



REVIEW OF EVIDENCE FOR THE LOSS OF LARGE BROWN MACROALGAE

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**A review for the Crown Estate
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1.0 EXECUTIVE SUMMARY

A literature review was undertaken of the changes that have been reported in the distribution of fifteen large brown macroalgal species that characterise temperate rocky shores and the shallow subtidal in the marine environment in the UK and related areas in the North East Atlantic. The 15 species included eight kelps (*Alaria esculenta*, *Chorda filum*, *Laminaria digitata*, *Laminaria hyperborea*, *Laminaria ochroleuca*, *Saccharina latissima*, and *Undaria pinnatifida* [non-native]), the kelp-like *Saccorhiza polyschides* and seven fucoids (*Ascophyllum nodosum*, *Fucus serratus*, *Fucus spiralis*, *Fucus vesiculosus*, *Himanthalia elongata*, *Pelvetia canaliculata*, and *Sargassum muticum* [non-native]). The northern and southern limits of these species occur outside the UK, with the exception of *Laminaria ochroleuca*, which is at its northern limit in the UK, and *Alaria esculenta* with its southern limit just into northern France. This makes the UK a stronghold for these large brown algae. Changes in the distribution of these species can be summarized as follows: i) decline in distribution: *Alaria esculenta*, *Ascophyllum nodosum*, *Chorda filum*, *Himanthalia elongata*, *Laminaria digitata*, *Laminaria hyperborean*, *Pelvetia canaliculata*, *Saccharina latissima*, and *Saccorhiza polyschides*, ii) depleted genetic diversity: *Fucus serratus* at southern end of its range, iii) range expansion: *Fucus vesiculosus*, *Laminaria ochroleuca*, *Sargassum muticum* and *Undaria pinnatifida* and iv) no change: *Fucus spiralis*. Although explanations for the documented changes tend to be attributed to climate change, reasons are multiple and complex, including reproductive biology, impact of mild winters on the interaction between grazers and sporelings, increase in non-native species, change in current regimes and turbidity in the North East Atlantic and change in nutrients. Most of the decline that has been reported is not for the UK. It is therefore concluded that there is a need for an assessment of change in distribution of these species for this geographical region.

2.0 INTRODUCTION

The large brown zone-forming fucoids (members of the order Fucales) and kelps (members of the order Laminariales) characterise temperate rocky shores and the shallow subtidal. However, in the past decade there have been an increasing number of reports that these macroalgae (seaweeds) are declining in distribution and abundance on UK shores and in other areas of the North East Atlantic. Whilst some of these reports are anecdotal, there is increasing evidence to support these observations. Some changes appear to be linked to climate change, although reasons are multiple and complex, and include reproductive biology, fertility and recruitment of brown algae, impact of milder winters on the interaction between sporelings and grazers (e.g. top shells and winkles), increase in number and spread of non-native species, and changes in current regimes and turbidity in the last half century in the North East Atlantic and North Sea and impact of nutrients.

Macroalgae are important primary producers, contributing significantly to coastal ecosystems (Ramus, 1992; Coelho *et al.*, 2000). They provide habitats for a diverse range of organisms, including substrata for numerous epiphytes (Duggins, 1980; Reed & Foster, 1984, Dunton & Schell, 1987), and protection for many epilithic and pelagic organisms (Steneck & Watling, 1982; Estes & Steinberg, 1988; Bustamante *et al.*, 1995). When submersed, macroalgae provide protection from the hydrodynamics of the marine system by removing energy from currents and waves (Boller & Carrinton, 2006). When emersed, they protect against desiccation by physically covering under-storey species (Jenkins *et al.*, 1999; Steneck, 2002). As a result of this dampening effect, many organisms utilize brown seaweeds, especially the kelp forests of the

shallow subtidal, as breeding and feeding grounds (Bernstein & Jung, 1980; Bologna & Steneck, 1993; Levin, 1994; Duarte, 1995; Anderson *et al.*, 1997; Steneck *et al.*, 2002). Consequently, a decline in macroalgal abundance will impact, both directly and indirectly, on all trophic levels of intertidal and shallow subtidal ecosystems (Hawkins *et al.*, 2008).

Whilst global distribution patterns of macroalgal species differ, each species is physiologically constrained within its geographical range by physical and biological parameters (Stebeck *et al.*, 2002). These environmental parameters impact on all developmental stages of the complex macroalgal life-history, which often exhibit differing environmental optima and tolerances. The ultimate impact of an environmental stressor on a species is its cumulative impact on all life-history stages (Fain & Murray, 1982; Ladah & Zertuche-González, 2007; Harley *et al.*, 2012). The majority of these impacts are largely unknown for individual stressors, let alone multiple stressor systems (Harley *et al.*, 2012).

Many coastal species reach their distribution limits in UK waters: several species with southern distributions reach their northern limits, whilst some species with northern distributions reach their southern limit (Table 2). The large brown macroalga, *Laminaria ochroleuca* reaches its northern limit in UK waters, whilst *Alaria esculenta*, although at its southern limit within Northern France, has showed local extirpations and a decrease in abundance in the southern UK (Mieszkowska *et al.* 2006). For many faunal intertidal species, historic biogeographical boundaries occurred between St David's Head, South Wales and Anglesey, North Wales, and between Plymouth and the Isle of Wight (Hawkins *et al.*, 2009), but in recent years, major changes have been documented across these boundaries, in response to climate change, extreme weather events and anthropogenic influences (Helmuth *et al.*, 2006). Equivalent range limits, and comparable retractions and expansions, have also been documented for some macroalgal

species (Simkanin *et al.*, 2005, Mieszkowska *et al.*, 2006). Ultimately, the distribution of any species is determined by its dispersal ability and tolerance to numerous stressors (Thompson *et al.*, 2002; Jenkins *et al.*, 2008). Understanding the governing mechanisms behind such patterns is fundamental to coastal ecology, and is often confused by the interaction of many multi-scale variables (Crain *et al.*, 2004; Saldaña *et al.*, 2007).

Given the paucity of scientific data on the decline and/or loss of the large brown algae for UK shores, coupled with an increasing interest from industry in harvesting and farming these species in order to exploit them for a range of products, including foodstuff, cosmetics, biofuels and pharmaceuticals, there is an urgent need to review the status of these species around our shores and to instigate long-term monitoring to assess changes in their distribution and abundance.

The aim of this study is to review currently available literature on the biology, status and distribution of fifteen species of large brown macroalgae found throughout the United Kingdom (Table 1). For a comprehensive review of the literature pertaining to the Laminariales *sensu lato* since 1979 when the previous review was undertaken (Kain 1979) the reader is also referred to Bartsch *et al.* (2008).

3.0 SPECIES OF LARGE BROWN ALGAE COVERED IN THIS REVIEW

The fifteen species in this review are listed in Table 1 and a summary of species-specific information is given in Table 2. A detailed summary of the distribution, description and biology of each species is given in the Appendix (section 9).

Table 1. Species and classification of large brown macroalgae (Phaeophyceae) in this review. Source for taxonomy: Guiry & Guiry (2013). Source for common names: Bunker *et al.* (2010).

Species	Authority	Order	Family	Common Names
<i>Ascophyllum nodosum</i>	(Linnaeus) Le Jolis	Fucales	Fucaceae	Knotted Wrack, Egg Wrack
<i>Fucus serratus</i>	Linnaeus	Fucales	Fucaceae	Toothed Wrack
<i>Fucus spiralis</i>	Linnaeus	Fucales	Fucaceae	Spiral Wrack
<i>Fucus vesiculosus</i>	Linnaeus	Fucales	Fucaceae	Bladder Wrack
<i>Pelvetia canaliculata</i>	(Linnaeus) Decaisne & Thuret	Fucales	Fucaceae	Channel Wrack
<i>Himanthalia elongata</i>	(Linnaeus) S.F. Gray	Fucales	Himanthaliaceae	Thongweed
<i>Sargassum muticum</i>	(Yendo) Fensholt	Fucales	Sargassaceae	Wireweed
<i>Alaria esculenta</i>	(Linnaeus) Greville	Laminariales	Alariaceae	Dabber-locks
<i>Undaria pinnatifida</i>	(Harvey) Suringar	Laminariales	Alariaceae	Wakame
<i>Chorda filum</i>	(Linnaeus) Stackhouse	Laminariales	Chordaceae	Mermaid's Tresses, Bootlace weed
<i>Laminaria digitata</i>	(Hudson) J.V. Lamouroux	Laminariales	Laminariaceae	Oarweed
<i>Laminaria hyperborea</i>	(Gunnerus) Foslie	Laminariales	Laminariaceae	Tangle-weed
<i>Laminaria ochroleuca</i>	Bachelot de la Pylaie	Laminariales	Laminariaceae	Golden Kelp
<i>Saccharina latissima</i>	(Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders	Laminariales	Laminariaceae	Sugar Kelp, Sea Belt
<i>Saccorhiza polyschides</i>	(Lightfoot) Batters	Tilopteridales	Phyllariaceae	Furbelows

Table 2. Summary of species-specific information including distribution, habitat, life-history, known physical tolerances, biotic interactions and key references

Species	Native/non-native	Biogeography	Distribution	Habitat	Littoral/sublittoral range	Exposure	Longevity	Sources
<i>Ascophyllum nodosum</i>	Native	Arctic to cold temperate	North Atlantic: S. Arctic to N. Portugal and N. Carolina	Rocky substrata	Mid-littoral	Sheltered shores	Estimated: 50-60 years	Burrows et al. (2010) Lüning (1990)
<i>Fucus serratus</i>	Native	Cold temperate	North Atlantic: Novaya Zemlya to N. Portugal and Gulf of St Lawrence	Rocky substrata	Lower littoral, near low water mark; rock pools mid-upper shore	Relatively sheltered shores	Perennial 3-4 years	Lüning (1990) Chapman, 1980
<i>Fucus spiralis</i>	Native	Cold temperate	North Atlantic: Newfoundland and N. Norway to N. Africa and Delaware	Rocky substrata	Upper littoral	Sheltered to moderately exposed shores	Perennial up to 4 years	Lüning (1990) Chapman, 1980
<i>Fucus vesiculosus</i>	Native	Arctic to cold temperate	North Atlantic species: S. Arctic to N. Africa and N Carolina	Rocky substrata	Mid-littoral	Sheltered shores (within estuaries and bays). forma <i>evesiculosus</i> on wave-exposed shores	Perennial c. 4-5 years	Lüning (1990) Chapman, 1980 White (2008b)
<i>Pelvetia canaliculata</i>	Native	Cold temperate	North Atlantic species: N. Norway to mid Portugal	Rocky substrata	Upper littoral, near high water mark	sheltered shores	Perennial c. 4 years	Lüning (1990) Chapman, 1980
<i>Himantalia elongata</i>	Native	Cold temperate	North Atlantic species: N. Norway to mid Portugal	Rocky substrata	Lower littoral, near low water mark	Semi-exposed shores	Biennial 2-3 years	Lüning (1990)
<i>Sargassum muticum</i>	Non-native	Cold temperate	Native to Pacific waters around Japan. Invasive to S Pacific, N and S Atlantic.	Rocky substrata and any hard surface including shells and small stones	Lower littoral and shallow sublittoral	Sheltered to semi-exposed shores	Perennial, 2-6+ years	Critchley et al.
<i>Alaria esculenta</i>	Native	Arctic to cold temperate	Amphioceanic species: Mid-Arctic to N. France and New Hampshire in Atlantic, S. Alaska and Vladivostok in Pacific	Rocky substrata	Upper sublittoral to c. 8 m depth; exceptionally to 35 m depth in areas of high exposure	Semi-exposed to exposed shores	Perennial 5-10 years	Lüning (1990) Chapman, (1980)
<i>Undaria pinnatifida</i>	Non-native	Cold temperate	Native to Pacific waters around Japan. Invasive to S Pacific, N and S	Rocky substrata although pre dominantly on	Upper sublittoral, 0-18 m depth	Sheltered to moderately exposed shores	Annual	Refs exist

			Atlantic.	floating artificial structures in the UK.				
<i>Chorda filum</i>	Native	Arctic to cold temperate	Amphioceanic: S. Arctic to N. Portugal and Connecticut in Atlantic, S. Alaska and S. Japan in Pacific	Rocky substrata often attached to small rocks and shells in sandy bays	Lower shore to upper sublittoral, to 5 m depth.	Sheltered coasts.	Annual	Lüning (1990)
<i>Laminaria digitata</i>	Native	Arctic to cold temperate	North Atlantic: Mid Arctic to N. France and Connecticut in Atlantic	Rocky substrata	Bottom of the lower-littoral to shallow sublittoral, to 2 m depth	At all levels of wave exposure, but favours moderately exposed shores	Perennial 6-10 years	Lüning (1990)
<i>Laminaria hyperborea</i>	Native	Sub-Arctic to cold temperate	North Atlantic: N. Norway to Mid Portugal in Atlantic	Rocky substrata	Upper sublittoral, to 8 m depth in coastal waters, 30 m in clear coastal waters and 47 m around St. Kilda.	At all levels of wave exposure, but favours exposed shores	Perennial	Lüning (1990)
<i>Laminaria ochroleuca</i>	Non-native; range expansion?	Warm temperate	North Atlantic: SW UK to N. Africa	Rocky substrata	Low water spring tide level to 25 m depth	Higher density on sheltered shores	Annual	Izquierdo <i>et al.</i> (2002), Roleda <i>et al.</i> (2004) John (1971)
<i>Saccharina latissima</i>	Native	Arctic to cold temperate	Amphioceanic: N. Arctic to N. Portugal and New York in Atlantic, and Oregon and Vladivostok in the Pacific	Rocky substrata; often attached to small rocks and shells in sandy bays.	Lower littoral and sublittoral, to 30 m depth	Sheltered coasts	Annual	Lüning (1990)
<i>Saccorhiza polyschides</i>	Native	Cold to warm temperate	North Atlantic: Mid Norway to N. Africa in Atlantic	Rocky substrata	Extreme low water spring to <35m	Sheltered coasts	Annual	Lüning (1990) Chapman, (1980)

4.0 METHODOLOGY FOR REVIEW

A literature review of available data on the biology, status and distribution of fifteen species of large brown macroalgae (Table 1) and the threats they face was undertaken using peer-reviewed papers, “grey” literature and web-based sources. The focus of this review was the potential for future change in the distribution of these species in relation to anthropogenic influences (e.g. climate change, pollution, and the direct and indirect influences of marine grazers) on the coastlines of the United Kingdom, and also within a North East Atlantic and global context. The predominant search tools used to compile this review were Web of Knowledge and Google Scholar. The Natural History Museum on-line library and Bangor University library were the other main sources of material. The report is a distillation taken from Bush *et al.* (unpubl.) *Review of the evidence for the loss of large brown macroalgae* (S1 supplementary document).

5.0 DOCUMENTED DISTRIBUTION CHANGES IN THE NORTH EAST ATLANTIC

Changes that have been reported in the distribution of the species in this report fall into four main categories: i) decline, ii) depleted genetic diversity, iii) no apparent change, and iv) range expansion. A summary of changes reported in the distribution of the 15 species of large brown seaweeds for the North East Atlantic is given in Table 3.

5.1 Decline in distribution

Species that have been reported to show recent distribution declines within the north-eastern Atlantic include *Alaria esculenta* (Simkanin *et al.*, 2005; Mieszkowska *et al.*, 2006; Merzouk & Johnson, 2011), *Ascophyllum nodosum* (Simkanin *et al.*, 2005), *Laminaria hyperborea* (Simkanin *et al.*, 2005; Müller *et al.*, 2009), *Laminaria digitata* (Cosson, 1999; Morizur, 2001), *Saccharina latissima* (Simkanin *et al.*, 2005; Pehlke & Bartsch, 2008; Brodie *et al.*, 2009; Andersen *et al.*, 2011; Roleda & Dethleff, 2011; Moy & Christie, 2012), *Saccorhiza polyschides* (Fernández, 2011), *Himanthalia elongata* (Lima *et al.*, 2007), *Chorda filum* (Eriksson *et al.*, 2002) and *Pelvetia canaliculata* (Lima *et al.*, 2007).

5.2 Depleted genetic diversity

Fucus serratus populations at their southern range limit show depleted genetic diversity and resilience to stress (Pearson *et al.*, 2009; Jueterbock *et al.*, 2012).

Table 3. Summary of changes in distribution of large brown seaweeds in the NE Atlantic.

Species	Decline in distribution	Depleted genetic diversity	No apparent change	Range expansion	References
<i>Alaria esculenta</i>	+				Simkanin <i>et al.</i> (2005), Mieszkowska <i>et al.</i> (2006), Merzouk & Johnson (2011)
<i>Ascophyllum nodosum</i>	+				Simkanin <i>et al.</i> (2005)
<i>Chorda filum</i>	+				Eriksson <i>et al.</i> (2002)
<i>Fucus serratus</i>		+ ²	+ ¹		¹ Lima <i>et al.</i> (2007), ² Pearson <i>et al.</i> (2009), ² Jueterbock <i>et al.</i> (2012)
<i>Fucus spiralis</i>			+		Lima <i>et al.</i> (2007)
<i>Fucus vesiculosus</i>				+	Lima <i>et al.</i> (2007)
<i>Himanthalia elongata</i>	+ ¹		+ ²		¹ Fernández & Neill (1982), ^{1,2} Lima <i>et al.</i> (2007), ¹ Davies <i>et al.</i> (2007), ² Simkanin <i>et al.</i> (2005), ² Merzouk & Johnson (2011)
<i>Laminaria digitata</i>	+				Cosson (1999), Morizur (2001)
<i>Laminaria hyperborea</i>	+ ¹		+ ²		¹ Simkanin <i>et al.</i> (2005), ¹ Müller <i>et al.</i> (2009) ² Lima <i>et al.</i> (2007)
<i>Laminaria ochroleuca</i> *				+	Parke (1948)
<i>Pelvetia canaliculata</i>	+				Lima <i>et al.</i> (2007)
<i>Sacchorhiza latissima</i>	+				Simkanin <i>et al.</i> (2005), Pehlke & Bartsch (2008), Brodie <i>et al.</i> (2009), Andersen <i>et al.</i> (2011), Roleda & Dethleff (2011), Moy & Christie (2012)
<i>Sacchorhiza polyschides</i>	+				Fernández (2011)
<i>Sargassum muticum</i>				+	Harries <i>et al.</i> (2007)
<i>Undaria pinnatifida</i> *				+	Fletcher & Farrell (1999)

*Reach northern limit in the UK

5.3 No apparent change

Conversely, *Fucus spiralis* has shown no reported distribution or abundance change within the north-eastern Atlantic (Lima *et al.*, 2007). *Ascophyllum nodosum* showed no significant change in abundance around Ireland between 1958 and 2003 (Simkanin *et al.*, 2005). Some studies report no change for other species (see Table 3), but all these have been observed to be declining in other areas.

5.4. Range expansion

Species that have been reported to show opposing range expansions within this region include *Laminaria ochroleuca*, *Sargassum muticum* and *Undaria pinnatifida* (Parke, 1948, Fletcher & Farrell, 1999; Harries *et al.*, 2007), whilst *Fucus vesiculosus* is reported to have increased its distribution in northern Portugal (Lima *et al.*, 2007).

5.5 Biogeographic boundaries

Two species considered in this report, *A. esculenta* and *L. digitata*, are near the southern edge of their distribution limits within UK waters with both reaching their southern limits in northern France. Several other species reach their biogeographic limits in continental Europe: *C. filum*, *S. latissima*, *F. serratus* and *A. nodosum* in Northern Portugal, and *L. hyperborea*, *P. canaliculata* and *H. elongata* in mid Portugal. Others, such as *F. spiralis*, *F. vesiculosus* and *S. polyschides* reach their southern distribution limits in northern Africa. Opposingly, *L. ochroleuca* and *U. pinnatifida* currently reach their northern range limits within UK waters, whilst *S. muticum* reaches higher latitudes in Norway and Alaska and is still expanding in range.

5.6 Comparative overview

Species of Fucales, being intertidal, are pre-adapted to cope with a high degree of environmental stress and are generally highly resilient. Nevertheless, reported changes in distribution patterns of native species have been highly variable. For example, Lima *et al.* (2007) reported no change in distribution pattern in Portugal, from the 1950s to 2006, for either *Fucus serratus* or *F. spiralis*, whilst several other native Fucales were reported to have altered their range. Although there have been no reports of change in distribution for *F. serratus* in northern Portugal, populations there have been reported to be maladapted, and potentially more vulnerable to stresses. Pearson *et al.* (2009) found that edge populations were less resilient to both desiccation and heat shock, with higher levels of heat shock gene expression at equivalent temperatures to those well within their range limits and concluded that despite their inherent resilience, on-going climate forcing is likely to induce extirpations within range edge populations. Allelic richness in southern populations has decreased over the last decade (Jueterbock *et al.*, 2012), with these same populations featuring a lower maximum shore height and thus shorter emersion period than northern populations.

Macroalgal community composition and species abundance along the Spanish coast, where many species are close to their range edge, have fluctuated through time. In northern Spain, *Himanthalia elongata* was present in the 1930s but later reported to be absent (Fernández & Neill, 1982), and a range retraction northwards of ca. 220 km, from São Martinho do Porto to Labruga in Portugal, was recorded from the 1950s to 2006 (Lima *et al.*, 2007). However, *Pelvetia canaliculata* was reported to have shown a 245 km range shift northwards, from the Berlengas Islands to Cabo do Mundo, in the same time period (Lima *et al.*, 2007).

Ascophyllum nodosum has been intensively harvested around UK coastlines for centuries, making it impossible to establish a baseline of abundance. No significant change in abundance was found around the coast of Ireland from 1958 to 2003 (Simkanin *et al.*, 2005), although Davies *et al.* (2007) reported a local reduction in abundance in Strangford Lough, Ireland between 1962 and 2002, where a previously continuous cover of *A. nodosum* was being replaced by barnacles.

Conversely, Lima *et al.* (2007) reported a 157 km shift south in the distribution of the northern species *Fucus vesiculosus*, from Vila Nova de Milfontes to Ingrina, between the 1950s and 2006 in Portugal, whilst further afield, in the Canadian Maritimes, *F. vesiculosus* has been gradually increasing its cover within *Ascophyllum nodosum* beds (Ugarte *et al.*, 2010).

The invasive species *Sargassum muticum* is increasing in abundance in UK waters where it was feared it would have a competitive advantage over indigenous intertidal and shallow subtidal species. There are several recorded incidents of *S. muticum* displacing native algae after natural die-backs (Fletcher & Fletcher, 1975a; Norton, 1976; Nicholson *et al.*, 1981; Ambrose & Nelson, 1982; DeWreede, 1983; Viejo, 1997; Cosson, 1999; Staehr *et al.*, 2000; Bartsch & Tittley, 2004; Britton-Simmons, 2004; Sánchez *et al.*, 2005), but, within the UK, it has had fewer detrimental ecological impacts than originally feared (Davison, 2009). Rather than displacing indigenous algae, *S. muticum* has been found to occur alongside them, supporting a diverse range of epibionts. Additionally it colonises a wider range of substratum than native algae, and can potentially increase biodiversity in some areas (Davison, 2009).

Subtidal species such as the Laminariales and Tilopterales are buffered from the majority of physical environmental changes by the water column. They are not adapted to cope with variability in environmental conditions and consequently may be more susceptible to climate

change. This is reflected in the reported northwards range retractions for all northern subtidal species covered in this review. *Laminaria hyperborea* has already shown an extension of its northern distribution limit to Spitsbergen, in addition to a recent progressive retraction of its southern distribution limit (Müller *et al.*, 2009). A significant decrease in the abundance of *L. hyperborea* was reported around the coast of Ireland from 1958 to 2003 (Simkanin *et al.*, 2005). Conversely, no change in abundance was observed in data from the 1950s to 2006 on the Iberian shore by Lima *et al.* (2007), and around Helgoland, Germany, Pehlke & Bartsch (2008) have reported an increase in the vertical distribution as a result of localised increasing water transparency since 1975. Regression of *Laminaria digitata* populations has occurred on the Atlantic coast of France where populations of *Sargassum muticum* have exploded, covering ~80% of the substratum in 1999 (Cosson, 1999; Morizur, 2001) whilst decreases in the abundance of *Saccharina latissima* have been recorded on several north-eastern Atlantic coasts, including Ireland, Norway and Germany (Pehlke & Bartsch, 2008; Brodie *et al.*, 2009; Andersen *et al.*, 2011). Significant decreases in abundance occurred around the coast of Ireland from 1958 to 2003 (Simkanin *et al.*, 2005). In 2002, *S. latissima* forests were observed to have disappeared in many areas since 1996, especially in the Skagerrak region (Moy & Christie, 2012). *S. latissima* has also decreased around the coast of Helgoland, in some areas being replaced by *L. hyperborea*, from 1970 to 2003 (Pehlke & Bartsch, 2008; Roleda & Dethleff, 2011). Along the south and west coast of Norway, Moy and Christie (2012) reported a large-scale shift from *S. latissima* forests to ephemeral macroalgae. *Chorda filum* was seen to disappear from the North Swedish coast of the Skagerrak Sea from 1941 to 1998 with a decrease in maximum penetration depth further south, the reasons for which are unknown. Major decreases in *Alaria esculenta* abundance and local extirpations have occurred in the northeast Atlantic, reported from the southwest of the UK from 1950 to 2006 (Mieszkowska *et al.*, 2006), Ireland from 1958 to 2003 (Simkanin *et al.*, 2005 and Norway since the 1950s (Merzouk & Johnson, 2011). *Saccorhiza*

polyschides now only occurs in isolated pockets south of Brittany associated with cold water upwellings. A decrease in abundance has been seen here, with adult sporophytes surviving for less than 6 months and often not reaching maturity (Fernández, 2011).

Warm water subtidal species are now increasing in abundance in the northeast Atlantic. The range extension of *Laminaria ochroleuca* into UK waters from Atlantic France is thought to be relatively recent (Parke, 1948). It is unlikely to have been present in the UK prior to this as no herbarium specimens were collected (Brodie *et al.*, 2009). The invasive macroalga *Undaria pinnatifida* was introduced to UK waters by leisure craft. It was initially discovered in southern England, at the Port Hamble Marina within the Hamble Estuary of Southampton Water in 1994 (Fletcher & Manfredi, 1995), and it has since spread to several other marinas. The spread from there has been relatively slow but progressive (Fletcher & Farrell, 1999). Although *U. pinnatifida* can now be found on the rocky shore in Plymouth, within the UK, it predominantly occurs on floating artificial substrata, despite its being known to colonize fixed artificial structures in abundance elsewhere (Hay, 1990; Brown & Lamare, 1994; Casas & Piriz, 1996; Floc'h *et al.*, 1996). This may be due to the nature of the long distance dispersal. Marinas tend to have high levels of suspended sediment and turbidity. This not only limits light penetration levels, but also spore adhesion, and thus recruitment (Fletcher & Farrell, 1999). This theory is supported by the fact that *U. pinnatifida* rapidly colonized fixed artificial structures in the clearer, less turbid waters of the coastal Torquay Marina (Fletcher & Farrell, 1999). Additionally *U. pinnatifida* is tolerant of decreased salinity, growing well in estuarine conditions where it out-competes many native macroalgae, especially kelps (Farrell, 2003). Consequently in marinas where *U. pinnatifida* is established, it is the dominant macroalga on the majority of pontoons, with native species of kelp generally only seen on the outer, more wave exposed pontoons in limited numbers. *U. pinnatifida* is likely to considerably extend its distribution polewards throughout Europe, being the dominant macroalga in marinas due to its high tolerance of low salinity,

turbidity and high suspended sediment (Farrell & Fletcher, 2006). However its impact on the indigenous communities of rocky shores is unknown.

6.0 CONCLUSIONS

Two clear points emerge from this review: 1) there is evidence of change in the distribution and status of thirteen of the fifteen species of large brown macroalgae studied and 2) reasons for these changes are multiple and complex. Strikingly, eight species show decline in at least some regions of the NE Atlantic and although there is only one report of a loss of genetic diversity, there is considerable scope for further studies to assess loss in other species and populations. However, the data are mostly from outside the UK which points to the need for a comprehensive assessment of these species from within this geographical region.

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9.0 APPENDIX

9.1 *Alaria esculenta*



Description: A perennial yellowy-brown seaweed that can live for up to 7 years, it attaches to the substratum by a claw-like holdfast, from which extends a flexible stipe continuing into a distinct midrib through the length of a narrow, slightly wavy blade that can reach up to 4 m in length (although generally is not more than 1.5 m). Around the base of the blade, flat sporophylls bearing the reproductive sori project to c. 10 cm in length. It occurs in the upper sublittoral zone, from the low water mark to depths of as much as 35 m (Tyler-Walters, 2008). It is rarely present in abundance at sheltered sites where it is outcompeted by *Saccharina latissima* and *Laminaria digitata*, but thrives on exposed shores where the stipe and midrib provide both strength and flexibility to the blade in rough seas, whilst allowing the blade to lie flat amongst the canopy at low tide (Hawkins & Hartnoll, 1985; Lüning, 1990; Merzouk & Johnson, 2011).

Reproduction: *Alaria esculenta* sporophytes generally appear in early spring in UK waters. Sporangia develop on multiple pairs of sporophylls that develop on the upper stipe at the base of the blade of the mature sporophyte. These release zoospores into the water column that settle out and develop into both male and female gametophytes (Gordon & Brawley, 2004). Widdowson (1971) suggested that the southern limit of *A. esculenta* was approximately the 20°C August isotherm, and later studies support this (in Gordon & Brawley, 2004). For photosynthesis the temperature optimum of sporophytes is between 13 and 17°C (Fredersdorf *et al.*, 2009). Zoospores have an upper survival limit of 18°C, and shown optimal germination at 2 to 12°C, with the germination process tolerant of UV-B (Müller *et al.*, 2008). Gametophytes are more temperature tolerant with an upper survival limit of 19 to 21°C (tom Dieck (Bartsch), 1993). Zoospores retain photosynthetic function at higher temperatures for longer, and have a greater capacity for photosynthetic recovery than *Laminaria digitata* and *Saccharina latissima*, sustaining 50% PSII function at 19°C for up to 24 hours, with a greatest capacity for photosynthetic recovery at 13°C (Roleda, 2009). Of note, water motion inhibits sperm release in *A. esculenta* gametophytes, whilst enhancing zoospore discharge from the sporophyte. It is suggested that water motion will inhibit sperm release by disrupting the gradient of the pheromone lamocirene from the egg, rather than directly impacting on the antheridia. The release of zoospores in periods of high water flow may aid dispersal and recruitment of gametophytes (Gordon & Brawley, 2004).

Distribution: *Alaria esculenta* is an amphioceanic cold-water species extending from the mid Arctic to Brittany, northern France within the Northeast Atlantic. Within the UK, it has been recorded around Scotland, most of Ireland and the west and southwest coasts of England. On the east coast, it only extends as far as Flamborough Head (Lüning, 1990).

9.2 *Ascophyllum nodosum*



Description: Thallus of long strap-like fronds up to 2 m in length bearing single gas-bladders at intervals. This slow-growing perennial is often the dominant seaweed in the mid region of sheltered shores. Fronds can reach 15 years old before breakage, and holdfasts, from which fresh fronds regenerate, exist for several decades (Hill & White, 2008). Maximum growth rates of 3.6 cm per month were recorded in April, in Maine (Mathieson *et al.*, 1976). Growth rate decreases with depth (Ramus *et al.*, 1977). The overall length of shoots varies with wave exposure, increasing with water velocities of up to 1 m s^{-1} and decreasing thereafter (Mathieson *et al.*, 1977). Sexual maturity is reached after 5 years old (Sundene, 1973).

Reproduction: Gametophytes are dioecious; receptacles are produced yearly on lateral branches from the main axis and bear numerous spherical conceptacles (Josselyn & Mathieson, 1979; Brawley *et al.*, 1999; Pearson & Serrão, 2006). These receptacles are initiated in April to June, induced by photoperiods of 8:16 to 12:12 hours light: dark (Terry & Moss, 1980). They may take up to a year to develop to fertility, ripening from April of the following year (Hill & White, 2008). Gamete release is predominantly in the late spring and early summer (Brawley & Johnson, 2007), correlated with temperature (Bacon & Vadas, 1991). Gamete release is commonly at low tide (Pearson & Serrão, 2006), often triggered by a period of overnight aerial exposure (Hill & White, 2008). Under calm conditions within dense populations, this will increase reproductive assurance as fertilization will occur within populations, especially on the incoming tide (Pearson & Serrão, 2006). Eggs release the pheromone finavarrene (Maier & Müller, 1986). Recruitment success is very poor (Printz, 1959), which is partially due to the short reproductive period of two months (Hill & White, 2008). Zygotes can remain in the water column for up to 10 days (Hill & White, 2008) and do not settle unless there has been a spell of very calm water, which does not often occur in UK waters (Vadas *et al.*, 1990). Additionally, the slow growth rate of this species reduces their competitive ability (Baardseth, 1970).

Distribution: A cold water species with a biogeographical range extending from the southern Arctic to northern Portugal in the northeast Atlantic. It occurs throughout UK coastlines with the exception of the southeast of England where no suitable habitat is available (Lüning, 1990). Within this range, it is excluded from the Basque coastline by a region of warm water and a lack of suitable substratum (Lüning, 1990).

9.3 *Chorda filum*



Description: An annual brown seaweed with elongated, unbranched cord-like fronds, up to 5 mm thick and to 8 m long, attached to the substratum by a small discoid holdfast, becoming hollow in older individuals, and frequently inflated with gases at the terminal region keeping them buoyant. This sublittoral fringe species extends from the low shore to 5 m deep, often in sheltered sandy bays, where it can attach to small rocks and shells (South & Burrows, 1967; White, 2006).

Reproduction: The sporophyte of the dioecious seaweed grows rapidly from late spring to early summer when energy resources are switched to reproductive growth. Peak reproduction occurs in autumn. Sporophytes form unilocular sporangia on all but the lower regions of the thallus, with each sporangium producing 16 motile haploid zoospores that settle out and germinate into male and female gametophytes. Gametophyte fertility appears to be irrespective of daylength, occurring at temperatures between 5 and 10°C, with temperatures greater than 15°C blocking reproduction completely (Lüning, 1980b; Novaczek *et al.*, 1986). These gametophytes remain fertile in culture for several months. They can persist *in situ* until the following spring in the UK (South & Burrows, 1967). Female gametophytes produce flask-shaped, positively phototropic oogonia, each containing a single egg, whilst male gametophytes produce numerous triangular antheridia, containing a single spermatozoid, complete with an eyespot (Kanda, 1938; South & Burrows, 1967). When eggs are released, they emit the pheromone multifidene which induces the release of the chemotactic spermatozoids from the antheridia (Maier & Muller, 1986). Fertilization occurs, and the zygote develops at the mouth of the oogonium (Guiry & Guiry, 2013) before it settles out and the sporophyte develops. Settlement and sporophyte development begin in spring in the UK and continue throughout the remainder of the year (South & Burrows, 1967). It is reported that *Chorda filum* sporophytes appear in the Gulf of St Lawrence after spring temperatures rise above 1°C, and persist throughout the summer months. Although new sporophytes appear in autumn after water temperatures drop below 15°C, they do not survive the winter. *In vitro* studies found that sporophytes have a temperature tolerance of 0 to 24°C, and reproduce between 0 and 15°C, favouring 5-12°C (Novaczek *et al.*, 1986).

Distribution: An amphiocenic cold water species extending from the south Arctic to north Portugal in the northeast Atlantic. Within this range it is absent from the majority of the Bay of Biscay, and the east coast of the UK. This species favours sheltered habitats, and is tolerant of high sedimentation (Lüning, 1990) and reduced salinity (South & Burrows, 1967).

9.4 *Fucus serratus*

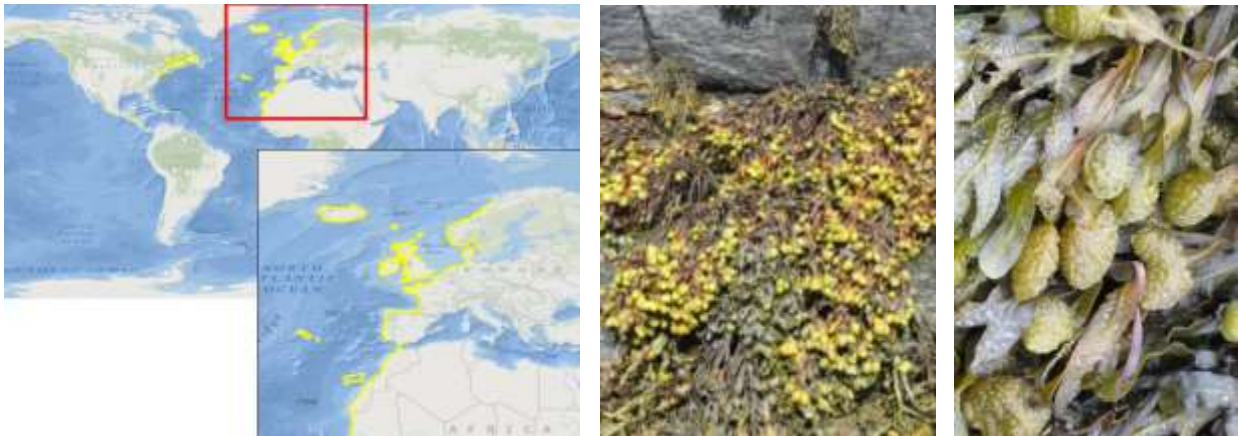


Description: This olive brown seaweed occurs on relatively sheltered shores, in the low intertidal, and extends into the sublittoral fringe. It has dichotomously branched flat fronds c. 2 cm wide and to c. 60 cm long with a serrated edge.

Reproduction: Gametophytes are dioecious. In reproductively active individuals, the apices of the main axis become fertile, subsequently dying back entirely (Knight & Parke, 1950); male receptacles frequently release their gametes at low tide (Brawley *et al.*, 1999). Sporophytes generally reproduce from late spring until autumn, predominantly in August to October, although reproduction tends to be earlier on sheltered shores. Broadcast spawning and external fertilization occur as with all *Fucus* spp. (Lobban & Harrison, 1997; Brawley *et al.*, 1999). Fertilized eggs settle and attach to the substratum where many are grazed upon by browsing molluscs. Mortality of germlings is high, with up to 83% recorded in a 77 day period on the Isle of Man. Adult sporophytes can also suffer high mortality during winter storms and periods of high wave action (Jackson, 2008).

Distribution: *Fucus serratus* is a cold water species restricted to the North Atlantic with its eastern distribution limits at Novaya Zemlya in the north, and northern Portugal (just north of the 20°C August isotherm) in the south. Within this range it is absent from the Basque coast (Lüning, 1990), but occurs on almost all UK coastlines. It was introduced to both Nova Scotia and Iceland from Europe within the last two centuries (Coyer *et al.*, 2006; Brawley *et al.*, 2009).

9.5 *Fucus spiralis*

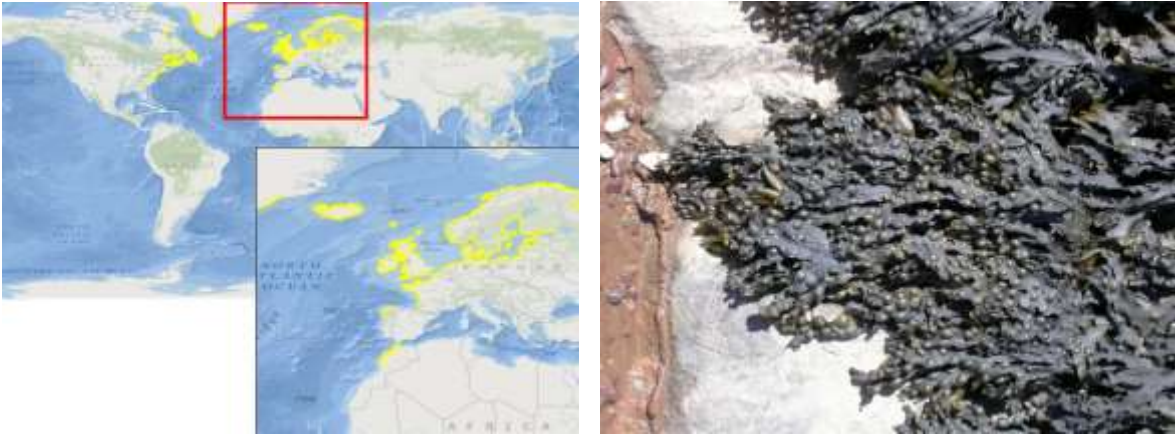


Description: An intertidal brown seaweed with flat, commonly spiralled, dichotomously branched fronds up to 40 cm in length. The terminal receptacles are characterized by a distinct ridge along their edge. This species inhabits the upper zone of sheltered to moderately exposed shores where it occurs below *Pelvetia canaliculata* and above *F. vesiculosus* and *Ascophyllum nodosum*, and this species is pre-adapted to a high level of desiccation stress (Perrin *et al.*, 2007; White, 2008a).

Reproduction: *Fucus spiralis* is a hermaphroditic fucoid. Sporophytes often release gametes throughout the day, and at all tides which increases the chance of reproductive success through self-fertilization, which is a common mode of reproduction within this species, assuring a high fertilization success even in turbulent conditions as occur on the exposed open coast (Coleman & Brawley, 2005; Engel *et al.*, 2005; Pearson & Serrão, 2006; Perrin *et al.*, 2007; Ladah *et al.*, 2008). Consequently, sporophytes can be expected to be less responsive to environmental cues for gamete release than the dioecious species *F. serratus* (Ladah *et al.*, 2008). *F. spiralis* sporophytes initiate receptacle formation from late January to February of their second year of growth (White, 2008a). Gametogenesis predominantly occurs in the summer (Brawley & Johnson, 2007). An increase in wave height induced by high winds can inhibit *F. spiralis* gamete release at high tide, but generally the monoecious *F. spiralis* is less responsive to environmental conditions than the dioecious *F. vesiculosus* or *F. serratus* (Ladah *et al.*, 2008).

Distribution: *Fucus spiralis* is a cold-water species that was historically restricted to the North Atlantic where its eastern range limit extends from northern Norway to northern Africa. It occurs throughout this distribution range. Invasive *F. spiralis* populations have been discovered along the northeast coast of the North Pacific (Lüning, 1990).

9.6 *Fucus vesiculosus*



Description: An intertidal seaweed with flat dichotomously branched fronds to 2 m long, with paired vesicles (air bladders) that can be found in high densities on more sheltered conditions within estuaries and bays (Perrin *et al.*, 2007) in the mid-littoral in a band below *F. spiralis*, and often co-habiting with *Ascophyllum nodosum* on more sheltered coasts (White, 2008b).

Reproduction: Dioecious with unisexual individuals, making cross-fertilization obligatory (Pearson & Serrão, 2006; Perrin *et al.*, 2007). In reproductively active individuals, often just the lateral branches become fertile, and die back after reproduction has occurred (Knight & Parke, 1950). Reproduction occurs in the autumn and winter at low water temperatures (Brawley & Johnson, 2007). Gametes are reported to be released during daylight hours in periods of calm weather, at high and low tide, increasing reproductive success (Pearson & Serrão, 2006). In comparison to monoecious *F. spiralis*, dioecious *F. vesiculosus* releases a greater number of eggs, later in the day and at a lower tide, thus minimising gamete dilution (Ladah *et al.*, 2008). Gamete release is determined, at least in part, by hydrodynamics with both male and female sporophytes requiring calm conditions (Pearson & Serrão, 2006). The high sensitivity of adult sporophytes to environmental conditions and the resultant synchrony of spawning in addition to the furoid adaptations of both sperm and egg to ensure fertilization, results in a fertilization success often above 90% (Serrão *et al.*, 1996; Brawley *et al.*, 1999).

Distribution: The cold-water species *Fucus vesiculosus*, is restricted to the North Atlantic, although it survives further north than *F. serratus* and *F. spiralis*, with its eastern range limit extending from the southern Arctic to Morocco in northern Africa. It is absent from much of the Spanish and Portuguese coast (Lüning, 1990), but occurs on almost all UK coastlines.

9.7 *Himanthalia elongata*



Description: A brown seaweed with a vegetative button-like base producing strap-shaped, dichotomously branched reproductive fronds, to 2 m in length. It is confined to semi-exposed shores, inhabiting the sublittoral fringe, predominantly near the low water mark but in some cases occurring subtidally (Moss *et al.*, 1973; White, 2008c). It can be very common.

Reproduction: Life-history biennial (although some individuals remain vegetative for an additional year; Gibb, 1937; Russell, 1990), with up to 98% of its total biomass devoted to reproduction (Benchley *et al.*, 1996). Early growth of recruits is during late winter and spring, in the absence of a dense protective parent canopy (Russell, 1990; Stengel *et al.*, 1999). Whilst zygotes can grow on a variety of substrata, sporophytes are less abundant in silty conditions (Moss *et al.*, 1973). For the first year, sporophytes are the vegetative phase, but from autumn of the following year, reproductively active individuals start to develop strap-like fertile receptacles. These grow slowly until the following spring when more rapid growth occurs before releasing gametes the following summer and autumn and starting to decay (Russell, 1990; Stengel *et al.*, 1999). The initiation of exclusive elongation growth in early spring coincides with an increase in both temperature and daylength, with the greatest receptacle growth rate occurring when seawater temperatures are 10 to 12°C both *in situ* and *in vitro* (Gibb, 1937; Stengel *et al.*, 1999). Stengel *et al.* (1999) observed gamete release at seawater temperatures of 16 to 18°C *in situ*, but this also coincided with increased daylength. Laboratory studies have found that gamete release occurs between 10 to 20°C in both light and dark. As with other members of the Fucales, gamete release may be triggered by water motion (Serrão *et al.*, 1996; Pearson *et al.*, 1998). *Himanthalia elongata* differs from the majority of large brown seaweeds as eggs do not produce pheromones to attract sperm (Lobban & Harrison, 1997).

Distribution: A cold water species restricted to European coastlines, its range extends from northern Norway to mid Portugal just north of the 20°C August isotherm (Lüning, 1990). Within this range it is absent from the majority of the Bay of Biscay, the east of the English Channel and the southern coasts of the North Sea. Within the UK, it is absent from many coastlines of south and east England.

9.8 *Laminaria digitata*



Description: A perennial kelp reaching up to 2 m in length. The broad frond extends from a smooth, flexible stipe that is oval in cross section, and is attached by a claw-like holdfast (Hill, 2008). It extends from the lower intertidal to the shallow subtidal to c. 2 m at all levels of wave exposure, favouring moderately exposed or hydrodynamic locations where it may extend up the shore in rock pools, and often occurring in association with other kelps (Hill, 2008; Merzouk & Johnson, 2011).

Reproduction: Sporophytes have sori on both surfaces of the blade from which they release zoospores during summer and autumn at periods of high seawater temperature (15 to 20°C in the North Sea), whilst gametogenesis and juvenile sporophyte development occur during winter and spring at low temperatures (4 to 12°C in the North Sea). The optimal temperature requirements for zoospores and juvenile gametophytes are very different from those of the eggs and juvenile sporophytes (Müller *et al.*, 2008). Sorus development decreases with increased temperature, with specimens from Helgoland showing reduced development at 18-19°C and no development at 20°C (I. Bartsch, unpublished data). Within the laboratory, zoospore germination was clearly inhibited at temperatures below 2°C and above 12°C, at temperatures outside the natural range (Sjoetun & Schoschina, 2002; Müller *et al.*, 2008). Whilst *L. digitata* shows significant additional negative responses to UV-B at optimal temperatures, gametogenesis appears to be tolerant to UV-B and actively enhanced by UV-A, especially at elevated temperatures. Zoospores show elevated germination after exposure to UV-A (Müller *et al.*, 2008). *L. digitata* zoospores sustain 50% PSII function at 19°C for just 4 hours, and greatest capacity for photosynthetic recovery at 7°C, compared to 24 hours and 13°C respectively in *Alaria esculenta* (Roleda, 2009).

Distribution: *Laminaria digitata* is a cold-water kelp species restricted to the Arctic and North Atlantic region, extending from the mid Arctic to southern Brittany, northern France. It is present round most of the UK, with the exception of the English east coast.

9.9 *Laminaria hyperborea*



Description: A perennial kelp that inhabits the mid-sublittoral from 1 to 2 m below low water mean to depths of up to 47 m dependent on light penetration, with the uppermost individuals periodically dying out due to exposure of the meristem at extreme low tide. This perennial macroalga favours exposed areas where it can live for up to 15 years. Large tough blades can reach up to 4 m in length and be supported 1 to 2 m above the seabed on an elongate rigid stipe. The rough stipe provides habitat for numerous epiphytes in shallower waters (Norton *et al.*, 1977; Kain, 1979; Lüning, 1990; Tyler-Walters, 2007), and gives the relatively slow-growing *L. hyperborea* a competitive advantage over other kelp: cleared areas of the mid sublittoral are colonized by many species of brown macroalgae, but after c. 4 years, *L. hyperborea* becomes dominant, overtopping other species and forming a dense canopy reducing light penetration to depth (Kain 1975, 1976).

Reproduction: Zoospore germination, gametogenesis and sporophyte formation in North Sea populations occur in winter and early spring. In laboratory studies, optimum zoospore germination occurred between 7 and 12°C (Müller *et al.*, 2008). Sori occur on both surfaces of the Kelp blade releasing oogonia and antheridia into the water column. Gametophytes require temperatures up to 14 to 15°C for optimum development, becoming established and surviving throughout the winter (Lüning, 1980a). In contrast to *L. digitata*, gametogenesis, zoospore germination and subsequent sporophyte formation and development in *L. hyperborea* are inhibited by UV-A (Wiencke *et al.*, 2006; Müller *et al.*, 2008).

Distribution: *Laminaria hyperborea* is a cold-water kelp of relatively limited distribution, restricted to European waters, extending from Cape Mondego in mid Portugal (near the 20°C August isotherm) to the Bay of Murmansk, northern Norway. Within this range, it is absent from the Bay of Biscay, and shows restricted distribution in south-east England (Lüning, 1990).

9.10 *Laminaria ochroleuca*

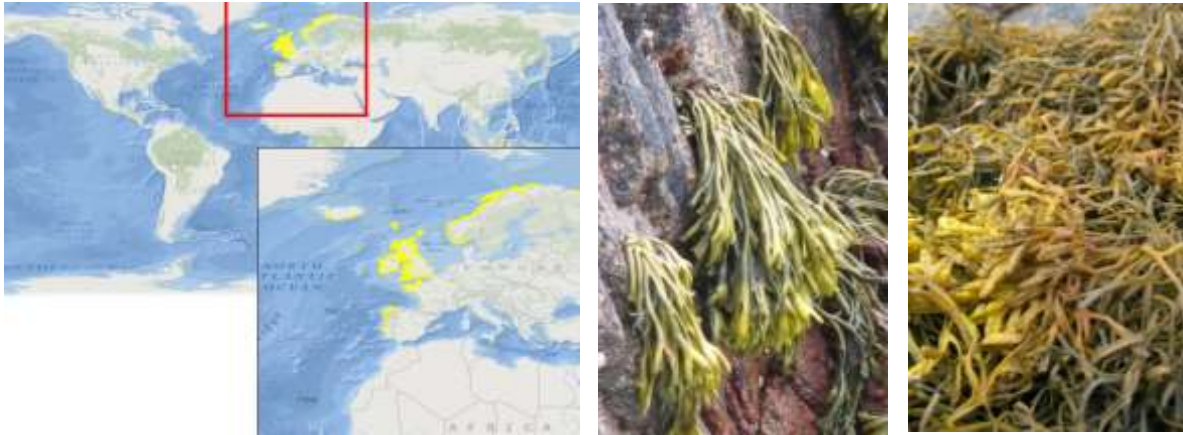


Description: A perennial kelp to 1.5 m in height with a distinct yellow region at the junction between the rigid round stipe and broad flat digitate blade. The population density of sporophytes varies with both water quality and wave exposure. Within UK waters, sporophytes predominantly inhabit the subtidal from low water spring tide level to the shallow subtidal, although, for example, in the Isle of Scilly, *L. ochroleuca* forms a stand deeper than *L. hyperborea* at depths of c. 25 m (Roleda *et al.*, 2004; Smirthwaite, 2007). In the Strait of Messina populations occur to depths of >100m, whilst in Spain and France, populations occur from c. 2 m above the low water spring tide level surviving aerial exposure (Roleda *et al.*, 2004). Vertical distribution is limited by light penetration with dense populations observed at depths of 100 m in the Straits of Messina, where light levels are 5% of surface PAR (Drew *et al.*, 1982).

Reproduction: Sporophyte vegetative growth occurs in the winter and spring, progressing to reproductive growth in summer and autumn (Pereira *et al.*, 2011). Elevated UV radiation is known to negatively impact on both zoospores (Wiencke *et al.*, 2000), and sporophytes of *Laminaria ochroleuca* (Roleda *et al.*, 2004). Temperature is the principal controlling factor governing zoospore germination (optimal between 15 and 18°C) in addition to optimal female gametophyte development, gametophyte sex ratios, fecundity and reproductive success (see Table 2) (Lee & Binkhuis, 1988; Izquierdo *et al.*, 2002). Cultured female gametophytes are unable to reproduce at temperatures of c. 10°C (Izquierdo *et al.*, 2002). The percentage of male gametophytes increases outside this optimal temperature range (Lee & Binkhuis, 1988; Izquierdo *et al.*, 2002). Additionally gametophytes do not survive at temperatures <5°C (tom Dieck, 1992). Maximum relative growth rate of young sporophytes occurs at temperatures of 15 to 20°C (tom Dieck, 1992; Izquierdo *et al.*, 2002), with an upper lethal temperature limit of 22 to 25°C (tom Dieck & de Oliveira, 1993). Although the minimum lethal temperature has not been determined, sporophytes of *L. ochroleuca* are exposed to average winter temperatures of c. 10°C in the English Channel (Pereira *et al.*, 2011), but are unable to survive 0°C for 2 weeks (tom Dieck, 1992). Pereira *et al.* (2011) suggested that gametophytes of *L. ochroleuca* may be outcompeted by the annual species *Saccorhiza polyschides* in northern populations. Additionally, populations in northern Brittany are less adapted to elevated temperature than *S. polyschides* despite these species having similar southern distribution boundaries. This may explain why *L. ochroleuca* is often found in deeper waters in the south of its range (Pereira *et al.*, 2011).

Distribution: *Laminaria ochroleuca* is unusual amongst species of *Laminaria* as it is the only digitate species with a warm temperate distribution (tom Dieck, 1992). Its range extends from the southwest of the UK in the north, to the north of Africa in the south, with populations in the Mediterranean Sea, specifically the Strait of Messina (Izquierdo *et al.*, 2002; Roleda *et al.*, 2004). Along the Portuguese coast, it is restricted to the northern and mid shores (Assis *et al.*, 2009). Southern populations are often deeper, with populations in the Gorringe bank, Azores occurring below 40 m depths. The northern limit of *L. ochroleuca* distribution unsurprisingly coincides with the 10°C February isotherm (van den Hoek, 1982), below which female gametophytes are unable to reproduce and sporophyte growth is not competitive (Izquierdo *et al.*, 2002). Within the UK it is present along the south west coast from Lundy to the Isle of Wight.

9.11 *Pelvetia canaliculata*



Description: A yellowish-brown seaweed, with regularly dichotomously branched inrolled fronds, to 15 cm in height, arising from a discoid-conical holdfast. It forms the dominant zone of the temperate upper intertidal, is very tolerant of desiccation, surviving up to 8 days emersion, and lives for up to 5 years.

Reproduction: Sporophytes are monoecious, becoming reproductively active after 2 to 3 years (Subrahmanyam, 1960; White, 2008d). They produce club-like apical receptacles, c. 1.5 cm long, initiated in January, and develop throughout the spring and summer (White, 2008d). Receptacles are simple, bearing numerous spherical conceptacles on the protuberant surface, each containing many oogonia and antheridia (Brawley *et al.*, 1999; Cho *et al.*, 2001). Two eggs develop within each oogonium of *P. canaliculata* in contrast to eight in *Fucus* spp. (Cho *et al.*, 2001). Gamete release occurs from August to early September, and external fertilization occurs (White, 2008d). Like *Fucus* spp., the sperm of *P. canaliculata* are negatively phototactic (Brawley & Johnson, 2007). *P. canaliculata* is unique in the Fucales in exhibiting post-fertilization: once the egg has been released from the conceptacle, the mucilaginous mesochiton wall does not break down. It is thought this is to protect the zygote from desiccation when it settles out on the high shore (Moss, 1974b; Hardy & Moss, 1979). This mesochiton attaches to the substratum, and the zygote produces a solid algininate wall inside this shield before beginning cell division and further development.

Distribution: Restricted to European North Atlantic coastlines, its distribution range extends from northern Norway to the 20°C August isotherm in mid Portugal. Within this range it is absent from the majority of the Bay of Biscay, a small area of south-eastern England and the southern coasts of the North Sea (Lüning, 1990).

9.12 *Saccharina latissima*



Description: A perennial (2 to 4 years), yellowish brown seaweed with a long, narrow, undivided frond with wavy edges and dimpled centre, up to 3 m in length and 20 cm in width, arising from a flexible cylindrical stipe attached to the substratum by a claw-like holdfast (White & Marshall, 2007). It extends from the low water mark to depths of up to 20 m (1% light depth) on sheltered shores (Dunton, 1985, Lüning, 1988; Moy & Christie, 2012).

Reproduction: Sporophytes show continuous growth with considerable seasonal variation, with rapid growth occurring in spring (Parke, 1948). Recruitment occurs throughout the year but is most successful in spring (Parke, 1948) when the rapid growth of the holdfast leads to rapid adhesion (Parke, 1948; Kain, 1979). Successful development is dependent on both habitat type and season, with abundance of adult sporophytes limited by juvenile survival rates, rather than gametogenesis (Hsiao & Druehl, 1973). In UK waters, sporophytes live to 3 years, reaching reproductive maturity at 6 to 12 months (Parke, 1948). Sorus formation is greatest in autumn and winter (Parke, 1948; Kain, 1979), induced by daylength reduction (Lüning, 1988). In the laboratory, seawater temperatures of 10 to 15°C, equivalent to natural autumnal temperatures, were required for sorus formation (Lüning, 1988). Optimal zoospore germination occurs at 0 to 12°C (Müller *et al.*, 2008). As with *Laminaria digitata*, *S. latissima* zoospores sustain 50% PSII function at 19°C for just 4 hours compared to 24 hours in *Alaria esculenta*. Additionally they have a lower capacity for non-photochemical quenching, and thus for regulating and protecting photosynthesis under combined light and temperature stress, suggesting *S. latissima* is more sensitive to climate change than other kelp species (Roleda, 2009; Sjoetun & Schoschina, 2002). Significant negative effects of UV-B exposure occur at elevated temperatures (Müller *et al.*, 2008). In temperate conditions, perennial gametophytes produce gametes throughout the year; however gametogenesis decreases in autumn and winter with decreased daylength (Schrieber, 1930; Parke, 1948; Hsiao & Druehl, 1973). A photoperiod of >6 hours of blue light irradiation is necessary for *in vivo* gametogenesis (Hsiao & Druehl, 1971; Lüning & Dring, 1972). Annualgametogenesis allows *S. latissima* to rapidly colonise available space after a disturbance event therefore successful repopulation can occur rapidly (Leinaas & Christie, 1996).

Distribution: *Saccharina latissima* is an amphiocenic cold water species extending from the northern Arctic to northern Portugal (just north of the 20°C August isotherm) in the northeast Atlantic. Within this range, it is absent from the northern coast of Spain and the Bay of Biscay, and has a restricted distribution on the coast of southeast England (Lüning, 1990).

9.13 *Saccorhiza polyschides*



Description: A large annual opportunistic kelp-like species with a distinctive large lumpy holdfast, and a flattened stipe with an undulating margin that widens into a flat divided blade. It occurs from extreme low water spring tides to 35 m depth, forming dense stands on sheltered coasts (White, 2008e). Sporophyte blade morphology varies strongly with water conditions, developing broad, thin, non-digitate forms in areas of low current, in comparison to elongate, tough, highly digitate forms in high current conditions. In regions of high wave exposure, short, tough blades with few digits dominate (Norton, 1969).

Reproduction: *Saccorhiza polyschides* features the heteromorphic, biphasic life history strategy similar to the Laminariales (see section 2) (Lobban & Wynne, 1981). The sporophytes of *S. polyschides* generally appear in spring to summer. Those settling later in the year in the south are removed over winter, although some survive further north. The mature sporophyte features sori on the bulbous holdfast, the stipe frills and the base of the blade from which the zoospores are released. Temperature is considered to be a critical determinant in the zoospore viability, gametophyte fertility and juvenile sporophyte survival (Norton, 1977). Temperatures of greater than 25°C prevent spore release and settlement, germination and gametophyte development (Fernández, 2011). Spore development is most efficient at temperatures of 5 to 17°C (Pereira, 2011). Gametophyte fertility has a critical upper temperature of 18 to 23°C, and juvenile sporophyte growth of 18 to 25°C. Temperature stress occurs in the summer, and thus may not affect the microscopic gametophyte, consequently sexual reproduction may not be able to continue in warm years (Fernández, 2011). However, the continuation of gametogenesis throughout the year allows *S. polyschides* to rapidly colonise available space after a disturbance event such as extreme wind, therefore, when conditions are suitable, successful repopulation can occur rapidly (Leinaas & Christie, 1996).

Distribution: *Saccorhiza polyschides* is temperate water kelp-like species of relatively restricted distribution. *S. polyschides* is restricted to European coastlines extending from Rörvik, west Norway, to Cape Jubi, Morocco within the 20°C August isotherm. Within this range it is absent from the majority of the Basque coastline, and is largely absent from the North Sea coast and the Mediterranean (Lüning, 1990), but it is the most abundant “Kelp” in southern Europe (Fernandez & Neill, 1982; Fernández, 2011)

9.14 *Sargassum muticum*



Description: A yellowish brown seaweed with a short perennial main axis attached by a < discoid holdfast to 5 cm diameter. Annual primary lateral branches and basal lanceolate laminae grow from this stalk. Primary laterals reach 5 mm in width and to 6 m long in British waters (Strangford Lough), although they are recorded to grow to 12 m in warmer waters (Davidson, 1998). Primary laterals have alternating secondary branches of up to 40 cm length that have smaller tertiary branches. All branches have numerous flattened lanceolate laminae and small (2 to 6 mm) buoyant spherical vesicles, and are shed annually, usually in late summer and autumn, when they fragment easily (Critchley, 1983b, 1983c; Critchley *et al.*, 1990). It grows on any shallow hard substrata, including shells and small stones that may move with local currents, facilitating dispersal (Jephson & Gray, 1977; Critchley, 1983b; Nicholson *et al.*, 1981; Pizzolla, 2008). It favours sheltered shores, fragmenting under high levels of wave exposure (Fletcher & Fletcher, 1975a; Viejo *et al.*, 1995), whilst its subtidal range is limited by light penetration and thus water depth (Norton, 1977; Thomsen *et al.*, 2006).

Reproduction: *Sargassum muticum* has an annual cycle of growth with juveniles and lateral branches developing from autumn. Rapid vegetative growth occurs in late winter and early spring before the initiation of reproductive growth in the summer months (Critchley, 1983c). Consequently, this species can reproduce sexually in the first year of its life, with almost every branch becoming fertile (Norton, 1977). This monoecious species produces lanceolate reproductive receptacles in the axil of the leafy lamina on tertiary branches. Conceptacles are arranged spirally on these stalked receptacles and contain either oogonia or antheridia, with 90% of conceptacles being female (Fletcher & Fletcher, 1975a; Nicholson *et al.*, 1981; Critchley, 1983c; Norton & Deysher, 1989). Gametes are released in 13 day cycles shortly after spring tides, not all at once, increasing the likelihood of encountering favourable environmental conditions (Fletcher & Fletcher, 1975b). Unlike the majority of brown seaweeds, *S. muticum* eggs do not produce a pheromone to attract sperm, although the non-motile eggs are surrounded by a sticky mesochiton that may promote sperm retention (Brawley & Johnson, 2007). Eggs are released from the conceptacles but remain attached to the receptacle, increasing the chances of fertilization success (Lobban & Harrison, 1997). A significant amount of self-fertilization occurs, with the potential for cross-fertilization maximized by different primary laterals releasing gametangia at different times (Monterio *et al.*, 2009). Following fertilization, zygotes remain attached to the outside of the receptacle for 2 to 3 days, beginning development into germlings prior to settlement (Fletcher & Fletcher, 1975a; Fletcher, 1980; Lobban & Harrison, 1997). The resultant larger size upon release to the water column is a very efficient settling

strategy (Deysher & Norton, 1982; Lobban & Harrison, 1997) and fast adhesion is facilitated by the associated premature development of rhizoids (Deysher & Norton, 1982; Monterio *et al.*, 2009). Following the initiation of sexual reproduction, the laterals are gradually shed from the adult sporophyte (Deysher, 1984; Norton & Deysher, 1989; Norton, 1977). Some reproductively mature branches are shed and float away from the parent plant remaining viable in the water column for up to 3 months, aiding dispersal of the gametes, and potentially zygotes (Farnham *et al.*, 1981; Deysher & Norton, 1982).

Egg release and embryo settlement follow a semi-lunar pattern. However, as with *Fucus* spp., their relationship to the state of the moon varies with location (Okuda, 1981; Fletcher, 1980; Norton, 1981; Monterio *et al.*, 2009). The initiation of the reproductive cycle is also dependent on water temperature and daylength, both of which vary with latitude (Deysher, 1984; Norton & Deysher, 1989). *S. muticum* is tolerant of a wide range of temperatures from 5 to 30°C, and can survive short periods of freezing, in addition to salinities from 6.8 to 34 psu, although it shows reduced growth rates at both low temperature and low salinity (Norton, 1977). The optimal growth conditions are reported to be a salinity of 34 psu and a temperature of 25°C (Eno & Clark, 1995). *S. muticum* is a successful invasive species, in part due to this wide temperature and salinity tolerance. Other properties typical of invasive species include high growth rates (2 to 4 cm per day) (Jephson & Gray, 1977; Lewey & Farnham, 1981; Critchley, 1983a), early fertility (Pizzolla, 2008), high fecundity, a monoecious perennial life history (Norton & Deysher, 1989), and effective sexual and asexual dispersal strategies (Norton, 1976). It can also colonize both disturbed habitats (DeWreede, 1983) and undisturbed macroalgal communities (Sánchez & Fernández, 2005).

Distribution: A native of the western Pacific (Yoshida, 1983) where it forms a relatively minor component of macroalgal communities (Norton, 1977; Critchley, 1983a). It has been introduced to coastlines in both the Pacific and the Atlantic, attached to Japanese oysters (*Crassostrea gigas*), also an invasive species transplanted for aquaculture (Scagel, 1956). It was first recorded in the UK in 1973, at Bembridge on the Isle of Wight (Farnham *et al.*, 1973), and has since spread rapidly along the south coast of England to the Isles of Scilly, and north to Wales, Ireland and Scotland (Pizzolla, 2008).

9.13 *Undaria pinnatifida*



Description: An annual kelp with a claw-like holdfast, above which the stipe gives way to undulating edges which progresses to a broad, flat blade with a distinct midrib and a wavy edge. The sporophyte rapidly grows to 1 to 3 m long (Oakley, 2007). This species occurs in the shallow sublittoral and infralittoral zone to depths of <18 m (Floc'h *et al.*, 1991).

Reproduction: Sporophytes generally recruit during winter, grow throughout the spring and reach reproductive maturity in the summer months as water temperatures increase (Thornber *et al.*, 2004; Báez *et al.*, 2012). However, in Northern Spain and California, two sporophyte recruitment periods have been reported: late summer and early winter (Thornber *et al.*, 2004). Sori are located in the sporophylls around the stipe from which the release of motile zoospores is induced when the 10 day average water temperature exceeds 14°C (Saito, 1975). This process has been reported from late April to December along the south coast of England (Farrell & Fletcher, 2006). The zoospores are reportedly motile for up to 5 hours (Saito, 1975; Akiyama & Kurogi, 1982; Hay & Luckens, 1987), before settling and developing into microscopic haploid gametophytes. Gametophyte production and persistence occurs during the summer months. These gametophytes can remain dormant for long periods, and can reportedly withstand temperatures of -1 to 29°C (Saito, 1975), whilst they wait for the optimal conditions to mature. Once the seawater temperature drops to below 20°C, with optima of 10 to 15°C (Morita *et al.*, 2003a), gametophyte development occurs. Consequently mature gametophytes undergo sexual reproduction giving rise to the new embryonic sporophyte in autumn. The sporophyte is tolerant of temperatures from 4 to 25°C (Akiyama & Kurogi, 1982; Morita *et al.*, 2003b) with 10 to 20°C the optimal growing temperatures for a vegetative sporophyte (Akiyama, 1965; Saito, 1975).

Distribution: A temperate species that originated in the Northwest Pacific, but has considerably extended its worldwide distribution over the past four decades. In the North Atlantic it was first introduced to Brittany for aquaculture purposes in 1983 from where it spread, with local wild populations discovered in 1987. The initial rate of both population growth and spread within Brittany was slow, with populations spreading stepwise out from the original farm sites into the wild. Unlike *Sargassum muticum*, *U. pinnatifida* is not equipped with an inherent long range dispersal strategy. However, the long range spread of this species is facilitated by anthropogenic activity through transfer of contaminated shellfish, and on the hulls of small leisure boats (Fletcher & Farrell, 1999). The unique life history pattern with easily transportable, highly tolerant, microscopic stages that are present in the summer months, when pleasure craft are in abundance, may be one reason why *U. pinnatifida* is the only reported invasive kelp species in North Atlantic waters (Ruiz *et al.*, 2000; Thornber *et al.*, 2004).