	*Omalosecosa ramulosa*	X	X
Bryozoa	*Oshurkovia (Umbonula) littoralis*	X	X
Bryozoa	*Phaeostachys spinifera*	X	
Bryozoa	*Schizomavella cornuta*		X
Bryozoa	*Schizomavella hastata*	X	X
Bryozoa	*Schizomavella linearis*	X	X
Bryozoa	*Scruparia chelata*	X	X
Bryozoa	*Scrupocellaria scrupea*	X	X
Bryozoa	*Scrupocellaria scruposa*	X	X
Bryozoa	*Smittina affinis*	X	
Bryozoa	*Tubulipora spp.*	X	X
Cirripedia	*Acasta spongites*	X	
Cirripedia	*Austrominius modestus*		X
Cirripedia	*Balanus balanus*	X	
Cirripedia	*Balanus crenatus*	X	X

Cirripedia	***Chirona hameri***	**X**		
Cirripedia	*Hesperibalanus fallax*	X	X	
Cirripedia	*Verruca stroemia*	X	X	
Hydrozoa	*Abietinaria filicula*	X		
Hydrozoa	*Amphisbetia operculata*	X	X	
Hydrozoa	*Diphasia attenuata*	X		
Hydrozoa	*Kirchenpaueria pinnata*	X	X	
Hydrozoa	*Kirchenpaueria similis*		X	
Hydrozoa	*Laomedea flexuosa*		X	
Hydrozoa	*Obelia spp.*	X	X	
Hydrozoa	*Plumularia setacea*	X	X	
Hydrozoa	*Sertularella spp.*	X	X	
Hydrozoa	*Sertularia distans*	X	X	
Polychaeta	*Serpulidae spp.*	X	X	
Polychaeta	*Spirorbidae spp.*	X	X	
Polychaeta	*Spirobranchus* spp.	X	X	X
Porifera	Demosponge A	X		
Porifera	Demosponge B	X	X	
Porifera	Demosponge C		X	
Porifera	Demosponge D	X	X	
Porifera	Demosponge E	X	X	
Porifera	Demosponge F	X	X	
Porifera	Demosponge G	X	X	
Porifera	Deomsponge H		X	
Porifera	Demosponge I		X	
Porifera	Demosponge J		X	
Porifera	*Dysidea fragilis*	X		
Porifera	Flat sponge	X	X	
Porifera	*Halicondriidae* spp.		X	
Porifera	*Hemedesmiidae* spp.		X	
Porifera	*Microionidae* spp.		X	
Porifera	*Mycalidae* spp.		X	
Porifera	*Sycon ciliata*	X	X	
Actinopterygii	*Gobiesocidae spp.*	X		
Amphipoda	*?Gitana sarsi*	X		
Amphipoda	*Abludomelita obtusata*	X		
Amphipoda	*Acanthonotozomatidae spp.*	X		X
Amphipoda	*Amphilochus manudens*	X		
Amphipoda	*Ampithoe spp.*	X		X
Amphipoda	*Aora typica*	X		X
Amphipoda	*Aoridae* ♀	X		X
Amphipoda	*Apherusa bispinosa*	X		X
Amphipoda	*Apherusa jurinei*	X		X
Amphipoda	*Apolochus neapolitanus*	X		
Amphipoda	*Caprella acanthifera*	X		X
Amphipoda	*Caprella fretensis*			X

Amphipoda	***Caprella penantis***		**X**
Amphipoda	*Caprella septentrionalis*	X	
Amphipoda	*Caprella sp. A*	X	
Amphipoda	*Caprella spp. complex*	X	
Amiphipoda	*?Caprella tuberculata*		X
Amphipoda	*Corophium acutum*		X
Amphipoda	*Dexamine spinosa*	X	x
Amphipoda	*Dexamine thea*	X	
Amphipoda	*Dexamine* spp.		X
Amphipoda	*Elasmopus rapax*	X	
Amphipoda	*Erichthonius brasiliensis*	X	X
Amphipoda	*Gammaropsis maculata*	X	X
Amphipoda	*Gitana sarsi*	X	X
Amphipoda	*Jassa spp.*	X	X
Amphipoda	*Lembos websteri*	X	
Amphipoda	*Leucothoe spinicarpa*	X	X
Amphipoda	*Liljeborgia pallida*	X	
Amphipoda	*Lysianassa certatina*	X	X
Amphipoda	*Maera grossimana*	X	
Amphipoda	*Melitidae spp.*	X	
Amphipoda	*Monocorophium sextonae*	X	X
Amphipoda	*Orchomene spp.*	X	
Amphipoda	*Othomaera othonis*	X	
Amphipoda	*Parajassa pelagica*	X	
Amphipoda	*Peltocoxa damnoniensis*		X
Amphipoda	*Pereionotus testudo*	X	
Amphipoda	*Phtisica marina*	X	
Amphipoda	*Podocerus variegatus*		X
Amphipoda	*Pseudoprotella phasma*	X	
Amphipoda	*Stenothoidae spp.*	X	X
Amphipoda	*Tritaeta gibbosa*	X	X
Amphipoda	*Tryphosella sarsi*	X	
Asteroidea	*Asterias rubens*	X	
Asteroidea	*Asterina gibbosa*	X	X
Asteroidea	*Asteroidea juv.*	X	
Decapoda	*Cancer pagurus*	X	
Decapoda	*Decapoda juv.CHANGE*	X	
Decapoda	*Eualus occultus*	X	
Decapoda	*Eualus pusiolus*	X	
Decapoda	*Eualus spp.*	X	
Decapoda	*Eurynome spinosa*	X	
Decapoda	*Eurynome spp.*	X	
Decapoda	*Galathea spp.*	X	
Decapoda	*Galathea strigosa*	X	
Decapoda	*Hippolyte varians*	X	X
Decapoda	*Hippolytidae spp.*	X	X

Decapoda	***Macropodia deflexa***			**X**
Decapoda	*Pilumnus hirtellus*	X		X
Decapoda	*Pisidia longicornis*	X		
Echinoidea	*Psammechinus miliaris*	X		
Gastropoda	*?Buccinidae spp.*	X		
Gastropoda	*?Manzonia zetlandica*	X		
Gastropoda	*Calliostoma ziziphinum*	X		
Gastropoda	*Alvania semistriata*			X
Gastropoda	*Cerithiopsis spp.*	X		
Gastropoda	*Cerithiopsis tubercularis/barleei*	X		X
Gastropoda	*Chauvetia brunnea*	X		
Gastropoda	*Crisilla semistriata*	X		
Gastropoda	*Doto* spp.			X
Gastropoda	*Fissurellidae spp.*	X		
Gastropoda	*Gibbula cineraria*	X		X
Gastropoda	*Lacuna parva*	X		X
Gastropoda	*Lacuna vincta*	X		X
Gastropoda	*Lamellaria perspicua/latens*	X		X
Gastropoda	*Margarites helicinus*	X		
Gastropoda	*Marshallora adversa*	X		
Gastropoda	*Nudibranchia spp.*	X		
Gastropoda	*Ocenebra erinaceus*	X		
Gastropoda	*Onchidorididae spp.*	X		
Gastropoda	*Onoba aculeus*	X		
Gastropoda	*Onoba semicostata*	X		
Gastropoda	*Onoba spp.*	X		
Gastropoda	*Opisthobracnchia spp.*	X		
Gastropoda	*Patella pellucida*	X	X	X
Gastropoda	*Retusa truncatula*	X		
Gastropoda	*Rissoa lilacina*	X		X
Gastropoda	*Rissoa parva (Rissoidae sp A)*	X		X
Gastropoda	*Rissoaidae sp. B (smooth)*	X		
Gastropoda	*Rissoidae sp. C*	X		
Gastropoda	*Spiralinella spiralis*	X		
Gastropoda	*Tectura virginea*	X		
Gastropoda	*Tricolia pullus*	X		X
Gastropoda	*Tritia incrassata*	X		
Gastropoda	*Trivia arctica*	X		
Gastropoda	*Trivia monacha*	X		
Gastropoda	*Velutina velutina*	X		
Holothuroidea	*Cucumariidae spp.*	X		
Isopoda	*?Idotea neglecta*	X		
Isopoda	*Anthura gracilis*	X		
Isopoda	*Astacilla damnoniensis*	X		X
Isopoda	*Cymodoce truncata*	X		
Isopoda	*Idotea gramulosa*	X		

Isopoda	***Idotea pelagica***	**X**	**X**
Isopoda	*Jaeropsis brevicornis brevicornis*	X	
Isopoda	*Janira maculosa*	X	
Isopoda	*Janiropsis breviremis*	X	
Isopoda	*Munna kroyeri*	X	
Isopoda	*Sphaeroma* spp.		X
Isopoda	*Stenosoma lancifer*	X	X
Leptostraca	*Nebalia bipes*	X	
Mysida	*Heteromysis norvegica*	X	
Mysida	*Mysidae spp.*	X	
Mysida	*Praunus inermis*	X	X
Nemertea	*Nemertea* spp.		X
Ophiuroidea	*Amphipholis squamata*	X	X
Ophiuroidea	*Ophiothrix fragilis*	X	X
Ophiuroidea	*Ophiurida spp.*	X	
Polychaeta	*?Amphiglena mediterranea*		X
Polychaeta	*?Eupolymnia/Neoamphitrite spp.*	X	
Polychaeta	*?Glycera capitata*	X	
Polychaeta	*?Harmothoe imbricata*	X	
Polychaeta	*?Oriopsis spp.*	X	
Polychaeta	*?Paraonidae spp.*	X	
Polychaeta	*?Proceraea scapularis*	X	
Polychaeta	*?Spio goniocephala*	X	
Polychaeta	*?Trypanosyllis spp.*	X	
Polychaeta	*Alentia gelatinosa*	X	
Polychaeta	*Amblyosyllis formosa*	X	
Polychaeta	*Aonides oxycephala*	X	
Polychaeta	*Autolytus/ Myrianida* spp.		X
Polychaeta	*Branchiomma bombyx*	X	
Polychaeta	*Capitella capitata*	X	
Polychaeta	*Cirratulidae spp.*	X	
Polychaeta	*Eulalia spp.*	X	
Polychaeta	*Eulalia viridis*	X	
Polychaeta	*Eumida spp.*	X	
Polychaeta	*Eunice spp.*	X	
Polychaeta	*Eurysyllis tuberculata*	X	
Polychaeta	*Eusyllis blomstrandi*	X	X
Polychaeta	*Flabelligera affinis*	X	
Polychaeta	*Glycera spp.*	X	
Polychaeta	*Harmothoe extenuata*	X	
Polychaeta	*Harmothoe impar*	X	X
Polychaeta	*Harmothoe pagenstecheri*	X	
Polychaeta	*Harmothoe spinifera*	X	
Polychaeta	*Harmothoe spp.*	X	
Polychaeta	*Jasmineria elegans*	X	
Polychaeta	*Lepidonotus clava*	X	X

Polychaeta	**Lepidonotus squamatus**	**X**	
Polychaeta	*Lysidice ninetta*	X	
Polychaeta	*Lysidice unicornis*	X	
Polychaeta	*Malacoceros spp.*	X	
Polychaeta	*Maldanidae spp.*	X	
Polychaeta	*Myrianida spp.*	X	
Polychaeta	*Nematonereis unicornis*		X
Polychaeta	*Nereidae* spp.		X
Polychaeta	*Nereimyra punctata*	X	
Polychaeta	*Nereis pelagica*	X	X
Polychaeta	*Nicolea venustula*	X	
Polychaeta	*Odontosyllis spp.*	X	X
Polychaeta	*Perinereis cultrifera*	X	
Polychaeta	*Perkinsiana spp.*	X	
Polychaeta	*Pherusa plumosa*	X	
Polychaeta	*Pholoe baltica (sensu Barnich 211)*	X	
Polychaeta	*Pholoe inornata (sensu Barnich 211)*	X	X
Polychaeta	*Phyllodoce greenlandia/laminacea*	X	
Polychaeta	*Phyllodoce maculata*	X	
Polychaeta	*Platynereis dumerilii*	X	X
Polychaeta	*Poecilochaetus serpens*	X	
Polychaeta	*Polycirrus spp.*	X	
Polychaeta	*Polydorid spp.*	X	
Polychaeta	*Polynaidae (Malnigrenia?)*	X	
Polychaeta	*Proceraea picta*	X	X
Polychaeta	*Proceraea spp.*	X	
Polychaeta	*Psamathe fusca*	X	
Polychaeta	*Sabellaria spinulosa*	X	
Polychaeta	*Sclerocheilus minutus*	X	
Polychaeta	*Spionidae sp. A*	X	
Polychaeta	*Sphaerodoridae spp.*	X	
Polychaeta	*Sphaerodorum gracilis*	X	
Polychaeta	*Sthenelais boa*	X	
Polychaeta	*Syllis spp.*	X	X
Polychaeta	*Terebellidae spp.*	X	
Polychaeta	*Trypanosyllis spp.*	X	
Polychaeta	*Websterinereis glauca*	X	
Polyplacophora	*?Callochiton achatinus*		X
Polyplacophora	*?Tonicella rubra/Lepidochitona cancreas*	X	
Polyplacophora	*Acanthochitona crinita*	X	X
Polyplacophora	*Ischnochitonidae spp.*	X	
Polyplacophora	*Polyplacophora juv.*	X	
Pycnogonida	*Achelia echinata*	X	X
Pycnogonida	*Ammothella longioculata*	X	X
Pycnogonida	*Ammothellia longipes*		X
Pycnogonida	*Anoplodactylus petiolatus*		X

Pycnogonida	***Callipallene tiberi***	**X**	
Pycnogonida	*Endeis spinosa*	X	X
Sipuncula	*Sipuncula spp.*	X	
Tanaidacea	*Apseudes talpa*	X	
Turbellaria	*Platyhelminthes (Turbellaria)*	X	
Turbellaria	*Turbellaria spp.*	X	X

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