

MarLIN Marine Information Network

Information on the species and habitats around the coasts and sea of the British Isles

Saccharina latissima and *Laminaria digitata* on sheltered sublittoral fringe rock

MarLIN – Marine Life Information Network Marine Evidence-based Sensitivity Assessment (MarESA) Review

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Laminaria saccharina and Laminaria digitata on sheltered sublittoral fringe rock Photographer: Keith Hiscock Copyright: Joint Nature Conservation Committee (JNCC)



Researched by Claire Jasper Refereed by Admin

Summary

UK and Ireland classification

EUNIS 2008	A3.3131	Laminaria saccharina and Laminaria digitata on sheltered sublittoral fringe rock
JNCC 2015	IR.LIR.K.Slat.Ldig	<i>Saccharina latissima</i> and <i>Laminaria digitata</i> on sheltered sublittoral fringe rock
JNCC 2004	IR.LIR.K.Lsac.Ldig	Laminaria saccharina and Laminaria digitata on sheltered sublittoral fringe rock
1997 Biotope	IR.SIR.K.Lsac.Ldig	Laminaria saccharina and Laminaria digitata on sheltered sublittoral fringe rock

Description

Sheltered bedrock and boulders in the sublittoral fringe may be characterized by a mixed canopy of the kelps *Laminaria digitata* (usually in its broad-fronded cape form) and *Saccharina latissima*

(both species generally frequent or greater). Beneath the canopy a wide variety of red seaweeds, including *Palmaria palmata*, *Corallina officinalis*, *Mastocarpus stellatus*, *Chondrus crispus* and *Plocamium cartilagineum*, may be present. The surface of the rock is usually covered with encrusting coralline algae; there may be patches of the sponge *Halichondria panicea* frequently occurs in cracks in the rock. Beneath and between boulders a variety of mobile crustaceans (*Carcinus maenas*, *Cancer pagurus* and *Porcellana platycheles*), spirorbid worms, starfish (*Asterias rubens*) and encrusting bryozoans are common. On such sheltered shores the transition between sublittoral fringe and the true sublittoral zone may not be distinct; this biotope therefore extends into the shallow sublittoral. (See Connor et al., 2004; JNCC)

↓ Depth range

Lower shore, 0-5 m

1 Additional information

-

✓ Listed By

- none -

% Further information sources

Search on:



Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

This biotope is characterized by the occurrence of both *Laminaria digitata* and *Saccharina latissima* in frequent or greater abundances, and may also have other green and brown algae present including *Ulva intestinalis*, *Fucus serratus* and ectocarpoids, and by high levels of siltation on bedrock, boulders and in some cases cobbles (Connor *et al.* 2004). However, the presence of *Laminaria digitata* suggests that siltation or disturbance by winter storms (and scour) is reduced in this biotope (IR.LIR.K.Slat.Ldig) in comparison with the IR.LIR.K.Slat.Ft or IR.LIR.K.Slat.Pk biotopes.

This biotope is found in sheltered inlets, fjordic sealochs and loughs (southwest England, Scotland and Ireland). The demarcation of each zone is not as well defined on sheltered shores as it is in more exposed shores, therefore there may be a physical overlap between biotopes. For example, IR.LIR.K.Slat.Ldig may occur in the sublittoral, above the IR.LIR.K.Slat.Ft on the shore, but in extremely sheltered conditions may occur up to the base of the *Fucus serratus* zone, although in extremely sheltered condition, IR.LIR.K.Slat.Ldig (may extend into the shallow sublittoral. Geographical location plays a major part in determining the characteristic biota associated with this biotope.

This biotope occurs in areas sheltered from wave action and strong water currents. The kelps *Saccharina latissima* and *Laminaria digitata* are the key characterizing species defining this biotope group, the sensitivity assessments are based largely on these species alone. Loss of either species would result in the loss of the biotope and its replacement with another biotope. However, IR.LIR.K.Slat.Ldig is defined by the relative abundance of the two kelp species. Increased shelter, sedimentation and scour would probably favour *Saccharina latissima* while increase wave action and reduced siltation would probably favour *Laminaria digitata*, and result in a change in the character of the biotope and its replacement by other kelp dominated biotopes. Although a range of species are associated with the biotope at low abundance, these species occur in a number of other rock biotopes and therefore do not specifically define this biotope group. Although these species contribute to the structure and function of the biotope they are not considered key species and are not specifically assessed.

Resilience and recovery rates of habitat

Saccharina latissima (studied as Laminaria saccharina) was the prominent kelp species on the concrete blocks (a minimum of 1.3 m in diameter) six months after removal of all vegetation (Kain, 1975). Without competition from other kelp species, Saccharina latissima populations increase their biomass within two years, while its density decreases (Mikhaylova, 1999). Re-attachment of dislodged Saccharina latissima may occur in certain conditions, with dislodged individuals growing new haperon (root-like structures) that subsequently attach to the substratum (Burrows, 1958). Unattached 'loose lying' populations of Saccharina latissima (studied as Laminaria saccharina) have been documented in Port Erin Bay, Isle of Man (Burrows, 1958). Indicating that apart from the earliest stages of sporophyte development, attachment to the substratum is not essential for growth. It is therefore possible that a few individuals could survive displacement, although this is not considered as a significant pathway for the biotope's recovery.

Saccharina latissima has a typical heteromorphic life history, in which a microscopic gametophyte alternates with a macroscopic adult, the sporophyte. The sporophyte's lifespan is normally two to four years, although older specimens have been recorded from a fjord in Greenland (Gayral &

Cosson, 1973, Borum *et al.*, 2002). Growth of the lamina occurs from its base, potentially enhancing its resistance to grazing (Kain, 1979). Juvenile sporophytes take eight months to reach an average size (1-2 m in length; Gerard, unpublished, cited in Gerard and Du Bois, 1988). Growth rates for sporophytes are greatest between 10-15°C, with tissue growth occurring from March to November (7 m depth, Bolton & Lüning, 1982, Nielsen *et al.*, 2014). Despite this, elongation of the frond only occurs between March and May due to high levels of abscission from July to November (Nielsen *et al.*, 2014). Temperature is a major factor affecting growth in *Saccharina latissima*, with decreased growth rates evidence above 16°C, and 50-70% growth reduction at 20°C (Bolton & Lüning, 1982).

Saccharina latissima's reproductive period is defined by the presence of sori (reproductive tissue) on its fronds. Sori are first produced by Saccharina latissima individuals of 4-5 months old and may occur for 1-9 concurrent months a year (studied as Laminaria saccharina, Parke 1948; Lüning 1979; Lee & Brinkhuis, 1988). This contrasts with other kelp species including Laminaria digitata and Laminaria hyperborea which reach maturity between 18-20 and 15 months respectively (Perez, 1971, Kain, 1975). Formation of sori (reproductive tissue) occurs at temperatures below 18°C (Bartsch et al., 2013) from October to March/April (Andersen et al., 2011). A minimum of 10 weeks a year between 5-18°C is needed for subsequent spore formation (Bartsch et al., 2013). Thus temperature and by default season impacts the level of reproductive activity. If environmental conditions for spore survival are not favourable, then development of the gametophytes can be delayed for a short period, creating a level of resistance against short-term environmental changes (Van den Hoek et al., 1995). Despite this ability, seaweeds in general are considered particularly vulnerable to short-term warming events (Dayton & Tegner, 1984; Smale & Wernberg, 2013; Wernberg et al., 2013; from Smale et al., 2013). Recruitment of Saccharina latissima generally occurs in the highest numbers from December to January (Andersen et al., 2011).

Evidence on *Saccharina latissima*'s spore dispersal is limited. The passive dispersal of spores is reliant on local current and wave mediated water movements (Cie & Edwards, 2011). Kelp larval dispersal varies with location and species, *Macrocystis* spores in Australia may travel 1 km (Gaylord *et al.*, 2006), while the spores of *Laminaria digitata* have a dispersal range of 600 m (Chapman, 1981). In conditions of low water movement, typical of this biotope, larval dispersal range is likely to be depressed, with the majority of recruitment occurring within the biotope. The reforestation of historic kelp beds off Norway, indicate that natural re-colonization was prevalent in the past (Moy and Christie, 2012). Andersen (2013) suggests that this, and other regional studies (see Andersen 2013 and the references herein) are illustrative of population connectivity and long distant dispersal in *Saccharina latissima*. *Saccharina latissima* exhibits a high degree of plasticity between populations with kelp from Maine, USA able to withstand greater temperatures than their northern, New York counterparts (Gerard and Du Bois, 1988).

There are a number of studies which specify the recovery of *Laminaria digitata* post removal. Recolonization of concrete blocks by *Laminaria digitata* was investigated by Kain (1975) at Port Erin, Isle of Man, *Laminaria digitata* was considered re-established two years after removal, while the characteristic red foliose algae returned one year later. Additionally after plant cutting, the standing crop of *Laminaria digitata* was re-established within 18-20 months (Kain, 1979). Like their host, the life cycles of many of the kelp associated organisms involve a planktonic stage. While colonization of young *Laminaria* sporophytes may occur soon after initial growth (1 year), the return of the biotope to its original biological functioning takes longer. Removal of 0.25m² areas of *Laminaria digitata* forest in the spring and autumn indicated differences in recovery rates between seasons, with autumn recovery more rapid than spring (taking a minimum of 12 months). Return to conditions prior to removal took 18-24 months, with competition for space by Saccorhiza polyschides impacting recovery rates in the first year of recolonization (Engelen et al., 2011). These findings agree with those of previous studies which showed that when 60% of sporophytes (adult algal stage) were removed from a location, 18 months were required for the stand to rejuvenate (Perez, 1971), while in France, CIAM (le Comité interprofessionel des algues marines) proposed that, regardless of collection method, the restoration of stands of Laminariales took up to 18 months after harvesting (Arzel, 1998). Some disparities between recovery rates do exist, with cleared plots in Helgoland taking, 25 months, probably because plots were burned to ensure all spores and germlings were also removed (Markham & Munda, 1980). Even after 25 months, although algal density had returned to pre-clearance levels, the Laminaria digitata plants were smaller than those on undisturbed plots, suggesting full recovery is longer than 25 months (Markham & Munda, 1980). This lag in total recovery is common for Laminarian species. Laminaria digitata has also been shown to regenerate if cut 5 cm from the base of the blade (above the meristem) and can withstand up to 4 blade removals, with younger individuals recovering faster than those of 5 years (Perez, 1971). Location also appears to play a major role in the recovery rates of Laminaria digitata, with the species exhibiting stunted growth for longer in some areas than others (Engelen et al., 2011). In addition, Birkett et al. (1998b) described how experimental canopy removal and clearance experiments conducted in Scotland and the Isle of Man showed that 3 years after canopy removal, some semblance of a kelp forest, in terms of macroalgal biomass and subsidiary algal species, was regained. However, the size of the kelp plants and age structure of the population was different from uncleared kelp forests.

Interactions with other species may also alter the recovery of this biotope and in some instances the interactions may be mediated by the effects of human activities. Grazers are responsible for less than 20% of kelp produced nutrients entering the food web; the majority enters as detritus or dissolved organic matter. Direct grazing of kelp is rare, with exceptions including the blue-rayed limpet (Krumhansl & Scheibling, 2012). However in conditions of stress, grazers may change their feeding activity and directly graze the kelp. Laboratory choice experiments indicated that Echinus esculentus preferentially feeds on bryozoan encrusted Saccharina latissima over Laminaria *digitata*, meaning that the key species of this biotope may be more vulnerable to grazing than its counterparts (Bonsdorff & Vahl, 1982). Uncontrolled grazing of kelps by herbivores, including sea urchins may result in detrimental consequences to the biotope. In Nova Scotia (Atlantic coast of Canada) a study on the kelp Laminaria longicruris and its understory of Laminaria digitata indicate that grazing sea urchins may have prevented the kelp biotope's regeneration after harvesting. Removal of the urchin's predators through direct harvesting (e.g. of fin fish) or indirect elimination of the kelp canopy, leads to an urchin population increase which, unchecked by predation may result in the formation of barrens and the loss of the biotope (Bernstein et al. 1981; Estes & Duggins 1995; Ling et al., 2009). Heavy biofouling has been indicated to cause premature death and decreased reproductive output in Saccharina latissima (Saier and Chapman, 2004, Andersen et al., 2011). This indicates that a decrease in grazers which feed on these epibionts could be detrimental to the biotope's identity, especially in the light of future global sea temperature increases, which favour the growth of ephemeral algae (Andersen et al., 2011).

Many of the Rhodophyta e.g. *Delesseria sanguinea*, are perennial species that may persist for several years. For instance, Dickinson (1963) suggested a lifespan of 5-6 years for *Delesseria sanguinea*. However, Kain (1984) estimated that 1 in 20 specimens of *Delesseria sanguinea* may attain 9 -16 years of age. Kain (1975) examined recolonization of cleared concrete blocks in a subtidal kelp forest at Port Erin, Isle of Man. Red algae colonized blocks within 26 weeks in the shallow subtidal (0.8 m) and 33 weeks at 4.4 m. *Delesseria sanguinea* was noted within 41 weeks (8 months) at 4.4 m in one group of blocks and within 56-59 days after block clearance in another

group of blocks. This recolonization occurred during winter months following spore release and settlement, but not in subsequent samples (Kain, 1975). This suggests that colonization of *Delesseria sanguinea* in new areas is directly dependent on spore availability. Rhodophyceae have non flagellate, and non-motile spores that stick on contact with the substratum. Norton (1992) noted that algal spore dispersal is probably determined by currents and turbulent deposition. However, red algae produce large numbers of spores that may settle close to the adult especially where currents are reduced by an algal turf or in kelp forests. However, in her recolonization experiments Kain (1975) while *Laminaria digitata* was considered re-established two years after removal, with the characterizing red foliose algae followed one year later, that is, took up to three years to reestablish prior abundance.

Resilience Assessment. The rapid maturation of Saccharina latissima (4-5 months), when compared to other kelps means that this species should have a relatively fast recovery phase (less than two years) as indicated by its initial growth in areas cleared of other kelp species. Saccharina latissima species has been noted as one of the first algal species to recolonize to disturbed substratum. The associated biota of Saccharina latissima are mainly substratum dwelling, their return to the biotope is likely to depend on the recovery of Saccharina latissima and is therefore likely to occur after the initial stages of recovery by Saccharina latissima. If removed completely red algae are likely to return within a year (Kain 1975) but do not reach the diversity and cover found at Port Erin, due to the inherent disturbance of this biotope due to scour. However, Laminaria digitata took up to 20-25 months to recover in similar experiments, depending on study and location, and may take longer to recover completely. Therfore, the biotope exhibits a mixture of opportunisticspeices and (e.g. Saccharina latissima and tube-worms) and species typical of more stable condtions (e.g. Laminaria digitata and red algae). Therefore, where the a proportion of the biotope is disturbed, damged or lost (e.g. resistance is 'Medium' to 'Low') then the resilience is probably 'High', but where the biotope is severely damaged (e.g. resitance is 'None'), resilience is probably 'Medium'.

Hydrological Pressures

	Resistance	Resilience	Sensitivity
Temperature increase	<mark>Medium</mark>	<mark>High</mark>	Low
(local)	Q: High A: Medium C: Medium	Q: High A: High C: High	Q: High A: Medium C: Medium

Saccharina latissima is found in the NW Atlantic and North Pacific (Wilce 1965; Druehl, 1970; Lüning, 1990), typically occurring between 40°N and 80°N. In Europe, *Saccharina latissima* occurs from Portugal to Spitbergen (Van den Hoek & Donze, 1967, Lüning, 1990). Its distribution suggests a tolerance to a chronic temperature change (e.g. by 2°C for a year). Other associated organisms to this biotope may fair less well. Exposure to high short-term temperature increases are likely to result in stress, however the recovery of this biotope is likely to be rapid. There is a general consensus in the literature that increases in temperature are likely to have a more detrimental effect than decreases in temperature (Andersen *et al.*, 2013, Nielsen *et al.*, 2014).

Temperature ecotypes have been suggested for *Saccharina latissima* populations near its southern limit off the USA coastline. Algae from New York, which experience water temperatures in excess of 20°C each summer, exhibit greater temperature tolerance than algae from Maine, where temperatures rarely exceed 17°C (Gerard & Du Bois, 1988). Three weeks of exposure to temperatures greater than 20°C in the field resulted in 50% mortality of algae from New York, while 100% of the algae from Maine died (Gerard & Du Bois, 1988). In comparison, individual

Saccharina latissima from Helgoland in the southern North Sea undergo disintegration of blade tissue after 3 month at 15°C (Lüning, 1988).

The life cycle of kelps are considered sensitive to temperature. At temperatures greater than 15° C, higher photon flux densities are required to reach similar proportions of fertility to their counterparts kept at lower temperatures (Lüning, 1990), while photon fluence rates have been noted to rise concomitantly whilst photosynthetic efficiency decreases (Davison *et al.*, 1991). Sporogenesis in *Saccharina latissima* requires a minimum period of 4 weeks at or below 15° C combined with short day lengths in order to occur (Müller *et al.*, 2009). Germination of zoospores is also sensitive to temperature and may be population specific, with germination inhibited at 20°C in the laboratory, but exceeding 90% in field populations collected in July when photo fluence rates were 5 μ E m⁻² sec⁻¹ (Lee & Brinkhuis, 1988). The same study found that gametophyte growth improved with increasing water temperatures between 4-17°C and that fecundity was greatest between 7-17°C.

Sporophyte growth has been recorded between 10-15°C with 50-70% reduction in growth at 20°C (Bolton & Lüning, 1982). For the gametophytes and young sporophytes of *Saccharina latissima*, the upper temperature tolerance is 22°C with exceptions including the growth of gametophytes in Long Island Sound at 23°C (Lee & Brinkhuis, 1988). A temperature of 23°C is also considered to be the maximum survival temperature for gametophytes from three European populations of *Saccharina latissima*, with disintegration occurring after 3 weeks (Bolton & Lüning, 1982). Although a more conservative estimate of *Saccharina latissima*'s upper temperature limit was considered by Lüning (1990) to be 20°C. In the summer of 1983 (the hottest on record before July 2009), bleaching of *Saccharina latissima* sporophytes was evident in Plymouth Sound and on the Isle of Man (Hawkins & Hartnoll, 1985). Research showed that growth reduction was evident at only 5°C above the optimum temperature range for *Saccharina latissima* (10-15°C) (Kain 1979; Bolton & Lüning 1982; Andersen *et al.*, 2013).

In an experiment observing gene expression in *Saccharina latissima*, a greater representation of genes associated with high temperature response than those for low temperatures was evident, suggesting that higher temperatures are more detrimental to *Saccharina latissima* (and therefore the biotope) than low temperatures (Heinrich *et al.*, 2012). A permanent change to the local temperature regime may result in a shift to ephemeral algae which then form a barrier to future settlement of *Saccharina latissima* slowing or stopping recovery of the biotope (Moy & Christie, 2012).

Laminaria digitata is distributed from Brittany to the Spitzbergen (Birkett *et al.*, 1998b; Blight & Thompson, 2008). The Northern/Boreal distribution of *Laminaria digitata* suggests it may be slightly vulnerable to temperature increases in its southern range. The thermal optimum of *Laminaria digitata* is between 10-15°C, with reproductive ability impaired to 20% at 18°C (Arzel, 1998). Spore production only occurs between 5-10°C and is the most temperature sensitive stage of reproduction in *Laminaria digitata*. Outside this temperature range, reproduction is severely reduced and the species is at risk from local extinction in the short-term. A temperature increase to 22-23 °C causes cell damage and death (Sudene, 1964; Bolton & Lüning, 1982). During an exceptionally warm summer in Norway Sundene (1964) reported the destruction of *Laminaria digitata* plants exposed to temperatures of 22-23°C. The sensitivity of this species therefore relies on the current sea temperatures of the specific location (Bartsch *et al.*, 2013). A minimum of 10 weeks a year between 5-18 °C is needed in order to ensure spore formation and hence reproduction and recruitment (Bartsch *et al.*, 2013).

Combining predicted sea surface temperate over the next century with the current distribution of *Laminaria digitata*, Merzouk & Johnson (2011) predict an expansion of it's northern limits and localised extinctions across it's southern range edge (Mid Bay of Biscay, Northern France and southern England; Birkett *et al*, 1998b). Suggesting at sites where sea temperature is artificially increased as a result of anthropogenic activity (e.g. effluent output) local extinction of the biotope may occur (Raybaud *et al.*, 2013) especially if combined with high summer sea temperature (Bartsch *et al.* 2013). In southern examples of the biotope, *Laminaria digitata* may also be outcompeted by it's Lusitanian competitor *Laminaria ochroleuca* which is regionally abundant across the south UK coastline (Smale *et al.*, 2014).

Increased temperatures bring with them increased growth of epiphytic ephemeral algae. Excessive growth on kelp by these species has been reported to result in high mortality rates within the kelp populations on the North American coast (Lee & Brinkhuis, 1988, Levin *et al.*, 2002, Scheibling & Gagnon, 2006). Krumhansl & Scheibling (2011) also found negative effects in growth in conjunction with increasing temperatures, however they also highlighted the role which ephiphytic loading enhances blade tissue loss (Andersen *et al.*, 2013). If environmental conditions for spore survival are not favourable, then development of the gametophytes can be delayed for a short period, creating a level of resistance against short-term environmental changes (Van den Hoek *et al.*, 1995). Despite this ability, seaweeds in general are considered particularly vulnerable to short-term warming events (Dayton & Tegner, 1984; Smale & Wernberg, 2013; Wernberg *et al.*, 2013; from Smale *et al.*, 2013). Recruitment of *Saccharina latissima* generally occurs in the highest numbers from December to January (Andersen *et al.*, 2011).

The tolerance of red algae to temperature changes varies considerably and those of the littoral zone typically have a greater tolerance to both increased and decreased temperature, than those of the sublittoral (see Gessner, 1970). Sublittoral red algal species, Sphondylothamnion multifidum, Cryptopleura ramosa and Rhodophyllis divaricata were capable of surviving at 27 °C, while other species such as Callophyllis laciniata, Calliblepharis ciliata, Plocamium cartilagineum and Heterosiphonia plumosa died within 12 hours in seawater at 27 °C. However, such a temperature increase exceeds that of the benchmark level. There is some evidence to suggest that blade growth in Delesseria sanguinea is delayed until ambient sea temperatures fall below 13°C, although blade growth is likely to be intrinsically linked to gametangia development (see Kain, 1987). Delesseria sanguinea is tolerant of 23°C for a week (Lüning, 1984) but dies rapidly at 25°C. North Sea and Baltic specimens grew between 0-20°C, survived at 23°C but died at 25°C rapidly (Rietema, 1993). Rietema (1993) reported temperature differences in temperature tolerance between North Sea and Baltic specimens. Lüning (1990) reports optimal growth in Delesseria sanguinea between 10 -15°C and optimal photosynthesis at 20°C. However, the upper limit of temperature tolerance is reduced by lowered salinity in Baltic specimens (Kinne, 1970; Kain & Norton, 1990). At low salinity photosynthesis is restricted to a narrow range of temperatures in adult thalli whereas juvenile thalli have a wider response range (Lobban & Harrison, 1997; fig 6.27). It is likely therefore that within the subtidal an increase in temperature of 2°C in the long-term will have limited effect on survival, although it may affect initiation of new growth at the southern limits of the population. An increase of 5°C in the short-term may affect survival if the ambient temperature is increased above 23°C.

Sensitivity assessment. Responses of this biotope to an increase in temperature are clearly population specific. Those at the extremes of the biotope's temperature range are likely to be more affected than those at the centre of their range. An increase of 5°C for one month may affect the fecundity of *Saccharina latissima* or *Laminaria digitata* for that year depending on when the increase occurs. An increase of 2°C is more likely to affect those at the extremes of the biotope's range, the

plasticity of *Saccharina latissima* may allow for populations to adapt to the new conditions over time, however this is uncertain. Similarly, *Laminaria digitata* may survive a short-term increase in temperature (5°C for one month) but a long-term increase (2°C for one year) may result in loss of a proportion of the population especially at its upper extent on the shore and/or in southern parts of its range in summer months. The red algae community may survive long-term increase in 2°C but may suffer mortality from short-term change by 5°C, especially if the resultant temperature exceeded 27°C. Therefore resistance of this biotope to an increase in temperature is therefore considered as '**Medium**' at the benchmark level. Resilience is likely to be '**High**' and sensitivity therefore '**Low**'. However, prolonged increases in temperature or espacially hot summers (see Sundene, 1964) may result in loss of *Laminaria digitata* from the biotope, and hence a loss of the biotope.

Temperature decrease (local)

High Q: High A: Medium C: Medium High Q: High A: High C: High Not sensitive Q: High A: Medium C: Medium

Saccharina latissima is found in the NW Atlantic and North Pacific (Wilce 1965; Druehl, 1970; Lüning 1990), typically occurring between 40°N and 80°N. In Europe, *Saccharina latissima* occurs from Portugal to Spitbergen (Van den Hoek & Donze, 1967, Lüning, 1990). Its distribution suggest that the species would tolerate a chronic temperature change (e.g. by 2°C for a year). *Laminaria digitata* is distributed from Brittany to the Spitzbergen (Birkett *et al.*, 1998; Blight & Thompson, 2008). The Northern/Boreal distribution of *Laminaria digitata* suggests it would tolerate a decrease in temperature at the benchmark level.

The life cycle of kelps, in particular their spore production stage is considered to be sensitive to temperature. The gametophytes of *Saccharina latissima* reportedly suppress growth below 10°C (Lüning, 1990). In a laboratory experiment with an Arctic population of *Saccharina latissima*, embryos achieved 100% germination at 0°C, but expressed lower rates of primary cell growth in comparison to those grown at 10°C. These lower rates of growth do not seem to impede the kelp's ability to compete successfully, with the species occurring in year round temperatures lower than 0°C in a high-arctic Fjord, Greenland (Borum *et al.*, 2002). Sjotun & Schoschina (2002) cultivated *Saccharina latissima* from embryospores at 0°C in the laboratory and showed that oogonia were produced 18-20 days after sporulation in comparison to a minimum of 20-24 days for *Laminaria hyperborea*, and 34 days for *Laminaria digitata*.

Under laboratory conditions chronic exposure to 5°C, after being maintained at 15°C, resulted in the adult sporophytes stage requiring a higher photon fluence rate to maintain net and light-saturated photosynthesis (studied as *Laminaria saccharina*, Davison *et al.*, 1991). This response is short-term, with the acclimation of growth temperatures over time buffering the depression in compensation point and light-saturated photosynthesis, allowing the alga to achieve similar rates of light-limited photosynthesis at both 5 and 15°C (Davison *et al.*, 1991). At 2°C, *Saccharina latissima* up-regulates the production of amino acids associated with Glutathione, an antioxidant, suggesting that below 2°C lowered growth rates are related to an increased energy expenditure on decreasing the effects of photo-oxidative stress (Heinrich *et al.*, 2012).

The thermal optimum of *Laminaria digitata* is between 10-15°C, with reproductive ability impaired to 20% at 18°C (Arzel, 1998). Spore production only occurs between 5-10°C and is the most temperature sensitive stage of reproduction in *Laminaria digitata*. Outside this temperature range, reproduction is severely reduced and the species is at risk from local extinction in the short-term. A temperature increase to 22-23°C causes cell damage and death (Sudene, 1964; Bolton & Lüning,

1982). During an exceptionally warm summer in Norway Sundene (1964) reported the destruction of Laminaria digitata plants exposed to temperatures of 22-23°C. The sensitivity of this species therefore relies on the current sea temperatures of the specific location (Bartsch, 2013). A minimum of 10 weeks a year between 5-18 °C is needed in order to ensure spore formation and hence reproduction and recruitment (Bartsch, 2013).

Cold damage usually changes the colour of red algae to a bright yellow orange. Sphondylothamnion multifidum, Cryptopleura ramosa and Rhodophyllis divaricata were partially or completely killed at 5°C. Callophyllis laciniata, Calliblepharis ciliata, Plocamium cartilagineum and Heterosiphonia plumosa survived -2°C. Delesseria sanguinea and Phycodrys rubens succumbed at temperatures of -3°C to -5°C. During experimental attempts to adapt red algae to cold by maintaining them at -1°C to + 1°C for several months, a drop in the lethal temperature tolerance of Delesseria sanguinea and a few other species was detected, in the order of 1 to 2°C (Gessner, 1970). However, it is unlikely that seawater temperatures would fall below 0°C in the UK.

Sensitivity assessment. A decrease in temperature at the benchmark is not likely to impact biotopes at the centre of their temperature tolerances, however those at its temperature limit are likely to experience decreases in abundance of Saccharina latissima (due to reduced reproduction and growth) if the temperature is lowered to 0°C for one year. As Laminaria digitata is a northern boreal species, a chronic reduction in temrpature is unlkely to be significant. If decreases of 5°C for one month occur, then the time of the year is vital in determining the response of this biotope as it may impact the fecundity of the Saccharina latissima population and growth of red algae. However, if the decrease is chronic the biotope should persist and is therefore considered to have a resistance of 'High' to this biotope. A resilience of 'High' is therefore also recorded, while the overall sensitivity of the biotope is 'Not sensitive', although beyond the benchmark, the loss of the biotope may occur.

Salinity increase (local)

Medium

Q: High A: Medium C: Medium

High Q: High A: High C: High Low

Q: High A: Medium C: Medium

IR.LIR.K.Slat.Ldig is recorded from full or variable salinity conditions but Saccharina latissima is also typical of reduced salinity conditions (Connor et al., 2004). In a laboratory experiment, Saccharina latissima (studied as Laminaria saccharina) survived successfully between 17-32 psu (Druehl, 1967). However, Gerard & Du Bois (1988) reported that Saccharina latissima had a salinity tolerance of 23-31 psu. Karsten (2007) tested the photosynthetic ability of Saccharina latissima under acute 2 and 5 day exposure to salinity treatments ranging from 5-60 psu. A control experiment was also carried at 34 psu. Saccharina latissima showed high photosynthetic ability at >80% of the control levels between 25-55 psu. Decreases in salinity to 5 psu for Saccharina latissima from Arctic Kongsfjorden (Spitsbergen) induced bleaching, indicative of cell damage after 5 days of incubation in the laboratory, while treatments decreasing from 20-10 psu were associated with decreasing photosynthetic performance (Karsten, 2007). However, Birkett et al. (1998b) suggested that kelps are stenohaline and, therefore, long-term increases in salinity may be detrimental.

Optimum growth rates in Saccharina latissima cultured from UK waters were achieved at 31 psu, while 16 psu dramatically decreased growth rates and 8 psu resulted in the death of the alga (Burrows & Pybus 1971). In contrast, Saccharina latissima from the White Sea responded with decreased photosynthetic rates at 6-8 psu, while severe growth reductions were noted at 2 psu (Drobyshev, 1971). Juvenile sporophytes of Saccharina latissima can survive salinities of 13 for 3 weeks however, at 10 psu the juveniles become severely stressed and the majority die (Spurkland & Iken, 2011a). In Arctic kelp, decreases in *Saccharina latissima* growth were associated with decreasing salinity (Spurkland & Iken 2011a). Nielsen *et al.* (2014) also associated low growth, with decreases in salinity in a field experiment in Danish waters; while Weile (1996), recorded low growths (5.4 mm/day) in areas <14 psu. Responses of *Saccharina latissima* to salinity changes are population specific. Exposure to salinities outside a kelp's tolerance range causes osmotic and ionic stress (Kirst 1990) resulting in decreased efficiency of their photosynthetic apparatus (<20-25%, Kirst & Wiencke, 1995).

At the extremes of *Laminaria digitata's* salinity tolerance, decreases in photosynthetic rates are evident, particularly at low salinities (Gordillo *et al.*, 2002). On the Norwegian coast which is subjected to seasonal fluctuations in salinity, healthy *Laminaria digitata* plants were found growing at 15-25 psu (Sundene, 1964). Long-term reductions in salinity may result in the loss of the kelp beds in the affected area, or the out-competition of *Saccharina latissima* by *Laminaria digitata*, and thus the loss of the biotope (Birkett *et al.*, 1998b). Kelp tolerate increases in salinity better than decreases in salinity, with no evidence of decreased photosynthetic activity at 55 psu (Karsten, 2007). *Laminaria digitata* tolerates a large salinity range within a 24 hour period (5-60psu; Karsten, 2007).

Sensitivity assessment. At the benchmark, an increase in salinity from 'full' to 'hypersaline' (>40 psu) conditions for a year is unlikely to adversely affect *Saccharina latissima* or *Laminaria digitata* as kelp tolerate increases in salinity better than decreases in salinity, with no evidence of decreased photosynthetic activity at 55psu (Karsten, 2007). Little evidence for the effects of hypersaline conditions on the associated flora and fauna was found. Therefore, the resistance is probably '**Medium**' to represent the potential loss of members of the associated flora and fauna. Resilience ins probably '**High**' so that sensitivity is assessed as '**Low**'.

Salinity decrease (local)

<mark>High</mark> Q: High A: Medium C: Medium <mark>High</mark> Q: High A: High C: High Not sensitive Q: High A: Medium C: Medium

IR.LIR.K.Slat.Ldig is recorded from full or variable conditions but Saccharina latissima is also typical of reduced salinity conditions (Connor et al., 2004). In a laboratory experiment, Saccharina latissima (studied as Laminaria saccharina) survived successfully between 17-32 psu (Druehl, 1967). However, Gerard & DuBois (1988) reported that Saccharina latissima had a salinity tolerance of 23-31 psu. Optimum growth rates in algae cultured from UK waters were achieved at 31 psu, while 16 psu dramatically decreased growth rates and 8 psu resulted in the death of the alga (Burrows &Pybus 1971). In contrast, Saccharina latissima from the White Sea responded with decreased photosynthetic rates at 6-8 psu, while severe growth reductions were noted at 2 psu (Drobyshev, 1971). Decreases in salinity to 5 psu for Saccharina latissima from Arctic Kongsfjorden (Spitsbergen) induced bleaching, indicative of cell damage after 5 days of incubation in the laboratory, while treatments decreasing from 20-10psu were associated with decreasing photosynthetic performance (Karsten, 2007). Juvenile sporophytes of Saccharina latissima can survive salinities of 13 for 3 weeks however, at 10 psu the juveniles become severely stressed and the majority die (Spurkland & Iken, 2011a). In Arctic kelp, decreases in Saccharina latissima growth were associated with decreasing salinity (Spurkland & Iken 2011a). Nielsen et al., (2014) also associated low growth, with decreases in salinity in a field experiment in Danish waters; while Weile (1996), recorded low growths (5.4 mm/day) in areas <14 psu. Responses of Saccharina latissima to salinity changes are population specific. Exposure to salinities outside a kelp's tolerance range causes osmotic and ionic stress (Kirst 1990) resulting in decreased efficiency of their photosynthetic apparatus (<20-25%, Kirst & Wiencke, 1995).

Laminaria digitata tolerates a large salinity range within a 24 hour period (5-60psu; Karsten, 2007). Exposure to salinities outside a kelp's tolerance range causes osmotic and ionic stress (Kirst 1990) resulting in decreased efficiency of their photosynthetic apparatus (<20-25, Kirst & Wiencke, 1995). At the extremes of *Laminaria digitata's* salinity tolerance, decreases in photosynthetic rates are evident, particularly at low salinities (Gordillo *et al.*, 2002). On the Norwegian coast which is subjected to seasonal fluctuations in salinity, healthy *Laminaria digitata* plants were found growing at 15-25 psu (Sundene, 1964). *Laminaria digitata* tolerates a large salinity range within a 24 hour period (5-60 psu; Karsten, 2007). However, Birkett *et al.* (1998b) reported that all kelps are stenohaline species that required regular salinities of 30-35 psu to maintain optimum growth rates. The associated biota are relatively tolerant to this changes in salinity, as most are typical of lower shore and sublittoral fringe biotopes. However, reduced salinity biotope have a lower species diversity, so some species may be lost due to a decrease in salinity at the benchmark level.

Sensitivity assessment. At the benchmark, a decrease in salinity from 'full' to 'reduced' (18-30 psu) for a year is unlikely to adversely affect *Saccharina latissima* or *Laminaria digitata* population, although their abundance may decrease slightly if growth rates are impaired. However, if the changes were prolonged the associated flora and fauna may change, reflecting an increase in red algae and ascidians tolerant of reduced salinity. In addition, while *Laminaria digitata* may tolerate reducced salinity conditions, it is replaced by *Saccharina latissima* in reduced salinity conditions, so that its abundance would probalby be uch reduced, and the so that the biotope may come to resemble IR.LIR.KVS.SlatPhyVS or IR.LIR.KVS.SlatPsaVS. However, at the benchmark level, IR.LIR.K.Slat.Ldig probably has a '**High**' resistance to the pressure. The biotope is considered to have '**High**' resilience and hence '**Not sensitive**' at the benchmark level.

Water flow (tidal	High	High	Not sensitive
current) changes (local)	Q: High A: Low C: Low	Q: High A: High C: High	Q: High A: Low C: Low

Saccharina latissima is unlikely to be directly affected by this pressure at the prescribed benchmark. Increased competition from other species (such as *Laminaria digitata*) with the change in environmental conditions will pose an indirect threat, as this biotope is defined by low levels of water movement, and *Saccharina latissima* thrives best in these conditions. Tidal streams of >0.5 m/s or lower as described by Connor *et al.* (2004).

Comparisons between biomass yields (dry weight) from two sites found significantly higher yields of Saccharina latissima at the moderately exposed site over the sheltered site, with light exposure and water velocity cited as the determining factors of both populations health (Peteiro & Freire, 2013). The turbulence created by friction at the frond-water interface acts as a transport mechanism for nutrients from the water column to the algae and is called the boundary layer. In conditions which lack water motion, the transportation of dissolved gases and nutrients within the boundary layer may be significantly reduced, leading to diminished growth (Wheeler, 1980, Parker, 1981, 1982); although conditions of no water motion are rare in the field (Gerard, 1982). Water activity (wave, tidal and current mediated) may also be important for reducing sedimentation and the growth of filamentous algae which may compete with the key species in this biotope (Norton, 1978; Pihl et al., 1994; Isæus, 2004; Moy et al., 2006) and are the suggested reason for the absence of this biotope from extremely sheltered Norwegian waters (Bekkby & Moy, 2011). Despite this, populations of loose lying Saccharina latissima have been identified in areas of low water motion, in these conditions, attachment to the substratum does not appear to be important (Burrows, 1958); however if a lack of water movement results in a change in the kelp's life history traits, this along with the likely change in associated species would be considered

as equivalent to the loss of the biotope.

Saccharina latissima is absent from extremely sheltered conditions with little water flow in Norway. This infers that *Saccharina latissima* needs a minimum amount of water movement in order to survive; perhaps because of decreased competition from filamentous algae and sedimentation, but also because water flow maintains a nutrient flux and enhances light penetration to juvenile sporophytes by moving the fronds (Norton, 1978; Pihl *et al.*, 1995; Lobban & Harrison, 1994; Hurd, 2000; Isæus, 2004; Moy *et al.*, 2006; Bekkby & Moy, 2011). Decreased wave exposure also causes localised stagnation and de-oxygenation of the water column which would decrease survivorship in the area.

Saccharina latissima's morphology was noted to differ between a moderately exposed and sheltered site, with those at the moderately exposed site exhibiting a large surface area than those at the sheltered site (Peteiro & Freire, 2013). Kelps typically have a plastic morphology, in controlled laboratory experiments juvenile *Saccharina latissima* (studied as *Laminaria saccharina*) altered their morphology under different water flow exposures; mechanical longitudinal stress resulted in narrower blades of increased cell elongation, while a lack of tension lead to greater blade widths after 6 weeks (Gerard, 1987). This plasticity is likely to protect thallus damage in areas of greater exposure or in stormier conditions. Stronger water currents may dislodge the kelp from bedrock or cause damage by moving boulders and cobbles.

However, *Laminaria digitata* forms dense forests in the fast flowing water of the rapids where water speeds vary from 4-6 knots (Bassindale *et al.*, 1948). *Laminaria digitata* is also found in very strong flows (> 6 knots) although it is often out-competed by *Alaria esculenta* under these conditions. The biotope is not found in areas where sand scour occurs (associated with high water flow rates). *Laminaria digitata* partially achieves survival in a range of water flow conditions due to its blade morphology, which varies with flow, becoming narrower and more digitate as water flow rate increases (Sundene, 1964). As a result in increased water flow is likely to favour *Laminaria digitata* over *Saccharina latissima*.

Red algae are found in a range of water flow regimes, e.g. *Delessaria sanguinea* is recorded from moderately strong to weak tidal flows. The ascidians are equaly found in a range of tidal flow, and good water flow is considered important for suspension feeders, depending on species. However, *Clavelina lepadiformis* thrives in areas where there is very little, if any, water movement (for instance, Abereiddy Quarry, Pembrokeshire (Hiscock & Hoare, 1975) and *Ciona intestinalis* is remarkably tolerant of low flow rates and is frequently found in areas with minimal water exchange and renewal such as harbours, marinas and docks.

Sensitivity assessment. This biotope is recorded from weak (>0.5 m/s) to negligible water flow in wave sheltered areas, so that wave meditated flow is also low. The presence of *Laminaria digitata* in this biotope suggests that in condition of increased water flow it could out-compete *Saccharina latissima*, and thus change the identity of the biotope, especially in the shallow subtidal extent of the biotope. A decrease in flow is not relevant as the biotope occurs in negligible flow. However, an increase in flow could result in loss of the biotope. An increase in water flow of 0.1-0.2m/s for a year may be enough to change the relative abundance of *Laminaria digitata* and *Saccharina latissima* and change character of the biotope but unlikely to result in its loss within one year. Therefore, a resistance of '**Medium'** is suggested at the benchmark level. The resilience is probably '**High'** so that this biotope is regarded as '**Not sensitive'** at the benchmark level, although prolonged increase in flow could result in loss of the biotope.

Emergence regime changes



Medium Q: High A: High C: High



Q: Medium A: Low C: Medium

This sublittoral fringe is dominated by predominantly sublittoral species. Air exposure causes desiccation prevents photosynthesis, and decreases growth rates in Saccharina latissima (studied as Laminaria saccharina, Kain, 1979). Kelps are generally less tolerant to desiccation than other brown macroalgae (e.g. Pelvetia canaliculata and fucoids) and are therefore likely to be competitively outcompeted at their upper limits (Davison & Pearson, 1996, Harker et al., 1999). Laminaria digitata can survive water losses of 40% and is therefore considered moderately tolerant to desiccation. Laminaria digitata's upper limits are set by competition with Fucus serratus (Hawkins & Harkin, 1985). Fucus serratus out-competes Laminaria digitata by controlling its respiration rates in tandem with its desiccation rates, allowing it to monitor and control water loss, which Laminaria digitata is unable to do. An increase in emergence would lead to a depression in the upper limit of the biotope; while its lower limits may extend down the shore as irradiance levels increase in areas previously too deep for light-saturated photosynthesis to occur.

In conditions of low summer temperatures, both Saccharina latissima and Laminaria digitata have been documented as occurring in sheltered bays at the inner Porsangerfjord, North Norway, where the stands are completely drained at low tide (Sivertsen & Bjorge, 2015), suggesting that unique exceptions do exist in relation to this pressure, but are not the norm and are mediated by other environmental factors, e.g. temperature regime. this may explain why most records occur in Scottish waters. The associated red macroalgae of this biotope will have species specific responses to both increases and decreases in emergence with those of a saccate morphology generally more resistant to increased emergence than their counterparts (Oates, 1985, 1986).

Both kelp species are able to tolerate both an increased and decreased emergence; however this tolerance is based on the free movement of these species within their environmental optima, shifting their spatial extent up or down the shore. Therefore if an obstacle to movement perpendicular to the shore line (e.g. sea defence) is then combined with a change in the emergence regime this biotope could undergo compression of its range and may result in its local extinction. However in the footprint of the impact, a spatial shift of the biotope would result in the loss of the biotope, causing this biotope to be sensitive to the pressure at the benchmark.

Sensitivity Assessment. Emergence is a key driver of biotope extent because the upper and lower limits of Laminaria digitata are set by inter-species competition. Additionally Saccharina latissima is likely to be less tolerant of increased emergence than its counterpart. In the case of a sea level rise, the change may allow the biotope to shift up the shore, remaining within the sublittoral zone. In the direct footprint of the impact resistance is therefore 'None' (loss of >75%). Resilience is suggested as 'Medium' (2-10 years) due to the scale of the impact, and suspected spatial relocation of the biotope under conditions of increased emergence and increased sea levels, provided there are no barriers to the biotope migration. This biotope is therefore considered to have 'Medium' sensitivity to the pressure.

Wave exposure changes Medium (local)

Q: High A: Medium C: Medium

High Q: High A: High C: High



Q: High A: Medium C: Medium

The occurrence of Saccharina latissima and therefore this biotope can be predicted by the level of wave action experienced by a location (Bekkby & Moy, 2011). Saccharina latissima rarely grows in wave exposed conditions, as it is vulnerable to dislodgement from wave action and additionally

may be attached to cobbles and boulders typical of this biotope, which may be overturned in conditions of increased wave action. Increased wave exposure is also likely to detrimentally affect deposit feeders and species inhabiting the sediment which typically overlays the substratum in this biotope. In conditions of increased wave action *Saccharina latissima* may gradually change position, shifting into the lower eulittoral (Birkett *et al.*, 1998b). Competition from other species such as *Laminaria digitata*, able to withstand higher levels of wave action, may out-compete *Saccharina latissima* under natural conditions. *Saccharina latissima* has been cultivated in the presence of 6.4 m high waves (Buck & Buchholz, 2005), indicating that this competition is the likely driver of Saccharina latissima's absence from exposed shores. In conditions of greater wave action, *Saccharina latissima* productivity (studied as *Laminaria saccharina*) was less than that of sheltered population; this may have been due to greater nutrient availability in the sheltered site from a current of 0.5 meters/second/second (Gerard & Mann, 1979). When considered in conjunction with emergence, wave exposure is beneficial to *Saccharina latissima*, with wave spray acting to hydrate individual alga which would otherwise suffer from desiccation and decreased growth rates (Kain, 1979).

While *Saccharina latissima* is generally absent from wave swept shores, it is also absent from extremely sheltered conditions in Norway. Inferring that *Saccharina latissima*'s needs a minimum amount of water movement in order to survive; perhaps because of decreased competition from filamentous algae and sedimentation, but also because wave action maintains a nutrient flux and enhance light penetration to juvenile and smaller sporophytes by moving the fronds (Norton, 1978, Pihl *et al.*, 1995, Lobban & Harrison, 1994, Hurd, 2000, Isæus *et al.*, 2004, Moy *et al.*, 2006 Bekkby & Moy, 2011). Decreasing wave exposure also causes localised stagnation and de-oxygenation of the water column which would decrease survivorship in the area.

Sheltered conditions favour the growth of epiphytes, which decrease *Saccharina latissima*'s ability to withstand storm events and increased wave action, potentially increasing the vulnerability of this biotope to the pressure. Growth of the epiphytic bryozoan, *Membranipora membranacea* reduces the ability of individual alga to withstand wave action, increasing frond breakages by making them brittle and reducing the maximum stress, toughness and extensibility of the kelp blade materials (Krumhansl *et al.*, 2011). Andersen, 2011 suggested that in conditions of increased wave activity, water movement may act to clear the fronds' surface of epibiota, thus improving the health of the population in comparison to those in deeper and more wave sheltered areas.

The structure of kelp enables them to survive a range of wave conditions (Harder *et al.*, 2006). Comparisons between biomass yields from two sites found significantly higher yields at the moderately exposed site over the sheltered site, with light exposure and water velocity cited as the determining factors of both populations health (Peteiro & Freire, 2013). The blades of *Saccharina latissima* at the moderately exposed site were also found to have a large surface area than those at the sheltered site. Kelps typically have a plastic morphology, controlled laboratory experiments indicating that juvenile *Saccharina latissima* (studied as *Laminaria saccharina*) individuals alter their morphology under exposure to different water flow conditions, with mechanical longitudinal stress resulting in narrower blades of increased cell elongation while a lack of tension lead to greater blade width after 6 weeks (Gerard, 1987). This plasticity is likely to protect thallus damage in areas of greater exposure or in stormier conditions, although stronger water currents may dislodge the kelp from bedrock or cause damage by moving boulders and cobbles.

The greatest wet weight of *Laminaria digitata* occurs at low wave exposure (mean significant wave height <0.4 m) decreasing by a mean of 83% in medium to high wave exposures (mean significant

wave height >0.4 m; Gorman *et al.*, 2013). At medium to high levels of wave exposure, *L.digitata* biomass has been shown to decrease by 83% in the field (Wernberg & Thomsen, 2005). A flexible stipe and low profile holdfast allows *Laminaria digitata* to flourish in moderately to strongly wave exposed areas. A transplant experiment of *Laminaria digitata*, from exposed to sheltered sites resulted in a changed morphology with the frond widening, while individuals transplanted from sheltered to exposed sites became thinner more streamlined (Sundene, 1964; Gerard, 1987). This morphological plasticity is evident during the spore stage; because of this it is suggested that if wave height is increased or decreased the kelp will adapt morphologically over time to optimise its survival in the new environment. The associated assemblage of the biotope also influences *Laminaria digitata*'s ability to withstand increases in wave action. The encrusting of the epiphytic *Membranipora membranacea* which reduces the ability of individual kelp to withstand wave action, increasing frond breakages and additionally reducing the maximum stress, toughness and extensibility of the kelp blade materials (Krumhansl *et al.*, 2011).

Sensitivity assessment. This biotope is characteristic of wave sheltered to extremely wave sheltered conditions (Connor *et al.*, 2004). The plastic nature of *Saccharina latissima*'s structure means that it is likely to withstand increase in wave exposure at the benchmark, however its fitness for the new environment will be diminished and it may not be able to out-compete other species including *Laminaria digitata*. This is likely to cause a shift in the biotope to those dominated by other kelp species through competition, especially at the shallow subtidal extent of the biotope. Where increased wave action resulted in increase scour due to the mobility of coarse substrata (e.g. cobbles) then the biotope may become impoverished but *Saccharina latissima* remain the dominant kelp, as it is a rapid colonizing species, simlar to the IR.KIR.KwSed biotopes. Alternatively, where coarse sediment is absent, then *Laminaria digitata* may come to dominate. However, a change of only 3-5% in significant wave height may not be significant even in such sheltered conditions. Therefore, the biotope probably has a resistance of '**Medium**' to represent some changes in the relative abundance of kelp species. Resilience is probably '**High**', so that the sensitivity is probably '**Low'**.

A Chemical Pressures

_	Resistance	Resilience	Sensitivity
Transition elements &	Not Assessed (NA)	Not assessed (NA)	Not assessed (NA)
contamination	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

This pressure is **Not assessed** but evidence is presented where available.

Hydrocarbon & PAH	Not Assessed (NA)	Not assessed (NA)	Not assessed (NA)
contamination	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

This pressure is **Not assessed** but evidence is presented where available.

Synthetic compound	Not Assessed (NA)	Not assessed (NA)	Not assessed (NA)
contamination	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

This pressure is **Not assessed** but evidence is presented where available.

Date: 2015-11-30

Radionuclide contamination

No evidence (NEv) q: NR A: NR C: NR Not relevant (NR) Q: NR A: NR C: NR

No evidence (NEv) Q: NR A: NR C: NR

No evidence

Introduction of other substances

Not Assessed (NA) Q: NR A: NR C: NR Not assessed (NA) Q: NR A: NR C: NR Not assessed (NA) Q: NR A: NR C: NR

This pressure is **Not assessed**.

De-oxygenation

High Q: Low A: NR C: NR High Q: High A: High C: High Not sensitive

Q: Low A: Low C: Low

No direct evidence on the effects of deoxygenation for *Saccharina latissima* or *Laminaria digitata* were found in the literature, but reduced oxygen concentrations have been shown to inhibiting both photosynthesis and respiration in macroalgae (Kinne, 1977). Despite this, macroalgae are thought to buffer the environmental conditions of low oxygen, thereby acting as a refuge for organisms in oxygen depleted regions, especially if the oxygen depletion is short-term (Frieder *et al.*, 2012). A rapid recovery from a state of low oxygen is expected if the environmental conditions are transient. Additionally this biotope occurs in areas of low water movement. If levels do drop below 4 mg/l, negative effects on these organisms can be expected with adverse effects occurring below 2mg/l (Cole *et al.*, 1999).

Sensitivity Assessment. Reduced oxygen levels are likely to inhibit photosynthesis and respiration but not cause a loss of the macroalgae population directly. However, small invertebrate epifauna may be lost, causing a reduction in species richness. As the biotope is not considered dependent in any way upon these species and as these are not considered key characterizing species this loss is not considered in the sensitivity assessment. In additon, sublittoral fringe extent of the biotope is exposed to the air on extreme low tides Therefore, based on *Saccharina latissima* and *Laminaria digitata* a resistance of '**High'** is recorded. Hence resilience is likely to be '**High'**, and the biotopes is probably '**Not sensitive'** at the benchmark level.

Nutrient enrichment

Not relevant (NR) Q: NR A: NR C: NR Not relevant (NR) Q: NR A: NR C: NR Not sensitive Q: NR A: NR C: NR

As a macroalgae, *Saccharina latissima* uptakes nitrogen and carbon from the water column in order to survive and grow. The nitrogen and carbon content of *Saccharina latissima* varies annually, in conjunction with growth periods and nitrogen availability (Nielsen *et al.*, 2014). Carbon is used for winter growth and is stored during the summer as carbohydrate, while nitrogen is used for summer growth, and is a limiting factor (Nielsen *et al.*, 2014). High ambient levels of phosphate and nitrogen enhance spore formation in *Saccharina latissima* (Nimura *et al.*, 2002), but will eventually inhibit spore production, particularly at the extremes of the alga's temperature tolerance (studied as *Laminaria saccharina*; Yarish *et al.*, 1990). *Saccharina latissima* from the east coast of Scotland, showed increased growth rates in the laboratory when nutrient levels were enhanced by 25% (Conolly & Drew, 1985). Enhancement of coastal nutrients is likely to favour those species with more rapid growth rates including turf forming algae (Gorgula & Connell, 2004). Epiphytic abundance and biomass on *Laminaria longicruris* for example increased under a eutrophic regime (Scheibling *et al.*, 1999) and resulted in a shift from kelp dominated biotopes to an ephemeral algae

dominated biotope in Norway (Moy & Christie, 2012).

A comparison of *Laminaria digitata* growth rates in Arbroath, Scotland with a more oligotrophic and a more eutrophic site appears to support the hypothesis that the growth of macroalgae in temperate coastal waters is generally limited by nitrogen in the summer period (Davison *et al.*, 1984). In Helgoland, where ambient nutrient concentrations are double those of the Scotland site *Laminaria digitata* grows in the summer months. *Laminaria digitata* does not accumulate the significant internal reserves seen in some other kelps. Higher growth rates have also been associated with plants situated close to sewage outfalls. However, after removal of sewage pollution in the Firth of Forth, *Laminaria digitata* became abundant on rocky shores from which they had previously been absent. Therefore, although nutrient enrichment may benefit *Laminaria digitata*, the indirect effects of eutrophication, such as increased light attenuation from suspended solids in the water column and interference with the settlement and growth of germlings, may be detrimental.

Sensitivity Assessment. The benchmark of this pressure (compliance with WFD 'good' status) allows for a slightly less diverse community of red, green and brown seaweeds with the greatest reduction in red species and an increase in the proportion of short lived species under the WFD criteria for good status. The algae diversity in this biotope is already low with those remaining resistant to shading by kelp fronds and siltation. A further reduction in algal diversity would alter the biotope but would not result in loss of the biotope. However, the biotope is considered '**Not sensitive'** at the pressure benchmark that assumes compliance with good status as defined by the WFD.

Organic enrichment

<mark>High</mark> Q: Low A: NR C: NR <mark>High</mark> Q: High A: High C: High

Not sensitive Q: Low A: Low C: Low

As a macroalgae, *Saccharina latissima* uptakes nitrogen and carbon from the water column in order to survive and grow. The nitrogen and carbon content of *Saccharina latissima* varies annually, in conjunction with growth periods and nitrogen availability (Nielsen *et al.*, 2014). Carbon is used for winter growth, and is stored during the summer as carbohydrate, while nitrogen is used for summer growth (Nielsen *et al.*, 2014).

The amount of organic nitrogen a *Saccharina latissima* stand may be able to uptake varies with location; with *Saccharina latissima*'s nitrogen uptake by a fish farm in Tristein, Central Norway estimated as 1.2 t of nitrogen per hectare of kelp over one growth season (Wang *et al.*, 2014), while a similar setup in north-western Scotland predicted the removal of 5% waste nitrogen from 500 tonnes salmon over 2 years (Sanderson *et al.*, 2012). The excrement and unused feed for fish farms increases the levels of organic matter in their local vicinity. Evidence from experimental culture of *Saccharina latissima* around fish farms show enhanced growth rates by up to 61% at certain times in the year (Sanderson *et al.*, 2012). The quality of the nutrient source are also important with depressed growth rates associated with *Saccharina latissima* growing near a sewage sludge dumping ground in Liverpool Bay, Irish Sea (Burrows, 1971).

A comparison of *Laminaria digitata* growth rates in Arbroath, Scotland with a more oligotrophic and a more eutrophic site appears to support the hypothesis that the growth of macroalgae in temperate coastal waters is generally limited by nitrogen in the summer period (Davison *et al.*, 1984). In Helgoland, where ambient nutrient concentrations are double those of the Scotland site *Laminaria digitata* grows in the summer months. *Laminaria digitata* does not accumulate the significant internal reserves seen in some other kelps. Higher growth rates have also been associated with plants situated close to sewage outfalls. However, after removal of sewage pollution in the Firth of Forth, *Laminaria digitata* became abundant on rocky shores from which they had previously been absent. Therefore, although nutrient enrichment may benefit *Laminaria digitata*, the indirect effects of eutrophication, such as increased light attenuation from suspended solids in the water column and interference with the settlement and growth of germlings, may be detrimental.

Sensitivity assessment. At the benchmark level (a deposit of $100\text{gC/m}^2/\text{yr}$) this biotope could be resistant to the pressure, as suggested by the survival and enhanced growth of *Saccharina latissima* near fish farms and *Laminaria digitata* near sewage outfalls, associated with high levels of organic matter. Resistance to this pressure is therefore regarded as **'High'**, although beyond the benchmark, negative consequences of enhanced organic enrichment are possible. Resilience is therefore also regarded as **'High'** and the biotope is therefore probably **'Not sensitive'** at the pressure benchmark.

A Physical Pressures

	Resistance	Resilience	Sensitivity
Physical loss (to land or	None	Very Low	<mark>High</mark>
freshwater habitat)	Q: High A: High C: High	Q: High A: High C: High	Q: High A: High C: High

All marine habitats and benthic species are considered to have a resistance of '**None**' to this pressure and to be unable to recover from a permanent loss of habitat (resilience is '**Very low**'). Sensitivity within the direct spatial footprint of this pressure is, therefore 'High'. Although no specific evidence is described confidence in this assessment is '**High'**, due to the incontrovertible nature of this pressure.

Physical change (to another seabed type)

<mark>None</mark> Q: High A: High C: High Very Low Q: High A: High C: NR

High Q: High A: High C: High

Sensitivity assessment. *Laminaria digitata* requires stable hard substratum for attachment. A change in substratum type from bedrock to sedimentary would render the habitat unsuitable because kelp requires a stable substratum on which to settle. *Saccharina latissima* can occur on sediment where enough large pebbles, cobbles or boulder occur to provide attachment. No evidence of this biotope occurring on sedimentary substratum was found in the literature (see SS.SMp.KSwSS biotopes). However, a change in seabed type would change the character of the biotope from rock biotope to a sedimentary biotope, so that *Laminaria digitata* and many of the red seaweed community would be or replaced. The biotope would be lost so that resistance is **'None'** to this pressure. As the pressure is permanent, resilience is **'Very low'** and hence the sensitivity is likely to be **'High'**.

Physical change (to another sediment type)

Not relevant (NR) Q: NR A: NR C: NR Not relevant (NR) Q: NR A: NR C: NR Not relevant (NR) Q: NR A: NR C: NR

Not relevant to bedrock biotopes

Habitat structure changes - removal of substratum (extraction)	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR
The species character	izing this biotope are epif	auna or epiflora occurring	g on rock and would be
sensitive to the remov	/al of the habitat. Howeve	er, extraction of rock subs	tratum is considered
unlikely and this press	sure is considered to be 'N	lot relevant' to hard subst	tratum habitats.

Abrasion/disturbance of the	Low	High	Low
substratum or seabed	Q: Low A: NR C: NR	Q: High A: High C: High	Q: Low A: Low C: Low

No direct evidence was found for this pressure on this biotope. Low-level disturbances (e.g. solitary anchors) are unlikely to cause harm to the biotope as a whole, due to the impact's small footprint. Natural abrasion of the lamina tips occurs continuously, even in calm conditions (Krumhansl, 2012) as a result of water friction, although this erosion may be beneficial to the plants, reducing drag on the thalli (Reed *et al.*, 2008, Krumhansl & Scheibling, 2011; Gunnill, 1985). While *Saccharina latissima* is usually permanently attached to the substratum, Burrows (1958) suggests that re-attachment to the substratum after dislodgement is possible with individuals regrowing hapteron branches. It is, therefore, possible that individuals may be able to withstand dislodgement and abrasion. Survival of *Saccharina latissima* in areas where high levels of abrasion occur (a glacial influenced shore) indicate the phenotypic plasticity of the species and suggest that this species, and therefore the habitat, may be resistant to a higher degree of abrasion than other kelp biotopes (Spurkland & Iken, 2011a). Additionally, *Saccharina latissima* was the only kelp species present on an exposed glacial shore, where high levels of abrasion, inorganic sediment and siltation occurred, while an adjacent sheltered site boasted five kelp species (Spurkland & Iken, 2011b).

In a review of the effects of trampling on intertidal habitats, Tyler-Walters & Arnold (2008) found no information on the effects of trampling on *Laminaria* species (*Laminaria digitata* and *Laminaria saccharina*). The authors suggested that laminarians are robust species but that trampling on blades at low tide could potentially damage the blade or growing meristem. Trampling on shallow algal communities in the Mediterranean reported that erect canopy forming species (e.g. *Cysterseira* spp., *Dictyota* spp.) were the worse affected, and suffered a reduction in abundance but were reduced to just holdfasts at high trampling intensities (Milazzo *et al.*, 2002; Tyler-Walters, 2005).

Sensitivity assessment. There is little evidence on sensitivity to abrasion in this biotope. Abrasion via trampling could damage parts of the adult kelp and red algae and lead to the removal of individuals. Abrasion by passing bottom trawls or similar gear may remove or damage large erect kelps, and the associated biological assemblage could also be damaged, dislodged or killed. Therefore, a resistance of 'Low' is suggested based on limited evidence. The resilience is probably 'High', and sensitivity is, therefore, 'Low'.

Penetration or	Not relevant (NR)	Not relevant (NR)	Not relevant (NR)
substratum subsurface	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

The species characterizing this biotope group are epifauna or epiflora occurring on hard rock,

which is resistant to subsurface penetration. Therefore, 'penetration' is '**Not relevant**'. The assessment for abrasion at the surface only is, therefore, considered to equally represent sensitivity to this pressure'. Please refer to 'abrasion' above.

Changes in suspended solids (water clarity)

LOW Q: High A: Medium C: Medium High Q: High A: High C: High Low

Q: High A: Medium C: Medium

Next to wave exposure, light was a key descriptor of *Saccharina latissima*'s distribution along the Norwegian coast, indicating its importance to this biotope's identity (Bekkby & Moy, 2011). This biotope typically occurs in silty conditions, with *Saccharina latissima* able to maintain a positive carbon budget in very low light conditions (Andersen *et al.*, 2011). As a photosynthetic organism, ultimately *Saccharina latissima*'s depth distribution is reliant on light availability (Lüning, 1979; Lüning & Dring, 1979; Gerard, 1988). Therefore, an increase in turbidity may lead to the mortality of algae at the biotope's deeper range limit and may limit the biotope to shallower waters.

Blue light is crucial for the gametophytic stages of *Saccharina latissima*, and several other congenic species (Lüning, 1980). Without blue light (1-4 nE cm/s) and in the presence of red light, female gametophytes do not become fertile or produce eggs (Lüning & Dring, 1975). In comparison to *Laminaria digitata* and *Laminaria hyperborea*, *Saccharina latissima* exhibits a higher level of tolerance to UV light (indicative of its opportunistic nature, Lüning, 1980). Dissolved organic materials (yellow substance or gelbstoff) absorbs blue light (Kirk, 1976), therefore changes in riverine input or other land based runoff are likely to influence kelp density and distribution. Populations of *Saccharina latissima*'s exhibit different rates of carbon assimilation and growth when exposed to different light acclimation levels in laboratory conditions with alga from turbid sites possessing the fastest growth across treatments (Gerard, 1988). Deep water populations also exhibit adapted characteristics, with daily irradiances exceeding an average of 20 E (radiant flux) /mI /day reduce growth rates. The tolerance of a particular population to this pressure must, therefore, be considered in isolation.

Decreases in suspended solids are initially likely to increase photosynthesis and productivity of *Saccharina latissima*. However, in conditions of greater water clarity (reduced suspended solids) *Laminaria digitata* typically out-competes *Saccharina latissima*, resulting in the loss of the biotope (Norton, 1978). An absence of this biotope in low silt environments is therefore expected, although, with greater water clarity, it may be able to shift its range to deeper waters.

Increases in the levels of suspended sediment were found to reduce growth rates in *Saccharina latissima* (studied as *Laminaria saccharina*) by 20% (Lyngby & Mortensen, 1996). Suspended Particle Matter (SPM) concentration has a linear relationship with subsurface light attenuation (Kd) (Devlin *et al.*, 2008). *Laminaria* spp. show a decrease of 50% photosynthetic activity when turbidity increases by 0.1/m (light attenuation coefficient = 0.1-0.2/m; Staehr & Wernberg, 2009).

Burrow & Pybus (1971) found that the mean thalli thickness of *Saccharina latissima* (studied as *Laminaria saccharina*) that had grown in the silted waters of Redcar, Souter Point and Robin Hood's Bay (North-East England) were significantly smaller than those grown in the clearer waters of St Abbs (North-East England) and Port Erin (Isle of Man). Because of the low water movement associated with this biotope, suspended solids are not likely to be removed by water currents or turbulence and subsequent siltation of the biotope is, therefore, likely. Decreases in siltation may also cause a shift in the identity of the associated assemblage, as suspension and deposit feeders receive fewer nutrients, due to the lower carbon input and suspension feeders benefit as their feeding apparatus suffer less from clogging by silt. Red algae are shade tolerant so less sensitive to

a reduction in light than the kelp species, although the increased siltation and scour may be detrimental to the less robust species.

Sensitivity assessment. A decrease in suspended particulates from e.g. intermediate to clear (see benchmark) is likely to reduce siltation and scour, and allow Laminaria digitata) to increase in abundance, especially at the shallow subtidal extent of the biotope with a resultant change in the character of the biotope. The biotope is likely to be replaced by mixed kelp biotopes, depending on the extent of the change in suspended solids and the presence of mobile coarse sediments. An increase in turbidity at the benchmark e.g. from clear to intermediate represents a change from 0.67 to 6.7 in light attenuation coefficient (extracted from Devlin et al., 2008), and a change from intermediate to turbid conditions is considerably greater. Based on the observation that Laminaria sp. show a 50% decrease in photosynthetic activity after a change in light attenuation of only 0.1/m it is likely that the growth of Saccharina latissima and Laminaria digitata would be significantly decreased. In addition, Laminaria digitata has a lower level of tolerance to suspended solids than Saccharina latissima. Therefore, an increase in suspended solid is likely to remove Laminaria digitata and change the composition of the red algal community due to increased scour. Although the effects of light attenuation may be reduced in the sublittoral fringe where the biotope is emersed for short periods of time, the abundance *Saccharina latissima* is also likely to decline, resulting in a change in the biotope. Therefore, resistance to decreased and increased turbidity is likely to be 'Low'. Resilience is probably 'High'. The biotope, therefore, has 'Low' sensitivity to the pressure.

Smothering and siltation High rate changes (light) Q: Low A

High Q: Low A: NR C: NR High Q: High A: High C: High Not sensitive Q: Low A: Low C: Low

Low levels of siltation have been shown to initially offer protection to *Saccharina latissima* from UVR in laboratory experiments with thallus samples (Roleda *et al.*, 2008). However, after burial under a variety of sediment types, for over 7 days, symptoms of degradation, bleaching, tissue loss and reduced PSII function, were evident (Roleda & Dethleff, 2011). Laboratory experiments show that even a very thin deposit of fine grained sediment (0.1 -0.2 cm thick) caused rotting of *Saccharina latissima*, resulting in 25% mortality if covered for 4 weeks, under conditions of no water movement (Lyngby & Mortensen 1996). In the field, these conditions (no water movement) rarely exist and might explain the survival of *Saccharina latissima* sporophytes in areas of siltation (Birkett *et al.*, 1998b).

The gametophytic and zoospore stages are more vulnerable than their adult counterpart. Laboratory experiments indicated the adverse effects of siltation on *Saccharina latissima*, including abnormal development of the zoospore (Burrows, 1971). Other studies have indicated that siltation inhibits spore settlement with spores failing to form attachments to the fine sediment or the hard bedrock beneath, resulting in their subsequent loss from the biotope by water activity (Devinny & Volse, 1978, Norton, 1978; Bartsch *et al.*, 2008). *Laminaria digitata* is more sensitive to this pressure than other subtidal brown algae (e.g. *Sargassum muticum*; Morrell & Furnham, 1982). Therefore, a smothering event may favour *Saccharina latissima*, which may allow it to out-compete *Laminaria digitata* and change the biotope's identity.

However, smothering of the whole sporophyte is unlikely to last for long, if deposition is light (<5 cm) silt is likely to fall from the fronds to the substratum, even in conditions of weak water movement, therefore the rates of photosynthesis and growth are likely to return to normal within a few days of the deposition event. Also, the characteristic kelps are large and unlikely to adversely affected by smothering by 5 cm sediment unless the deposition occurred at low tide.

The understorey of red algae and fucoids may experience some mortality but the character of the biotope is unlikely to change.

Sensitivity assessment. Where smothering is short-term (less than 7 days), then this biotope should be relatively resistant. This biotope is recorded from low energy habitats (wave sheltered and weak tidal streams) deposited sediment may remain for some time, depending on the local conditions and topography. Nevertheless, a resistance of **'High** is suggested, although long-term smothering would be detrimental. The resilience of the biotope is considered to be '**High**' and the sensitivity of this biotope is, therefore **'Not sensitive'** at the benchmark, although confidence is low and local hydrography may increase or decrease the resistance.

Smothering and siltation Low rate changes (heavy)

Q: Low A: NR C: NR

Medium

Q: High A: High C: High

Medium

Q: Low A: Low C: Low

Low levels of siltation have been shown to initially offer protection to *Saccharina latissima* from UVR in laboratory experiments with thallus samples (Roleda *et al.*, 2008). However, after burial under a variety of sediment types, for over 7 days, symptoms of degradation, bleaching, tissue loss and reduced PSII function, were evident (Roleda & Dethleff, 2011). Laboratory experiments show that even a very thin deposit of fine grained sediment (0.1 -0.2 cm thick) caused rotting of *Saccharina latissima*, resulting in 25% mortality if covered for 4 weeks, under conditions of no water movement (Lyngby & Mortensen 1996). In the field, these conditions (no water movement) rarely exist and might explain the survival of *Saccharina latissima* sporophytes in areas of siltation (Birkett *et al.*, 1998b).

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Sensitivity Assessment. While a light covering may fall from fronds and be transported from the biotope relatively quickly, a deposition of 30 cm is likely to remain in place and therefore have a greater effect on the biotope, potentially resulting in the death of *Saccharina latissima* and therefore the loss of the biotope. *Laminaria digitata* may be tall enough to escape direct smothering of the thallus but smothering of the stipe and holdfast may result in deoxygenation and rot, and/or scour. Smothering of the associated epifauna and flora may also result in mortality, depending on the how long the deposit remained over the biotope. This biotope is regarded as having 'Low' resistance. Since the biotope is likely to be slow or non-existent. Resilience to this pressure is therefore regarded as 'Medium' Sensitivity to this pressure is therefore also assessed as 'Medium' although confidence is low and local hydrography may increase or decrease the resistance.

Litter

Not Assessed (NA) Q: NR A: NR C: NR Not assessed (NA) Q: NR A: NR C: NR Not assessed (NA) Q: NR A: NR C: NR Not assessed. It is feasible that discarded fishing line, plastic netting, or similar discards could tangle on kelp fronds and potentially damage or remove individuals. However, no doucmented evidence was found.

Electromagnetic changes	No evidence (NEv)	Not relevant (NR)	No evidence (NEv)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR
No evidence			
Underwater noise	Not relevant (NR)	Not relevant (NR)	Not relevant (NR)
changes	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR
Not relevant			
Introduction of light or shading	Low	Very Low	<mark>High</mark>
	Q: Low A: NR C: NR	Q: High A: High C: High	Q: Low A: Low C: Low

Next to wave exposure, light was a key descriptor of *Saccharina latissima*'s distribution along the Norwegian coast, indicating its importance to this biotope's identity (Bekkby & Moy, 2011). This biotope typically occurs in silty conditions, with *Saccharina latissima* able to maintain a positive carbon budget in very low light conditions (Andersen *et al.*, 2011). As a photosynthetic organism, ultimately *Saccharina latissima*'s depth distribution is reliant on light availability (Lüning, 1979; Lüning & Dring, 1979; Gerard, 1988). Therefore an increase in turbidity may lead to the mortality of algae at the biotope's deeper range limit and may limit the biotope to shallower waters.

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Sensitivity assessment. An increase in incident light is likely to increase plant productivity and increase the density of the kelps. However, there is no evidence that artificial light sources have

caused an increase in macroalgal productivity. Constant artificial light may affect the reproductive cues, development of gametophytes etc, but no evidence was found. However, shading, especially from permanent structures (e.g pontoons, jetties) are likely to reduce incident light, and will probably result in the reduction in kelp density, or even its exclusion from the affected area. Therefore, a resistance of **'Low'** is suggested. Resilience is probably 'High' if the shading is temporary but '**Very low'** if permanent. Therefore, a precautionary sensitivity of **'High'** is suggested.

Barrier to species movement

Not relevant (NR) Q: NR A: NR C: NR Not relevant (NR) Q: NR A: NR C: NR Not relevant (NR) Q: NR A: NR C: NR

Not relevant – this pressure is considered applicable to mobile species, e.g. fish and marine mammals rather than seabed habitats. Barriers to propagule (larvae, zoospores) supply could adversely affect the population because it is dependent on rapid recolonization after disturbance. However, most of the community, including the kelps, are widespread and also may be self-recruiting within the habitat or between adjacent habitats. Any permanent structures that completely block water exchange would be detrimental but mainly due to the permanent change in hydrography. No evidence of direct impacts was found.

Death or injury by	Not relevant (NR)	Not relevant (NR)	Not relevant (NR)
collision	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

Injury or mortality from collisions of biota with both static and/or moving structures is most relevant to mobile species. Intertidal habitat may be damaged due to grounding of vessels (boats, ships, tankers etc), and is addressed under 'abrasion' above.

Visual disturbance	Not relevant (NR) Q: <u>NR</u> A: <u>NR</u> C: <u>NR</u>	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR		
Not relevant					
Biological Pressures					
	Resistance	Resilience	Sensitivity		
Genetic modification & translocation of indigenous species	No evidence (NEv)	Not relevant (NR)	No evidence (NEv)		
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR		

No evidence regarding the genetic modification of key characteristic species was found. Cultivation of this species is becoming more common and may be achieved in coastal waters far from shore, increasing the species' potential larval dispersal range. There is a high degree of plasticity within *Saccharina latissima*, as indicated by Gerard (1988) suggesting that this species would be resistant to the introduction of genetically modified populations. No evidence that *Saccharina latissima* cross- breeds with any of its congenic species was found. Cultivation of this species from translocated individuals does occur, however the effects of this process on the natural populations of this species are not known. (Peteiro *et al.*, 2014). Harvesting is carried out on wild kelp stands in a sustainable 5 year cycle (Vea and Ask, 2011), therefore, translocation of species is unlikely. Additionally if translocation of populations does occur, a loss in genetic diversity is not regarded as an issue for *Laminaria digitata*, unless additional pressures result in the isolation and fragmentation of wild coastal populations (Valero *et al.*, 2011). Genetic differentiation in wild populations occurs within 10 km with genetic flow occurring between adjacent species (Billot *et al.*, 2003). No evidence that *Laminaria digitata* cross-breeds with any of its sister species was found.

Sensitivity assessment. No direct evidence was found that might indicate the effects of this pressure on the biotope. Inter-breeding between populations occurs in most *Laminaria* species; therefore the resistance of this biotope to the pressure may be **'High'**, with **'High'** resilience. Sensitivity for this pressure is also suggested as **'Not sensitive'**.

Introduction or spread of invasive non-indigenous	Low	Very Low	High
species	Q: High A: High C: High	Q: High A: High C: High	Q: High A: High C: High

The effects of invasive species on *Saccharina latissima* appear to be limited, or been fully documented in the literature. Strong & Dring (2011) found that the invasive macroalgae, *Sargassum muticum*, did not pose a threat to *Saccharina latissima* stands in Strangford Lough, Northern Ireland, indicating the ability of this species to withstand competition from the invader. However, the grazer, *Lacuna vincta* preferentially grazes on *Saccharina latissima* over the invasive macroalgae *Codium fragile* in the Gulf of Maine, USA (Chavanich & Harris., 2004). If similar conditions exist in UK waters, where native grazers preferentially feed on the native *Saccharina latissima*, then the invasive species will have an initial advantage, and may potentially out-compete *Saccharina latissima*, leading to the loss of the biotope.

The survival of *Saccharina latissima* in harbours and docks despite heavy fouling by epibionts has been documented in the south west of England (Johnston *et al.*, 2011), while the health of these kelp is undetermined; their presence illustrates the resilience of this biotope against this pressure. However, if *Saccharina latissima* is out-competed by an invasive macroalgae, its recolonization could be prevented by heavy fouling of non-native origin, in a similar way that native fouling organisms have prevented re-colonization and recovery of *Saccharina latissima* beds in the Skagerrak area (Andersen *et al.*, 2011).

Competition with invasive macroalgae posing a potential threat to this biota, include Undaria pinnatifida and Sargassum muticum (Rueness, 1989). Sargassum muticum has been shown to competitively replace Laminaria species in Denmark (Staehr et al., 2000). In Nova Scotia Codium fragile competes successfully with native kelps for space including Laminaria digitata, by exploiting gaps within the kelp beds. Once established the algal mat created by this species prevents recolonization by other macroalgaes (Scheibling et al., 2008). Despite this, the associated assemblages of the respective macroalgaes do not differ significantly (Schmidt & Scheibling, 2006).

Undaria pinnatifida has received a large amount of research attention as a major Invasive Non Indigenous Species (INIS) which could out-compete native UK kelp habitats (see Farrell & Fletcher, 2006; Thompson & Schiel, 2012, Brodie *et al.*, 2014; Hieser *et al.*, 2014). *Undaria pinnatifida* was first recorded in the UK, Hamble Estuary, in June 1994 (Fletcher & Manfredi, 1995) and has since spread to a number of British ports. *Undaria pinnatifida* is an annual species, sporophytes appear in Autumn and grow rapidly throughout winter and spring during which they can reach a length of 1.65 m (Birkett *et al.*, 1998b). Farrell & Fletcher (2006) suggested that native short lived species that occupy similar ecological niches to *Undaria pinnatifida* are likely to be worst affected and outcompeted by *Undaria pinnatifida*. Where present an abundance of *Undaria pinnatifida* has corresponded to a decline in *Laminaria* sp. (Farrel & Fletcher, 2006; Hieser *et al.*, 2014).

In New Zealand, Thompson & Schiel (2012) observed that intertidal fucoids could out-compete *Undaria pinnatifida* and re-dominate the substratum. However, Thompson & Schiel (2012) suggested the fucoid recovery was partially due to an annual *Undaria pinnatifida* die back, which as noted by Heiser *et al.* (2014) does not occur in Plymouth Sound, UK. *Undaria pinnatifida* was successfully eradicated on a sunken ship in Clatham Islands, New Zealand, by applying a heat treatment of 70°C (Wotton *et al.*, 2004) however numerous other eradication attempts have failed and, as noted by Fletcher & Farrell (1999), once established *Undaria pinnatifida* resists most attempts of long-term removal. The biotope is unlikely to fully recover until *Undaria pinnatifida* is fully removed from the habitat, which (as stated above) is unlikely to occur.

Sensitivity assessment. Resistance to the pressure is considered '**Low**', and resilience '**Very Low**'. The sensitivity of this biotope to INIS is assessed as '**High'**.

Introduction of microbial	High
pathogens	Q: Low A: N

: Low A: NR C: NR

<mark>High</mark>

Q: High A: High C: High

Not sensitive Q: Low A: Low C: Low

Little direct evidence was found in the literature with only two studies found on microscopic algal pathogens. Saccharina latissima (studied as Laminaria saccharina) may be infected by the microscopic brown alga Streblonema aecidioides which may manifest to different degrees from dark spots to heavy deformations and crippled thalli and reduce growth rates. Infection rates have been recorded as 87% (±13%) in Kiel Bay, Western Baltic (Peters & Scaffelke, 1996). Association of Saccharina latissima with a marine bacterium, Pseudomonads in the Baltic Sea protects the algae from 2 algal pathogens, Pseudoalteromonas elyakovii and Algicola bacteriolytica. Pseudomonads produces antibiotics which prevent Saccharina latissima's infection, suggesting that this biotope's resistance to disease is population and location specific (Nagel et al., 2012). Symptoms of disease are regularly seen on Laminaria species, however little evidence in the literature is apparent. Infection of Laminaria japonica sporophytes by Pseudoalteromonas, Vibrio and Halomonas results in the characteristic symptoms of hole-rotten disease (Wang et al., 2008). Additionally red spot disease may be caused by bacteria of the genus Alteromonas (Sawabe et al., 1998). Hyperplasia or gall growths are often seen as dark spots on Laminaria digitata and have been associated with endophytic brown filamentous algae. It can be inferred from these observations that microbial pathogens may impact growth rates of individuals.

There is no evidence in the literature that infection by microbial pathogens results in mass death of *Laminaria* populations and the kelp themselves are known to regulate bacterial infections through iodine metabolism (Cosse *et al.*, 2009). No evidence was found regarding introduction of pathogens or metazoan disease vectors to kelp biotopes.

Sensitivity Assessment. Due to the evidence for resistance, biotope continuation under a high pathogen load, and the evidence of disease resistance in kelps, resistance to this pressure is regarded as **'High'** and resilience is therefore also **'High'**. Hence **'Not sensitive'** is recorded.

Removal of target species







Q: High A: Medium C: High

In the UK, harvesting of *Saccharina latissima* is confined to manual harvesting on a small scale, and farming. Manual harvesting may involve individual blade or whole alga removal. Only two seaweed leases exist in the UK illustrating the low impact of this species' harvesting in the wild in UK waters. Mechanical harvesting of *Saccharina latissima* is done in Italy, but the preferred method of commercial harvesting in Europe is by farming on ropes (Seaweed Industry in Europe, Netalgae, 2012). Low level removal of individuals from the shoreline is unlikely to have an effect on the local biotope, however if harvesting of *Saccharina latissima* increased, the time window for harvesting (Low tide) is relatively small and could act as a buffer against excessive harvesting of the species. However if gathering by diving also increased there would be little resistance to the pressure. Associated species are unlikely to be affected by low level removal of *Saccharina latissima* unless protection from desiccation on the lower shore is important.

Overfishing of apex predators (in particular fin fish), has been occurring for centuries in UK and Irish waters, resulting in habitats dominated by invertebrates and commercially undesirable fish such as the lesser spotted catshark (Molfese *et al.*, 2014) suggesting an ecosystem level shift in the functioning of these food webs. The urchin barrens recorded off the coast of Norway and in the North West Atlantic, are not common to UK waters with deforestation by urchins instead restricted and patchy and could be a result of this shift, leading to a temporally more stable, less dynamic biotope (although some have been noted in Scotland; Smale *et al.*, 2013).

Unlike *Saccharina latissima*, *Laminaria digitata* is mechanically harvested in Europe, particularly in Brittany, France; although it is only harvested manually or by farming in the UK (Seaweed Industry in Europe, Netalgae, 2012). In France, *Laminaria digitata* is harvested with a 'Scoubidou' (a curved iron hook which is mechanically operated). This device is considered to be selective only harvesting individuals older than 2 years (Arzel, 2002). France reportedly harvests 75,000t kelp, mainly consisting of *Laminaria digitata* annually (FAO, 2007).

Debate exists on whether kelp harvesting is detrimental to fish stocks. While some state that no negative consequences of harvesting have been documented (Vea and Ask, 2011); others suggest that as important foraging and nursery grounds for birds and fish, removal will inevitably result in negative consequences (Lorentsen *et al.*,2010). Canopy removal of *Laminaria digitata* has been shown to reduce shading, resulting in the bleaching of sub canopy algae (Hawkins & Harkin, 1985). Harvesting may also result in habitat fragmentation, a major threat to this biotope's ecosystem functioning (Valero *et al.*, 2011). Conflicts in the literature may arise from the comparisons of different fisheries. Maintaining a sustainable crop of *Laminaria digitata* has been suggested as possible if the industry continues employing small vessels evenly dispersed along the coastline. This would protect against habitat fragmentation and buffer over exploitation (Davoult *et al.*, 2011). A fallow period of 18-24 months has been suggested for *Laminaria digitata* in France, where competition between the juvenile sporophytes of *Laminaria digitata* and *Saccorhiza polyschides* has been indicated as a threat to the continued harvesting effort of *Laminaria digitata* (Engelen *et al.*, 2011).

Sensitivity assessment. *Saccharina latissima* is harvested via on aquaculture rather than wild harvesting. However, *Laminaria digitata* could be harvested from wild beds. Therefore, if harvesting of the species occurred extensively in an area then there would be little resistance to the pressure. Resistance is regarded as 'None' as the pressure is defined as the removal of key characterizing species from the biotope. Resilience to this pressure is probably '**Medium**'. Sensitivity to this pressure is defined as '**Medium**'.

Removal of non-target species



<mark>High</mark> Q: High A: High C: High

<mark>Low</mark> Q: Low A: Low C: Low

No direct evidence was found for the removal of *Saccharina latissima* or *Laminaria digitata* from a biotope as by-catch. However if they were removed as by-catch, the result would be the loss of the biotope.

Sensitivity assessment. Resistance to this pressure is considered **'Low'** as removal of the structuring species would significantly alter the character of the biotope. Resilience is therefore assessed as **'High'** and sensitivity **'Low'**.

Bibliography

Lüning, K., 1979. Growth strategy of three *Laminana* species (Phaeophyceae) inhabiting different depth zones in the sublittoral region of Hegloland (North Sea). *Marine Ecological Progress Series*, **1**, 195-207.

Andersen, G.S., 2013. Patterns of Saccharina latissima recruitment. Plos One, 8 (12), e81092.

Andersen, G.S., Pedersen, M.F. & Nielsen, S.L., 2013. Temperature, Acclimation and Heat Tolerance of photosynthesis in Norwegian *Saccharina latissima* (Laminariales, Phaeophyceae). *Journal of Phycology*, **49** (4), 689-700.

Andersen, G.S., Steen, H., Christie, H., Fredriksen, S. & Moy, F.E., 2011. Seasonal patterns of sporophyte growth, fertility, fouling, and mortality of *Saccharina latissima* in Skagerrak, Norway: implications for forest recovery. *Journal of Marine Biology*, **2011**, Article ID 690375, 8 pages.

Arzel, P., 2002. La laminaire digitée. Les nouvelles de l'Ifremer, 33 (4).

Arzel, P., 1998. Les laminaires sur les côtes bretonnes. Évolution de l'exploitation et de la flottille de pêche, état actuel et perspectives. Plouzané, France: Ifremer.

Bartsch, I., Vogt, J., Pehlke, C. & Hanelt, D., 2013. Prevailing sea surface temperatures inhibit summer reproduction of the kelp *Laminaria digitata* at Helgoland (North Sea). *Journal of Phycology*, **49** (6), 1061-1073.

Bartsch, I., Wiencke, C., Bischof, K., Buchholz, C.M., Buck, B.H., Eggert, A., Feuerpfeil, P., Hanelt, D., Jacobsen, S. & Karez, R., 2008. The genus *Laminaria* sensu lato: recent insights and developments. *European Journal of Phycology*, **43** (1), 1-86.

Bassindale, R., Ebling, F.J., Kitching, J.A. & Purchon, R.D. 1948. The ecology of the Lough Ine rapids with special reference to water currents. I. Introduction and hydrography. *Journal of Ecology*, **36**, 305-322.

Bekkby, T. & Moy, F.E., 2011. Developing spatial models of sugar kelp (*Saccharina latissima*) potential distribution under natural conditions and areas of its disappearance in Skagerrak. *Estuarine Coastal and Shelf Science*, **95** (4), 477-483.

Bernstein, B.B., Williams, B.E. & Mann, K.H., 1981. The role of behavioral responses to predators in modifying urchins' (*Strongylocentrotus droebachiensis*) destructive grazing and seasonal foraging patterns. *Marine Biology*, **63** (1), 39-49.

Billot, C., Engel, C.R., Rousvoal, S., Kloareg, B. & Valero, M., 2003. Current patterns, habitat discontinuities and population genetic structure: the case of the kelp *Laminaria digitata* in the English Channel. *Marine Ecology Progress Series*, **253** (111), 21.

Birkett, D.A., Maggs, C.A., Dring, M.J. & Boaden, P.J.S., 1998b. Infralittoral reef biotopes with kelp species: an overview of dynamic and sensitivity characteristics for conservation management of marine SACs. *Natura 2000 report prepared by Scottish Association of Marine Science (SAMS) for the UK Marine SACs Project.*, Scottish Association for Marine Science. (UK Marine SACs Project, vol V.). Available from: http://www.ukmarinesac.org.uk/publications.htm

Blight, A.J. & Thompson, R.C., 2008. Epibiont species richness varies between holdfasts of a northern and a southerly distributed kelp species. *Journal of the Marine Biological Association of the United Kingdom*, **88** (03), 469-475.

Bolton, J.J. & Lüning, K., 1982. Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species (Phaeophyta) in culture. *Marine Biology*, **66**, 89-94.

Bonsdorff, E. & Vahl, O., 1982. Food preferences of the sea urchins *Echinus actus* and *Echinus esculentus*. *Marine Behaviour and Physiology*, **8** (3), 243-248.

Borum, J., Pedersen, M.F., Krause-Jensen, D., Christensen, P.B. & Nielsen, K., 2002. Biomass, photosynthesis and growth of *Laminaria saccharina* in a high-arctic fjord, NE Greenland. *Marine Biology*, **141**, 11-19.

Bradshaw, C., Veale, L.O., Hill, A.S. & Brand, A.R., 2000. The effects of scallop dredging on gravelly seabed communities. In: *Effects of fishing on non-target species and habitats* (ed. M.J. Kaiser & de S.J. Groot), pp. 83-104. Oxford: Blackwell Science.

Brodie J., Williamson, C.J., Smale, D.A., Kamenos, N.A., Mieszkowska, N., Santos, R., Cunliffe, M., Steinke, M., Yesson, C. & Anderson, K.M., 2014. The future of the northeast Atlantic benthic flora in a high CO₂ world. *Ecology and Evolution*, **4** (13), 2787-2798.

Buck, B.H. & Buchholz, C.M., 2005. Response of offshore cultivated *Laminaria saccharina* to hydrodynamic forcing in the North Sea. *Aquaculture*, **250** (3-4), 674-691.

Burrows, E.M. & Pybus, C., 1971. *Laminaria saccharina* and marine pollution in North-East England. *Marine Pollution Bulletin*, **2**, 53-56.

Burrows, E.M., 1958. Sublittoral algal population in Port Erin Bay, Isle of Man. *Journal of the Marine Biological Association of the United Kingdom*, **37**, 687-703.

Burrows, E.M., 1971. Assessment of pollution effects by the use of algae. *Proceedings of the Royal Society of London, Series B*, **177**, 295-306.

Chapman, A.R.O., 1981. Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, Eastern Canada. *Marine Biology*, **62**, 307-311.

Chavanich, S. & Harris, L.G., 2004. Impact of the non-native macroalga *Codium fragile* (sur.) *hariot* ssp. *tomentosoides* (van goor) *silva* on the native snail *Lacuna vincta* (montagu, 1803) in the gulf of maine. *Veliger*, **47** (2), 85-90.

Cie, D.K. & Edwards, M.S., 2011. Vertical distribution of kelp zoospores. *Phycologia*, **50** (4), 340-350.

Cole, S., Codling, I.D., Parr, W. & Zabel, T., 1999. Guidelines for managing water quality impacts within UK European Marine sites.

Natura 2000 report prepared for the UK Marine SACs Project. 441 pp., Swindon: Water Research Council on behalf of EN, SNH, CCW, JNCC, SAMS and EHS. [UK Marine SACs Project.], http://www.ukmarinesac.org.uk/

Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B., 2004. The Marine Habitat Classification for Britain and Ireland. Version 04.05. ISBN 1 861 07561 8. In JNCC (2015), *The Marine Habitat Classification for Britain and Ireland Version* 15.03. [2019-07-24]. Joint Nature Conservation Committee, Peterborough. Available from https://mhc.jncc.gov.uk/

Conolly N.J. & Drew, E.A., 1985. Physiology of *Laminaria*. III. Effect of a coastal eutrophication on seasonal patterns of growth and tissue composition in *Laminaria digitata* and *L. saccharina*. *Marine Ecology*, *Pubblicazioni della Stazione Zoologica di Napoli I*, **6**, 181-195.

Cosse, A., Potin, P. & Leblanc, C., 2009. Patterns of gene expression induced by oligoguluronates reveal conserved and environment-specific molecular defence responses in the brown alga *Laminaria digitata*. New Phytologist, **182** (1), 239-250.

Davison, I.R. & Pearson, G.A., 1996. Stress tolerance in intertidal seaweeds. *Journal of Phycology*, **32** (2), 197-211.

Davison, I.R., Greene, R.M. & Podolak, E.J., 1991. Temperature acclimation of respiration and photosynthesis in the brown alga *Laminaria saccharina*. *Marine Biology*, **110**, 449-454.

Davoult, E., Engel, C.R., Arzel, P., Knoch, D. & Laurans, M., 2011. Environmental factors and commercial harvesting: exploring possible links behind the decline of the kelp *Laminaria digitata* in Brittany, France. *Cah. Biol. Mar*, **52**, 1-6.

Dayton, P.K. & Tegner, M.J., 1984. Catastrophic storms, El-Nino, and patch stability in a southern-california kelp community. *Science*, **224** (4646), 283-285.

Devinny, J. & Volse, L., 1978. Effects of sediments on the development of *Macrocystis pyrifera* gametophytes. *Marine Biology*, **48** (4), 343-348.

Devlin, M.J., Barry, J., Mills, D.K., Gowen, R.J., Foden, J., Sivyer, D. & Tett, P., 2008. Relationships between suspended particulate material, light attenuation and Secchi depth in UK marine waters. *Estuarine, Coastal and Shelf Science*, **79** (3), 429-439.

Dickinson, C.I., 1963. British seaweeds. London & Frome: Butler & Tanner Ltd.

Drobyshev, V.P., 1971. Acclimatisation of marine algae when maintained in media of differing salinities. Ékologiya, 1, 96-98.

Druehl, L.D., 1967. Distribution of two species of *Laminaria* as related to some environmental factors 1. *Journal of Phycology*, **3**(2), 103-108.

Druehl, L.D., 1970. The pattern of Laminariales distribution in the northeast Pacific. Phycologia, 9 (3), 237-247.

Engelen, A.H., Leveque, L., Destombe, C. & Valer, M., 2011. Spatial and temporal patterns of recovery of low intertidal *Laminaria digitata* after experimental spring and autumn removal. *Cahiers De Biologie Marine*, **52** (4), 441-453.

Estes, J.A. & Duggins, D.O., 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs*, **65**, 75-100.

FAO, 2007. Aquaculture production: values 1984-2005. FISHSTAT Plus - Universal software for fishery statistical time series [online or CD-ROM]. Fishery Information, Data and Statistics Unit. Food and Agriculture Organization of the United Nations, Rome, Italy.

Farrell, P. & Fletcher, R., 2006. An investigation of dispersal of the introduced brown alga *Undaria pinnatifida* (Harvey) Suringar and its competition with some species on the man-made structures of Torquay Marina (Devon, UK). *Journal of Experimental Marine Biology and Ecology*, **334** (2), 236-243.

Fletcher, R.L. & Manfredi, C., 1995. The occurrence of *Undaria pinnatifida* (Phyaeophyceae, Laminariales) on the South Coast of England. *Botanica Marina*, **38** (4), 355-358.

Frieder, C., Nam, S., Martz, T. & Levin, L., 2012. High temporal and spatial variability of dissolved oxygen and pH in a nearshore California kelp forest. *Biogeosciences*, **9** (10), 3917-3930.

Gaylord, B., Reed, D.C., Raimondi, P.T. & Washburn, L., 2006. Macroalgal spore dispersal in coastal environments: Mechanistic insights revealed by theory and experiment. *Ecological Monographs*, **76** (4), 481-502.

Gayral, P. & Cosson, J., 1973. Exposé synoptique des données biologiques sur la laminaire digitée *Laminaria digitata*. Synopsis FAO sur les pêches, no. **89**.

Gerard, V., 1982. In situ water motion and nutrient uptake by the giant kelp Macrocystis pyrifera. Marine Biology, 69 (1), 51-54.

Gerard, V.A. & Du Bois, K.R., 1988. Temperature ecotypes near the southern boundary of the kelp Laminaria saccharina. Marine Biology, **97**, 575-580.

Gerard, V.A. & Mann, K.H., 1979. Growth and production of *Laminaria longicruris* (Phaeophyta) populations exposed to different intensities of water movement 1. *Journal of Phycology*, **15** (1), 33-41.

Gerard, V.A., 1987. Hydrodynamic streamlining of *Laminaria saccharina* Lamour. in response to mechanical stress. *Journal of Experimental Marine Biology and Ecology*, **107**, 237-244.

Gessner, F., 1970. Temperature - Plants. In Marine Ecology: A Comprehensive Treatise on Life in Oceans and Coastal Waters. Vol. 1 Environmental Factors Part 1. (ed. O. Kinne), pp. 363-406. Chichester: John Wiley & Sons

Gordillo, F.J.L., Dring, M.J. & Savidge, G., 2002. Nitrate and phosphate uptake characteristics of three species of brown algae cultured at low salinity. *Marine Ecology Progress Series*, **234**, 111-116.

Gorgula, S.K. & Connell, S.D., 2004. Expansive covers of turf-forming algae on human-dominated coast: the relative effects of

increasing nutrient and sediment loads. Marine Biology, 145 (3), 613-619.

Griffiths, A.B., Dennis, R. & Potts, G.W., 1979. Mortality associated with a phytoplankton bloom off Penzance in Mount's Bay. *Journal of the Marine Biological Association of the United Kingdom*, **59**, 515-528.

Gunnill, F., 1985 Population fluctuations of seven macroalgae in southern California during 1981-1983 including effects of severe storms and an El Nino. *Journal of Experimental Marine Biology and Ecology*, **85**, 149-164.

Harder, D.L., Hurd, C.L. & Speck, T., 2006. Comparison of mechanical properties of four large, wave-exposed seaweeds. *American Journal of Botany*, **93** (10), 1426-1432.

Harker, M., Berkaloff, C., Lemoine, Y., Britton, G., Young, A.J., Duval, J.-C., Rmiki, N.-E. & Rousseau, B., 1999. Effects of high light and desiccation on the operation of the xanthophyll cycle in two marine brown algae. *European Journal of Phycology*, **34** (1), 35-42.

Hawkins, S.J. & Harkin, E., 1985. Preliminary canopy removal experiments in algal dominated communities low on the shore and in the shallow subtidal on the Isle of Man. *Botanica Marina*, **28**, 223-30.

Hawkins, S.J. & Hartnoll, R.G., 1985. Factors determining the upper limits of intertidal canopy-forming algae. *Marine Ecology Progress Series*, **20**, 265-271.

Heinrich, S., Valentin, K., Frickenhaus, S., John, U. & Wiencke, C., 2012. Transcriptomic analysis of acclimation to temperature and light stress in *Saccharina latissima* (Phaeophyceae). *Plos One*, **7** (8), e44342.

Heiser, S., Hall-Spencer, J.M. & Hiscock, K., 2014. Assessing the extent of establishment of *Undaria pinnatifida* in Plymouth Sound Special Area of Conservation, UK. *Marine Biodiversity Records*, **7**, e93.

Hiscock, K. & Hoare, R., 1975. The ecology of sublittoral communities at Abereiddy Quarry, Pembrokeshire. *Journal of the Marine Biological Association of the united Kingdom*, **55**, 833-864.

Hurd, C.L., 2000. Water motion, marine macroalgal physiology, and production. Journal of Phycology, 36 (3), 453-472.

Isaeus, M., 2004. Factors structuring *Fucus communities* at open and complex coastlines in the Baltic Sea. Department of Botany, Botaniska institutionen, Stockholm.

Jensen, A.C., Collins, K.J., Lockwood, A.P.M., Mallinson, J.J. & Turnpenny, W.H., 1994. Colonization and fishery potential of a coalash artificial reef, Poole Bay, United Kingdom. *Bulletin of Marine Science*, **55**, 1263-1276.

JNCC, 2015. The Marine Habitat Classification for Britain and Ireland Version 15.03. (20/05/2015). Available from https://mhc.jncc.gov.uk/

Johnston, E., Marzinelli, E., Wood, C., Speranza, D. & Bishop, J., 2011. Bearing the burden of boat harbours: Heavy contaminant and fouling loads in a native habitat-forming alga. *Marine Pollution Bulletin*, **62** (10), 2137-2144.

Kain, J.M., 1984. Seasonal growth of two subtidal species of Rhodophyta off the Isle of Man. *Journal of Experimental Marine Biology* and Ecology, **82** (2), 207-220.

Kain, J.M., 1975a. Algal recolonization of some cleared subtidal areas. Journal of Ecology, 63, 739-765.

Kain, J.M., 1979. A view of the genus Laminaria. Oceanography and Marine Biology: an Annual Review, 17, 101-161.

Kain, J.M., 1987. Photoperiod and temperature as triggers in the seasonality of *Delesseria sanguinea*. *Helgolander Meeresuntersuchungen*, **41**, 355-370.

Kain, J.M., & Norton, T.A., 1990. Marine Ecology. In *Biology of the Red Algae*, (ed. K.M. Cole & Sheath, R.G.). Cambridge: Cambridge University Press.

Karsten, U., 2007. Research note: salinity tolerance of Arctic kelps from Spitsbergen. Phycological Research, 55 (4), 257-262.

Kinne, O. (ed.), 1970. Marine Ecology: A Comprehensive Treatise on Life in Oceans and Coastal Waters. Vol. 1 Environmental Factors Part 1. Chichester: John Wiley & Sons

Kinne, O., 1977. International Helgoland Symposium "Ecosystem research": summary, conclusions and closing. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **30**(1-4), 709-727.

Kirk, J., 1976. Yellow substance (gelbstoff) and its contribution to the attenuation of photosynthetically active radiation in some inland and coastal south-eastern Australian waters. *Marine and Freshwater Research*, **27** (1), 61-71.

Kirst, G., 1990. Salinity tolerance of eukaryotic marine algae. Annual review of plant biology, 41 (1), 21-53.

Kirst, G.O. & Wiencke, C., 1995. Ecophysiology of polar algae. Journal of Phycology, **31** (2), 181-199.

Krumhansl, K.A. & Scheibling, R.E., 2011. Detrital production in Nova Scotian kelp beds: patterns and processes. *Marine Ecological Progress Series*, **421**, 67-82.

Krumhansl, K.A. & Scheibling, R.E., 2012. Detrital subsidy from subtidal kelp beds is altered by the invasive green alga Codium fragile ssp fragile. Marine Ecology Progress Series, **456**, 73-85.

Krumhansl, K.A., 2012. *Detrital production in kelp beds*. degree of Doctor of Philosophy, Department of Biology, Dalhousie University, Halifax, Nova Scotia.

Krumhansl, K.A., Lee, J.M. & Scheibling, R.E., 2011. Grazing damage and encrustation by an invasive bryozoan reduce the ability of kelps to withstand breakage by waves. *Journal of Experimental Marine Biology and Ecology*, **407** (1), 12-18.

Lüning, K. & Dring, M., 1979. Continuous underwater light measurement near Helgoland (North Sea) and its significance for characteristic light limits in the sublittoral region. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **32** (4), 403-424.

Lauzon-Guay, J.-S. & Scheibling, R., 2007. Seasonal variation in movement, aggregation and destructive grazing of the green sea

urchin (Strongylocentrotus droebachiensis) in relation to wave action and sea temperature. Marine Biology, 151 (6), 2109-2118.

Lee, J.A. & Brinkhuis, B.H., 1988. Seasonal light and temperature interaction effects on development of *Laminaria saccharina* (Phaeophyta) gametophytes and juvenile sporophytes. *Journal of Phycology*, **24**, 181-191.

Levin, P.S., Coyer, J.A., Petrik, R. & Good, T.P., 2002. Community-wide effects of nonindigenous species on temperate rocky reefs. *Ecology*, **83**(11), 3182-3193.

Lewis, G.A. & Nichols, D., 1980. Geotactic movement following disturbance in the European sea-urchin, *Echinus esculentus* (Echinodermata: Echinoidea). *Progress in Underwater Science*, **5**, 171-186.

Ling, S.D., Johnson, C.R., Frusher, S.D. & Ridgeway, K.R., 2009. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proceedings of the National Academy of Sciences USA*, **106**, 22341-22345.

Lobban, C.S. & Harrison, P.J. (eds.), 1994. Seaweed Ecology and Physiology. Cambridge, uk: Cambridge University Press, pp. 366.

Lorentsen, S.-H., Sjøtun, K. & Grémillet, D., 2010. Multi-trophic consequences of kelp harvest. *Biological Conservation*, **143** (9), 2054-2062.

Lüning, K., 1990. Seaweeds: their environment, biogeography, and ecophysiology: John Wiley & Sons.

Lüning, K. & Dring, M.J., 1975. Reproduction, growth and photosynthesis of gametophytes of *Laminaria saccharina* grown in blue and red light. *Marine Biology*, **29**, 195-200.

Lüning, K., 1980. Critical levels of light and temperature regulating the gametogenesis of three laminaria species (Phaeophyceae). *Journal of Phycology*, **16**, 1-15.

Lüning, K., 1984. Temperature tolerance and biogeography of seaweeds: the marine algal flora of Helgoland (North Sea) as an example. *Helgolander Meeresuntersuchungen*, **38**, 305-317.

Lüning, K., 1988. Photoperiodic control of sorus formation in the brown alga *Laminaria saccharina*. *Marine Ecology Progress Series*, **45**, 137-144.

Lyngby, J.E. & Mortensen, S.M., 1996. Effects of dredging activities on growth of Laminaria saccharina. Marine Ecology, Publicazioni della Stazione Zoologica di Napoli I, **17**, 345-354.

Müller, R., Laepple, T., Bartsch, I. & Wiencke, C., 2009. Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. *Botanica Marina*, **52** (6), 617-638.

Markham, J.W. & Munda, I.M., 1980. Algal recolonisation in the rocky eulittoral at Helgoland, Germany. Aquatic Botany, 9, 33-71.

Merzouk, A. & Johnson, L.E., 2011. Kelp distribution in the northwest Atlantic Ocean under a changing climate. *Journal of Experimental Marine Biology and Ecology*, **400** (1), 90-98.

Mikhaylova, T.A., 1999. The initial stages of experimental forming of *Laminaria* communities in the White Sea. *Botanicheskii Zhurnal* (St. Petersburg), **84** (3), 56-66.

Milazzo, M., Chemello, R., Badalamenti, F. & Riggio, S., 2002. Short-term effect of human trampling on the upper infralittoral macroalgae of Ustica Island MPA (western Mediterranean, Italy). *Journal of the Marine Biological Association of the UK*, **82** (05), 745-748.

Molfese, C., Beare, D. & Hall-Spencer, J.M., 2014. Overfishing and the Replacement of Demersal Finfish by Shellfish: An Example from the English Channel. *Plos One*, **9** (7).

Morrell, S.L. & Farnham, W.F., 1982. Some effects of substratum on *Sargassum muticum*. British Phycological Journal, **17** (2), 236-237.

Moy, F., Alve, E., Bogen, J., Christie, H., Green, N., Helland, A., Steen, H., Skarbøvik, E. & Stålnacke, P., 2006. Sugar Kelp Project: Status Report No 1. SFT Report TA-2193/2006, NIVA Report 5265 (in Norwegian, with English Abstract), 36 pp.

Moy, F.E. & Christie, H., 2012. Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along the south and west coast of Norway. *Marine Biology Research*, **8** (4), 309-321.

Nagel, K., Schneemann, I., Kajahn, I., Labes, A., Wiese, J. & Imhoff, J.F., 2012. Beneficial effects of 2,4-diacetylphloroglucinol-producing pseudomonads on the marine alga *Saccharina latissima*. *Aquatic Microbial Ecology*, **67** (3), 239-249.

Netalgae, 2012. Seaweed industry in Europe. http://www.netalgae.eu/publications.php: (24/04/2014).

Nielsen, M., Krause-Jensen, D., Olesen, B., Thinggaard, R., Christensen, P. & Bruhn, A., 2014a. Growth dynamics of *Saccharina latissima* (Laminariales, Phaeophyceae) in Aarhus Bay, Denmark, and along the species' distribution range. *Marine Biology*, **161** (9), 2011-2022.

Nimura, K., Mizuta, H. & Yamamoto, H., 2002. Critical contents of nitrogen and phosphorus for sorus formation in four Laminaria species. *Botanica Marina*, **45**, 184-188.

Norton, T.A., 1978. The factors influencing the distribution of *Saccorhiza polyschides* in the region of Lough Ine. *Journal of the Marine Biological Association of the United Kingdom*, **58**, 527-536.

Norton, T.A., 1992. Dispersal by macroalgae. British Phycological Journal, 27, 293-301.

O'Brien, J.M., Scheibling, R.E. & Krumhansl, K.A., 2015. Positive feedback between large-scale disturbance and density-dependent grazing decreases resilience of a kelp bed ecosystem. *Marine Ecology Progress Series*, **522**, 1-13.

Oates, B.R., 1985. Photosynthesis and amelioration of desiccation in the intertidal saccate alga *Colpornema peregrina*. *Marine Biology*, **89**, 109-119.

Oates, B.R., 1986. Components of photosynthesis in the intertidal saccate alga *Halosaccion americanum* (Rhodophyta, Palmariales). *Journal of Phycology*, **22**, 217-223.

Parke, M., 1948. Studies on British Laminariaceae. I. Growth in Laminaria saccharina (L.) Lamour. Journal of the Marine Biological Association of the United Kingdom, **27**, 651-709.

Parker, H., 1981. Influence of relative water motion on the growth, ammonium uptake and carbon and nitrogen composition of *Ulva lactuca* (Chlorophyta). *Marine Biology*, **63** (3), 309-318.

Parker, H., 1982. Effects of simulated current on the growth rate and nitrogen metabolism of *Gracilaria tikvahiae* (Rhodophyta). *Marine Biology*, **69** (2), 137-145.

Pérez, R., 1971. Écologie, croissance et régénération, teneurs en acide alginique de Laminaria digitata sur les cotes de la Manche. Revue des Travaux de l'Institut des Peches Maritimes, **35**, 287-346.

Peteiro, C. & Freire, O., 2013. Biomass yield and morphological features of the seaweed Saccharina latissima cultivated at two different sites in a coastal bay in the Atlantic coast of Spain. *Journal of Applied Phycology*, **25**(1), 205-213.

Peteiro, C., Sánchez, N., Dueñas-Liaño, C. & Martínez, B., 2014. Open-sea cultivation by transplanting young fronds of the kelp *Saccharina latissima. Journal of Applied Phycology*, **26** (1), 519-528.

Peters, A.F. & Schaffelke, B., 1996. *Streblonema* (Ectocarpales, Phaeophyceae) infection in the kelp *Laminaria saccharina* in the western Baltic. *Hydrobiologia*, **326/327**, 111-116.

Pihl, L., 1994. Changes in the Diet of Demersal Fish due to Eutrophication-Induced Hypoxia in the Kattegat, Sweden. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**(2), 321-336.

Raybaud, V., Beaugrand, G., Goberville, E., Delebecq, G., Destombe, C., Valero, M., Davoult, D., Morin, P. & Gevaert, F., 2013. Decline in kelp in west Europe and climate. *Plos One*, **8** (6), e66044.

Reed, D.C., Rassweiler, A. & Arkema, K.K., 2008. Biomass rather than growth rate determines variation in net primary production by giant kelp. *Ecology and evolution*, **89**, 2493-2505

Rietema, H., 1993. Ecotypic differences between Baltic and North Sea populations of *Delesseria sanguinea* and *Membranoptera alata*. *Botanica Marina*, **36**, 15-21.

Robins, P.E., Neill, S.P., Giménez, L., Jenkins, S.R. & Malham, S.K., 2013. Physical and biological controls on larval dispersal and connectivity in a highly energetic shelf sea. *Limnology and Oceanography*, **58**(2), 505-524.

Roleda, M.Y. & Dethleff, D., 2011. Storm-generated sediment deposition on rocky shores: Simulating burial effects on the physiology and morphology of *Saccharina latissima* sporophytes. *Marine Biology Research*, **7** (3), 213-223.

Roleda, M.Y., Dethleff, D. & Wiencke, C., 2008. Transient sediment load on blades of Arctic *Saccharina latissima* can mitigate UV radiation effect on photosynthesis. *Polar Biology*, **31** (6), 765-769.

Rueness, J., 1989. *Sargassum muticum* and other introduced Japanese macroalgae: biological pollution of European coasts. *Marine Pollution Bulletin*, **20** (4), 173-176.

Saier, B. & Chapman, A.S., 2004. Crusts of the alien bryozoan *Membranipora membranacea* can negatively impact spore output from native kelps (*Laminaria longicruris*). Botanica Marina, **47** (4), 265-271.

Sanderson, J., Dring, M., Davidson, K. & Kelly, M., 2012. Culture, yield and bioremediation potential of *Palmaria palmata* (Linnaeus) Weber & Mohr and *Saccharina latissima* (Linnaeus) adjacent to fish farm cages in northwest Scotland. *Aquaculture*, **354**, 128-135.

Sawabe, T., Makino, H., Tatsumi, M., Nakano, K., Tajima, K., Iqbal, M.M., Yumoto, I., Ezura, Y. & Christen, R., 1998. *Pseudoalteromonas bacteriolytica* sp. nov., a marine bacterium that is the causative agent of red spot disease of *Laminaria japonica*. *International Journal of Systematic Bacteriology*, **48** (3), 769-774.

Scheibling, R.E. & Gagnon, P., 2006. Competitive interactions between the invasive green alga *Codium fragile* ssp tomentosoides and native canopy-forming seaweeds in Nova Scotia (Canada). *Marine Ecology Progress Series*, **325**, 1-14.

Scheibling, R.E., Hennigar, A.W. & Balch, T., 1999. Destructive grazing, epiphytism, and disease: the dynamics of sea urchin-kelp interactions in Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences*, **56** (12), 2300-2314.

Scheibling, R.E., Lyons, D.A. & Sumi, C.B., 2008. Grazing of the invasive alga *Codium fragile* ssp. *tomentosoides* by the common periwinkle *Littorina littorea*: effects of thallus size, age and condition. *Journal of Experimental Marine Biology and Ecology*, **355** (2), 103-113.

Schmidt, A.L. & Scheibling, R.E., 2006. A comparison of epifauna and epiphytes on native kelps (*Laminaria* species) and an invasive alga (*Codium fragile* ssp tomentosoides) in Nova Scotia, Canada. *Botanica Marina*, **49** (4), 315-330.

Sebens, K.P., 1985. Community ecology of vertical rock walls in the Gulf of Maine: small-scale processes and alternative community states. In *The Ecology of Rocky Coasts: essays presented to J.R. Lewis, D.Sc.* (ed. P.G. Moore & R. Seed), pp. 346-371. London: Hodder & Stoughton Ltd.

Sebens, K.P., 1986. Spatial relationships among encrusting marine organisms in the New England subtidal zone. *Ecological Monographs*, **56**, 73-96.

Sivertsen, K. & Bjorge, A., 2015. On the brink of the Arctic: Unusual intertidal sub-Arctic kelp associations in the Porsangerfjord, North Norway. *Marine Biology Research*, **11** (4), 405-413.

Sjøtun, K. & Schoschina, E.V., 2002. Gametophytic development of *Laminaria* spp. (Laminariales, Phaeophyta) at low temperatures. *Phycologia*, **41**, 147-152.

Smale, D.A. & Wernberg, T., 2013. Extreme climatic event drives range contraction of a habitat-forming species. *Proceedings of the Royal Society B-Biological Sciences*, **280** (1754).

Smale, D.A., Burrows, M.T., Moore, P., O'Connor, N. & Hawkins, S.J., 2013. Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecology and evolution*, **3** (11), 4016-4038.

Spurkland, T. & Iken, K., 2011a. Salinity and irradiance effects on growth and maximum photosynthetic quantum yield in subarctic *Saccharina latissima* (Laminariales, Laminariaceae). *Botanica Marina*, **54**, 355-365.

Spurkland, T. & Iken, K., 2011b. Kelp Bed Dynamics in Estuarine Environments in Subarctic Alaska. *Journal of Coastal Research*, 133-143.

Staehr, P.A. & Wernberg, T., 2009. Physiological responses of *Ecklonia radiata* (Laminariales) to a latitudinal gradient in ocean temperature. *Journal of Phycology*, **45**, 91-99.

Steneck, R.S., Vavrinec, J. & Leland, A.V., 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the western North Atlantic. *Ecosystems*, **7** (4), 323-332.

Strong, J.A. & Dring, M.J., 2011. Macroalgal competition and invasive success: testing competition in mixed canopies of *Sargassum muticum* and *Saccharina latissima*. *Botanica Marina*, **54** (3), 223-229.

Sundene, O., 1964. The ecology of *Laminaria digitata* in Norway in view of transplant experiments. *Nytt Magasin for Botanik*, **11**, 83-107.

Thompson, G.A. & Schiel, D.R., 2012. Resistance and facilitation by native algal communities in the invasion success of *Undaria* pinnatifida. Marine Ecology, Progress Series, **468**, 95-105.

Tyler-Walters, H., 2005b. Assessment of the potential impacts of coasteering on rocky intertidal habitats in Wales. *Report to Cyngor Cefn Gwlad Cymru / Countryside Council for Wales from the Marine Life Information Network (MarLIN)*. Marine Biological Association of the United Kingdom, Plymouth, 129 pp.

Tyler-Walters, H. & Arnold, C., 2008. Sensitivity of Intertidal Benthic Habitats to Impacts Caused by Access to Fishing Grounds. Report to Cyngor Cefn Gwlad Cymru / Countryside Council for Wales from the Marine Life Information Network (MarLIN) [Contract no. FC 73-03-327], Marine Biological Association of the UK, Plymouth, 48 pp. Available from: www.marlin.ac.uk/publications

Valero, M., Destombe, C., Mauger, S., Ribout, C., Engel, C.R., Daguin-Thiebaut, C. & Tellier, F., 2011. Using genetic tools for sustainable management of kelps: a literature review and the example of *Laminaria digitata*. *CBM-Cahiers de Biologie Marine*, *52*(4), 467.

Van den Hoek, C. & Donze, M., 1967. Algal phytogeography of the European Atlantic coasts. *Blumea*, **15** (1), 63-89.

Van den Hoek, C., Mann, D.G. & Jahns, H.M., 1995. Algae: an introduction to phycology: Cambridge University Press.

Vea, J. & Ask, E., 2011. Creating a sustainable commercial harvest of *Laminaria hyperborea*, in Norway. *Journal of applied Phycology*, **23**(3), 489-494.

Wang, G., Shuai, L., Li, Y., Lin, W., Zhao, X. & Duan, D., 2008. Phylogenetic analysis of epiphytic marine bacteria on Hole-Rotten diseased sporophytes of *Laminaria japonica*. *Journal of applied phycology*, **20** (4), 403-409.

Wang, X., Broch, O.J., Forbord, S., Handa, A., Skjermo, J., Reitan, K.I., Vadstein, O. & Olsen, Y., 2014. Assimilation of inorganic nutrients from salmon (*Salmo salar*) farming by the macroalgae (*Saccharina latissima*) in an exposed coastal environment: implications for integrated multi-trophic aquaculture. *Journal of Applied Phycology*, **26** (4), 1869-1878.

Weile, K., 1996. Baseline study of *Laminaria* populations in Øresund. Doc. nr. 95/120/1E. By VRI/Toxicon AB for Øresundskonsortiet

Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T., Bennett, S. & Rousseaux, C.S., 2013. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, **3** (1), 78-82.

Wheeler, W.N., 1980. Effect of boundary layer transport on the fixation of carbon by the giant kelp *Macrocystis pyrifera*. *Marine Biology*, **56**, 103–110.

Wilce, R., 1965. Studies in the genus *Laminaria*. III. A revision of the north Atlantic species of the Simplices section of *Laminaria*. *Bot. gothoburg.*, **3**, 247-256.

Yarish, C., Penniman, C.A. & Egan, B., 1990. Growth and reproductibe responses of *Laminaria longicruris* (*Laminariales, Phaeophyta*) to nutrient enrichment. *Hydrobiologia*, **204**, 505-511.