



# MarLIN

## Marine Information Network

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

# Grazed *Saccharina latissima* with *Echinus*, brittlestars and coralline crusts on sheltered infralittoral rock

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

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**Please note.** This MarESA report is a dated version of the online review. Please refer to the website for the most up-to-date version [<https://www.marlin.ac.uk/habitats/detail/263>]. All terms and the MarESA methodology are outlined on the website (<https://www.marlin.ac.uk>)

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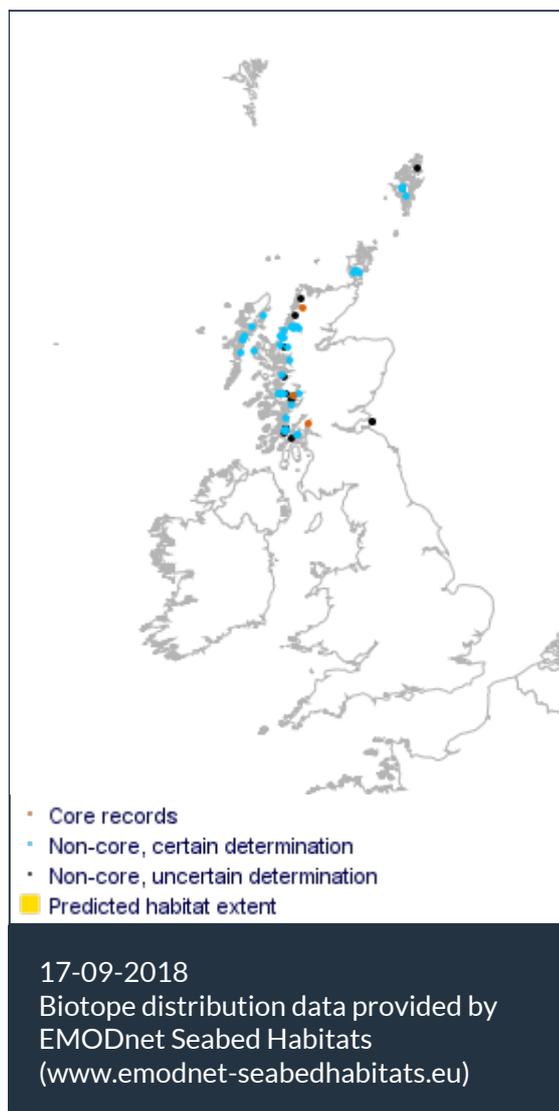
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Grazed *Saccharina latissima* with *Echinus*, brittlestars and coralline crusts on sheltered infralittoral rock

Photographer: Keith Hiscock

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Researched by Frances Perry      Referred by This information is not refereed.

## Summary

### ☰ UK and Ireland classification

EUNIS 2008	A3.3134	Grazed <i>Laminaria saccharina</i> with <i>Echinus</i> , brittlestars and coralline crusts on sheltered infralittoral rock
JNCC 2015	IR.LIR.K.Slat.Gz	Grazed <i>Saccharina latissima</i> with <i>Echinus</i> , brittlestars and coralline crusts on sheltered infralittoral rock
JNCC 2004	IR.LIR.K.Lsac.Gz	Grazed <i>Laminaria saccharina</i> with <i>Echinus</i> , brittlestars and coralline crusts on sheltered infralittoral rock
1997 Biotope	IR.SIR.K.EchBriCC	<i>Echinus</i> , brittlestars and coralline crusts on grazed lower infralittoral rock

### 🔍 Description

This biotope often looks bare, with few large species present. *Saccharina latissima* may be present, but always at low abundance. The biotope is characterized by relatively high abundances of the

urchin *Echinus esculentus* and/ or brittlestars (*Ophiocomina nigra* or *Ophiothrix fragilis*). As a result of the high grazing pressure the rock surfaces look bare, though they are usually covered by coralline algal crusts with scattered tufts of various red and filamentous brown algae. Grazing molluscs may also be abundant in this biotope.

### ↓ Depth range

-

### Additional information

-

### ✓ Listed By

- none -

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## Sensitivity review

### Sensitivity characteristics of the habitat and relevant characteristic species

This biotope is an example of a grazed infralittoral kelp biotope. *Saccharina latissima* is the dominant macroalgae species within this biotope, the presence of grazing echinoderms keeps its abundance between rare and occasional. The removal of these grazers would allow the abundance of *Saccharina latissima* to increase and would consequently change the biotope to one that has a far higher coverage of this kelp species, e.g. IR.LIR.K.Slat.Pk or IR.LIR.K.LhypSlat.Pk. If *Echinus esculentus* were released from competitive pressure, then these species would graze away the remaining *Saccharina latissima*, and lead to a biotope with reduced biodiversity. The substratum within this biotope is usually covered in red coralline crust with grazed tufts of red algae species such as *Phycodrys rubens*, *Delesseria sanguinea* and *Brongniartella byssoides*. Grazing molluscs such as *Gibbula cineraria* can also be found within this biotope and contribute to the limitation of the spread of the dominant algal species. The interactions between the dominant species within this biotope *Saccharina latissima*, and *Echinus esculentus*, have been chosen to characterize the sensitivity of the biotope. A change in an abundance of either of species would result in a change in the biotope. The sensitivity of other species will be taken into consideration when appropriate.

### Resilience and recovery rates of habitat

*Saccharina latissima* (studied as *Laminaria saccharina*) was the prominent kelp species on concrete blocks (a minimum of 1.3 m in diameter) six months after the experimental 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 harpoon (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), which indicates 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 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 2 to 4 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 8 months to reach an average size (1-2 m in length, Gerard, unpublished, cited in Gerard & Du Bois, 1988). Growth rates for sporophytes are greatest between 10-15°C, with tissue growth occurring from March to November (at 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% reduction in growth rate 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 that are 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* that 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 season will affect 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 recolonization was prevalent in the past (Moy & Christie, 2012). Andersen (2013) suggests that this, and other regional studies 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 populations found further north (Gerard & Du Bois, 1988).

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*, (Bonsdorff & Vahl, 1982). Uncontrolled grazing of kelps by herbivores, including sea urchins may result in detrimental consequences to the biotope. In Nova Scotia, a study on the kelp *Saccharina longicuris* and its understory of *Laminaria digitata* indicated that grazing sea urchins might 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 & Chapman, 2004, Andersen *et al.*, 2011). This indicates that a decrease in grazers that 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).

*Echinus esculentus* is a sea urchin found within Northeast Atlantic, recorded from Murmansk Coast, Russia to Portugal (Hansson, 1998). *Echinus esculentus* is estimated to have a lifespan of 8-16 years (Nichols, 1979; Gage, 1992) and reach sexual maturity within 1-3 years (Tyler-Walters, 2008). Maximum spawning occurs in spring although individuals may spawn over a protracted period throughout the year. Gonad weight is at its maximum in February/March in English Channel (Comely & Ansell, 1989) but decreases during spawning in spring and then increases again through summer and winter until the next spawning season. Spawning in *Echinus esculentus*, occurs just

before the seasonal rise in temperature in temperate zones but is not thought to be triggered by rising temperature (Bishop, 1985). *Echinus esculentus* is a broadcast spawner, with a complex larval life history which includes a blastula, gastrula and a characteristic four armed echinopluteus stage that forms an important component of the zooplankton. MacBride (1914) observed planktonic larval development could take 45-60 days in captivity. Recruitment is sporadic or variable depending on locality, e.g. Millport populations showed annual recruitment, whereas few recruits were found in Plymouth populations during Nichols' studies between 1980-1981 (Nichols, 1984). Bishop & Earll (1984) suggested that the population of *Echinus esculentus* at St Abbs had a high density and recruited regularly whereas the Skomer population was sparse, ageing and had probably not successfully recruited larvae in the previous 6 years (Bishop & Earll, 1984). Comely & Ansell (1988) noted that the largest number of *Echinus esculentus* occurred below the kelp forest.

*Echinus esculentus* is a mobile species and could therefore migrate and re-populate an area quickly if removed. For example, Lewis & Nichols (1979) found that adults were able to colonize an artificial reef in small numbers within 3 months and the population steadily grew over the following year. If completely removed from a site and local populations are naturally sparse then recruitment may be dependent on larval supply that can be highly variable. As suggested by Bishop & Earll (1984) the Skomer, Wales, *Echinus esculentus* population had most likely, not successfully recruited for six years, which would suggest the mature population would be highly sensitive to removal and may not return for several years. On 19 November 2002 the *Prestige* oil tanker spilled 63 000t of fuel 130 nautical miles off Galicia, Spain. High wave exposure and strong weather systems increased mixing of the oil to "some" depth within the water column, causing sensitive faunal communities to be effected. Preceding and for nine years following the oil spill, the biological community of Guéthary, France was monitored. Following the oil spill taxonomic richness decreased significantly from 57-recorded species to 41, which included the loss of *Echinus esculentus* from the site. Spill taxonomic richness had increased to pre-spill levels and *Echinus esculentus* had returned 2-3 years after the oil (Castège *et al.*, 2014).

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* might 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 (0.8m) 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 turfs, or in kelp forests. However, in her recolonization experiments Kain (1975) noted that for *Laminaria digitata* and the characterizing red foliose algae understory to re-establish to prior abundances took three years.

Studies by Edyvean & Forde (1984a; 1986; 1987) of populations of coralline crusts of *Lithophyllum incrustans*, suggest that reproduction may be sexual or asexual (on average early in the third year), and spores are released throughout the year with seasonal variation (less spores were produced in the summer). The authors also found that spore survival was extremely low and young plant mortality was high, but that individuals over the age of 10 appear relatively long-lived (up to 30

years). Some repair of damaged encrusting coralline occurs through vegetative growth, so recolonization by propagules may also be an important mechanism for rapid recovery (Chamberlain, 1996; Airoldi, 2000).

**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. If removed completely red algae are likely to return within a year (Kain 1975) but their abundance may not be as great as prior to disturbance for three years. *Echinus esculentus* can reportedly reach sexual maturity within 1-2 years (Tyler-Walters, 2008). However, as highlighted by Bishop & Earll (1984) and Castège *et al.* (2014) recovery may take 2-6 years, possibly more if local recruitment is poor. Taking into consideration the ability of the characterizing species to recover it is likely that where impacts remove a significant proportion of the population, recovery will require larval recolonization, as well as adult migration. Therefore, where a significant part of the population is lost resilience is assessed as 'Medium' (2-10 years). Within this time period, it is likely that most species could have re-established biomass and age structured populations.

**NB** The resilience and the ability to recover from human induced pressures is a combination of the environmental conditions of the site, the frequency (repeated disturbances versus a one-off event) and the intensity of the disturbance. Recovery of impacted populations will always be mediated by stochastic events and processes acting over different scales including, but not limited to, local habitat conditions, further impacts and processes such as larval-supply and recruitment between populations. Full recovery is defined as the return to the state of the habitat that existed prior to impact. This does not necessarily mean that every component species has returned to its prior condition, abundance or extent but that the relevant functional components are present and the habitat is structurally and functionally recognizable as the initial habitat of interest. It should be noted that the recovery rates are only indicative of the recovery potential.

## Hydrological Pressures

	Resistance	Resilience	Sensitivity
Temperature increase (local)	Medium Q: High A: High C: Medium	High Q: High A: High C: Medium	Low Q: High A: High C: Medium

*Saccharina latissima* is found in the north west 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 Spitsbergen (Van den Hoek & Donze, 1967, Lüning, 1990). Its distribution suggests a resistance to a chronic temperature change (e.g. by 2°C for a year). Exposure to high short-term temperature increases are likely to result in stress. 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 three months at 15°C (Lüning, 1988).

Sporogenesis in *Saccharina latissima* requires a minimum period of four weeks at or below 15°C combined with short day lengths (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 photofluence rates were 5  $\mu\text{E m}^{-2} \text{sec}^{-1}$  (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 three weeks (Bolton & Lüning, 1982). However, Lüning (1990) estimated the upper temperature limit 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).

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).

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 that then form a barrier to future settlement of *Saccharina latissima* slowing or stopping recovery of the biotope (Moy & Christie, 2012). Increased temperatures bring with them increased growth of epiphytic ephemeral algae. Excessive epiphyte growth on kelp 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 epiphytic loading enhances blade tissue loss (Andersen *et al.*, 2013).

Bishop (1985) suggested that *Echinus esculentus* cannot tolerate high temperatures for prolonged periods due to increased respiration rate and resultant metabolic stress. Ursin (1960) reported *Echinus esculentus* occurred at temperatures between 0-18°C in Limfjord, Denmark. Bishop (1985) noted that gametogenesis occurred at 11-19°C, however, continued exposure to 19°C disrupted gametogenesis. Embryos and larvae developed abnormally after 24hr exposure to 15°C but normally at 4, 7 and 11°C (Tyler & Young 1998).

**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* for that year depending on when the increase occurs, because sporogenesis in *Saccharina latissima* requires a minimum period of four weeks at or below 15°C combined with short day lengths. An increase of 2°C is more likely to affect those at the extremes of the biotope's range, but the plasticity of *Saccharina latissima* may allow for populations to adapt to the new conditions over time. Minor declines in *Echinus esculentus* may occur within this biotope. Therefore, resistance has been assessed as 'Medium', and resilience has been assessed as 'High' so that sensitivity has been assessed as 'Low'.

#### Temperature decrease (local)

**High**

Q: High A: High C: Medium

**High**

Q: High A: High C: Medium

**Not sensitive**

Q: High A: High C: Medium

*Saccharina latissima* is found in the north west 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 Spitzbergen (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).

Other species found in this biotope may fair less well. For example, the urchin *Psammechinus miliaris* was adversely affected by the 1962/63 winter, while the crinoid (rosy feather star) *Antedon bifida* may have been lost from the Menai Straits following winter 1947 (D.J. Crisp pers. comm. to K. Hiscock).

The life cycle of kelps, in particular their spore production stage is considered to be sensitive to temperature. The gametophytes of *Saccharina latissima* 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). Sjutun & 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, which suggests 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).

*Echinus esculentus* has been recorded from the Murmansk Coast, Russia. Due to the high latitude at which *Echinus esculentus* can occur, it is unlikely to be affected at the pressure benchmark.

**Sensitivity assessment.** A decrease in temperature at the benchmark is not likely to impact examples of this biotope at the centre of their temperature range. 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 2°C for one year. 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 affect the fecundity of the *Saccharina latissima* population. *Echinus esculentus* is not thought to be sensitive to this pressure at the benchmark. This biotope is considered to have a resistance of 'High', a resilience of 'High' and an overall sensitivity of 'Not sensitive' at the benchmark level

### Salinity increase (local)

**None**

Q: High A: High C: Medium

**High**

Q: High A: High C: Medium

**Medium**

Q: High A: High C: Medium

*Saccharina latissima* can be found in full, variable or 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 two and five 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 five days of incubation in the laboratory, while treatments decreasing from 20-10 psu were associated with decreasing photosynthetic performance (Karsen, 2007).

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). 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 the Arctic, 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 growth (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).

Echinoderms are generally stenohaline owing to the lack of an excretory organ and a poor ability to osmo- and ion-regulate (Booolootian, 1966; Stickle & Diehl, 1987; Russell, 2013). Therefore, an increase in salinity may cause both *Echinus esculentus* and the brittlestars within this biotope mortality. A review by Russell (2013) confirmed that none of the brittlestar species within this biotope occurs in hypersaline conditions, although Pagett (1981) suggested that localised physiological adaptation to reduced or variable salinities may occur in near shore areas subject to freshwater runoffs.

**Sensitivity assessment.** IR.LIR.K.Slat.Gz is found within variable salinity conditions. An increase in this pressure at the benchmark would mean that conditions would become fully saline, and the physical characteristics of the biotope would be changed. The characterizing species within this biotope would all be able to survive within this new salinity regime. The new salinity may even provide conditions in which more species would be able to survive and cause a shift to a biotope such as IR.LIR.K.Slat.Pk. This shift in biotope would not result in a loss of the characterizing

species. However, there would be a shift of the biotope. Therefore, a resilience of 'None' is recorded. However, when the pressure abated the biotope would rapidly return, which means resilience is assessed as 'High'. Therefore, sensitivity is assessed as 'Medium'.

**Salinity decrease (local)** Low Medium Medium  
 Q: High A: High C: Medium      Q: High A: High C: Medium      Q: High A: High C: Medium

*Saccharina latissima* can be found within full, variable or 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 (Karsen, 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).

Echinoderms are generally unable to tolerate low salinity (stenohaline) owing to the lack of an excretory organ and a consequent poor ability to osmo- and ion-regulate (Booolootian, 1966; Stickle & Diehl, 1987; Russell, 2013). At low salinity, urchins gain weight, and the epidermis loses its pigment as patches are destroyed; prolonged exposure is fatal. However, evidence shows some resilience to reduced salinity within *Echinus esculentus* through intracellular regulation of osmotic pressure due to increased amino acid concentrations. Furthermore, as *Echinus esculentus* is found within a number of variable and reduced salinity biotopes, e.g. IR.LIR.KVS.SlatPsaVS (Connor *et al.*, 2004).

**Sensitivity assessment.** A reduction in this pressure at the benchmark within this biotope would create a reduced salinity regime. *Saccharina latissima* may be able to cope with this reduction as this species is found within other biotopes with reduced salinity regimes. However, the evidence suggests that a decrease in salinity may result in significant mortality of some of the other characterizing species within this biotope. The lack of osmoregulatory organ within echinoderms means that *Echinus esculentus* is likely to suffer significant mortality. The loss of this characterizing grazer will lead to a significant change in the biotope. Resistance is therefore assessed as 'Low' and resilience as 'Medium'. Sensitivity is therefore assessed as 'Medium'.

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

Although *Saccharina latissima* is unlikely to be directly affected by this pressure at the benchmark.

However, comparisons between biomass yields (dry weight) from two sites found significantly higher yields of *Saccharina latissima* at the moderately wave exposed site over the sheltered site, with light exposure and water velocity cited as the determining factors of both populations health (Peteiro & Freire, 2013). 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). These factors are also the suggested reason for the absence of this biotope from extremely sheltered Norwegian waters (Bekkby & Moy, 2011). 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. 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 that 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.

*Echinus esculentus* occurred in kelp beds on the west coast of Scotland in currents of about 0.5 m/sec. Outside these beds, specimens were occasionally seen being rolled by the current (Comely & Ansell, 1988), which may have been up to 1.4 m/sec. Urchins are removed from the stipe of kelps by wave and current action. *Echinus esculentus* are also displaced by storm action. After disturbance, *Echinus esculentus* migrates up the shore, an adaptation to being washed to deeper water by wave action (Lewis & Nichols, 1979). Therefore, increased water flow may remove the population from the affected area and into deeper water. However, individuals not killed in the process could recolonize the area quickly.

**Sensitivity assessment.** This biotope is recorded in areas subject to weak to negligible water flow. Therefore, an increase in water flow would probably result in a change in the biotope. The characterizing species *Saccharina latissima* and *Echinus esculentus* are unlikely to be directly affected by this pressure at the prescribed benchmark. Therefore, this biotope is considered to have 'High' resistance and 'High' resilience resulting in an overall sensitivity assessment score of, 'Not Sensitive'.

#### Emergence regime changes

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

This biotope does not occur in the intertidal, and consequently an increase in emergence is considered not relevant to this biotope.

**Wave exposure changes (local)****High**

Q: High A: High C: High

**High**

Q: High A: High C: High

**Not sensitive**

Q: High A: High C: High

*Saccharina latissima* rarely grows in wave exposed conditions, as it is vulnerable to dislodgement by wave action and, is typically attached to cobbles and boulders in this biotope, which may be overturned in conditions of increased wave action. 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*. *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). Urchins have been noted to migrate out of kelp biotopes during storms and periods of high wave action, probably to avoid damage by algal whiplash. Hence, grazing pressure would be temporarily decreased (Lauzon-Gauy, 2007). When considered in conjunction with emergence, wave exposure is beneficial to *Saccharina latissima*, with wave spray acting to hydrate individual alga that 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. This suggests 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 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, 2004, Moy *et al.*, 2006 Bekkby & Moy, 2011). Decreasing wave exposure also causes localised stagnation and de-oxygenation of the water column that 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 (Krumhansl *et al.*, 2011). Andersen *et al.* (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.

*Echinus esculentus* occurred in kelp beds on the west coast of Scotland in currents of about 0.5 m/sec. Outside these beds, specimens were occasionally seen being rolled by the current (Comely & Ansell, 1988), which may have been up to 1.4 m/sec. Urchins are removed from the stipe of kelps by wave and current action. *Echinus esculentus* are also displaced by storm action. After disturbance, *Echinus esculentus* migrates up the shore, an adaptation to being washed to deeper water by wave action (Lewis & Nichols, 1979). Therefore, increased water flow may remove the population from the affected area and into deeper water. However, individuals not killed in the process could recolonize the area quickly.

**Sensitivity assessment.** This biotope is recorded from very wave sheltered sites. A decrease in wave exposure, to extremely sheltered, may be detrimental and *Saccharina latissima* requires some water movement. However, an increase in wave action would probably result in a change in the

biotope due either to a decrease in urchin grazing and/or completion from other kelp species. However, a change in water flow at the benchmark level is not likely to have an effect on this biotope. Therefore, this biotope is considered to have 'High' resistance and 'High' resilience resulting in an overall sensitivity assessment score of, 'Not Sensitive' at the benchmark level.

## Chemical Pressures

	Resistance	Resilience	Sensitivity
<b>Transition elements &amp; organo-metal contamination</b>	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** but evidence is presented where available.

<b>Hydrocarbon &amp; PAH contamination</b>	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** but evidence is presented where available.

<b>Synthetic compound contamination</b>	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** but evidence is presented where available.

<b>Radionuclide contamination</b>	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
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No evidence.

<b>Introduction of other substances</b>	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**.

<b>De-oxygenation</b>	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
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At the time of writing there was insufficient evidence on which to assess the effect of this pressure on the characterizing species within this biotope. No direct evidence on the effects of deoxygenation for *Saccharina latissima* 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). In general, respiration in most marine invertebrates does not appear to be significantly affected until extremely low concentrations are reached. For many benthic invertebrates this concentration is about 2 ml l<sup>-1</sup>, or even less (Herreid,

1980; Rosenberg *et al.*, 1991; Diaz & Rosenberg, 1995).

A rapid recovery from a state of low oxygen is expected if the environmental conditions are transient. However, this biotope occurs in areas of low water movement, which suggests that a degree of hypoxia may be inherent in the system. 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:** Due to the lack of information regarding the effect of this pressure on the characterizing species within this biotope has led to an assessment of 'No evidence'.

## Nutrient enrichment

High

Q: High A: Medium C: Medium

High

Q: High A: High C: Medium

Not sensitive

Q: High A: Medium C: Medium

The nutrient enrichment of a marine environment leads to organisms no longer being limited by the availability of certain nutrients. The consequent changes in ecosystem functions can lead to the progression of eutrophic symptoms (Bricker *et al.*, 2008), changes in species diversity and evenness (Johnston & Roberts, 2009) decreases in dissolved oxygen and uncharacteristic microalgae blooms (Bricker *et al.*, 1999, 2008).

Johnston & Roberts (2009) undertook a review and meta-analysis of the effect of contaminants on species richness and evenness in the marine environment. Of the 47 papers reviewed relating to nutrients as a contaminants, over 75% found that it had a negative impact on species diversity, <5% found increased diversity, and the remaining papers finding no detectable effect. Although the papers reviewed within this report did not consider this exact biotope this finding is still relevant as the meta-analysis revealed that the effect of marine pollutants on species diversity were 'remarkably consistent' between habitats (Johnston & Roberts, 2009). It was found that any single pollutant reduced species richness by 30-50% within any of the marine habitats considered (Johnston & Roberts, 2009). Throughout their investigation there were only a few examples where species richness was increased due to the anthropogenic introduction of a contaminant.

These examples were almost entirely from the introduction of nutrients, either from aquaculture or sewage outfalls.

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).

It was suggested by Comely & Ansell (1988) that *Echinus esculentus* could absorb dissolved organic material for the purposes of nutrition. Nutrient enrichment may encourage the growth of ephemeral and epiphytic algae and therefore increase sea-urchin food availability. Lawrence (1975) reported that sea urchins had persisted over 13 years on barren grounds near sewage outfalls, presumably feeding on dissolved organic material, detritus, plankton and microalgae, although individuals died at an early age. No information was available on the effects of nutrient enrichment on other parts of the *Echinus esculentus* life cycle.

**Sensitivity assessment.** The evidence suggests that nutrient enrichment could benefit the macroalgae in the biotope, in the short-term, but that long-term or high levels of nutrient enrichment would probably be detrimental due to an increase competition form in epiphytes and opportunistic green algae.

However, the biotope is recorded as 'Not sensitive' at the pressure benchmark of compliance with good status as defined by the WFD.

## Organic enrichment

**High**

Q: Medium A: Medium C: Medium

**High**

Q: High A: High C: Medium

**Not sensitive**

Q: Medium A: Medium C: Medium

Johnston & Roberts (2009) undertook a review and meta-analysis of the effect of contaminants on species richness and evenness in the marine environment. Of the 49 papers reviewed relating to sewage as a contaminant, over 70% found that it had a negative impact on species diversity, <5% found increased diversity, and the remaining papers finding no detectable effect. Although the papers reviewed within this report did not consider this exact biotope this finding is still relevant as the meta-analysis revealed that the effect of marine pollutants on species diversity were 'remarkably consistent' between habitats (Johnston & Roberts, 2009). It was found that any single pollutant reduced species richness by 30-50% within any of the marine habitats considered (Johnston & Roberts, 2009). Throughout their investigation there were only a few examples where species richness was increased due to the anthropogenic introduction of a contaminant. These examples were almost entirely from the introduction of nutrients, either from aquaculture or sewage outfalls.

The amount of organic nitrogen a *Saccharina latissima* stand may be able to uptake varies with location. *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 is also important with depressed growth rates associated with *Saccharina latissima* growing near a sewage sludge dumping ground in Liverpool Bay, Irish Sea (Burrows, 1971).

It was suggested by Comely & Ansell (1988) that *Echinus esculentus* could absorb dissolved organic material for the purposes of nutrition. Organic enrichment may encourage the growth of ephemeral and epiphytic algae and therefore increase sea-urchin food availability. Lawrence (1975) reported that sea urchins had persisted over 13 years on barren grounds near sewage outfalls, presumably feeding on dissolved organic material, detritus, plankton and microalgae, although individuals died at an early age.

**Sensitivity assessment:** There is little empirical evidence to determine the effect of the pressure at the benchmark to the characterizing species within this biotope. Organic enrichment can cause significant negative effects on marine species, however, at the benchmark it is not considered to be excessively damaging. Therefore, resistance and resilience are assessed as 'High', giving the biotope an overall assessment of 'Not sensitive'.

## A Physical Pressures

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

	Resistance	Resilience	Sensitivity
<b>Physical change (to another seabed type)</b>	<b>None</b> Q: High A: High C: High	<b>Very Low</b> Q: High A: High C: High	<b>High</b> Q: High A: High C: High

If rock were replaced with sediment, this would represent a fundamental change to the physical character of the biotope and the species would be unlikely to recover. The biotope would be lost.

**Sensitivity assessment.** Resistance to the pressure is considered 'None', and resilience 'Very low'. Sensitivity has been assessed as 'High'.

	Resistance	Resilience	Sensitivity
<b>Physical change (to another sediment type)</b>	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

This biotope occurs only on bedrock and boulders, therefore, this pressure is not relevant to this biotope.

	Resistance	Resilience	Sensitivity
<b>Habitat structure changes - removal of substratum (extraction)</b>	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 characterizing this biotope are epifauna or epiflora occurring on rock and would be sensitive to the removal of the habitat. However, extraction of rock substratum is considered unlikely and this pressure is considered to be 'Not relevant' to hard substratum habitats.

	Resistance	Resilience	Sensitivity
<b>Abrasion/disturbance of the surface of the substratum or seabed</b>	<b>Low</b> Q: High A: Medium C: Medium	<b>Medium</b> Q: High A: High C: Medium	<b>Medium</b> Q: High A: Medium C: Medium

No direct evidence was found for this pressure on *Saccharina latissima*. Jennings & Kaiser (1998) suggested that the main direct effects of fishing on marine ecosystems usually include scraping, scouring and re-suspension of substratum. 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 *Saccharina latissima* 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 as individuals can re-growing hapeteron (root) 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).

Species with fragile tests, such as *Echinus esculentus* were reported to suffer badly as a result of scallop or queen scallop dredging (Bradshaw *et al.*, 2000; Hall-Spencer & Moore, 2000). Kaiser *et al.* (2000) reported that *Echinus esculentus* were less abundant in areas subject to high trawling disturbance in the Irish Sea. Jenkins *et al.* (2001) conducted experimental scallop trawling in the North Irish sea and recorded the damage caused to several conspicuous megafauna species, both when caught as bycatch and when left on the seabed. The authors recorded 16.4% of *Echinus esculentus* were crushed/dead, 29.3% would have >50% spine loss/minor cracks, 1.1% would have <50% spine loss and the remaining 53.3% would be in good condition. The trawling examples mentioned above were conducted on sedimentary habitats and thus the evidence is not directly relevant to the rock based biotopes. However, it does indicate the likely effects of abrasion on *Echinus esculentus*.

**Sensitivity assessment.** Epifaunal species and communities are considered to be amongst the most vulnerable to bottom gears (Jennings & Kaiser, 1998) and the impact of surface abrasion will depend on the footprint, duration and magnitude of the pressure. While *Saccharina latissima* may recover quickly, the urchin population may take longer to return to its prior abundance, so that a different biotope would form. Therefore, based on the evidence, resistance to a single abrasion event is assessed as 'Low' and resilience as 'Medium', so that sensitivity is assessed as 'Medium'. However, Veale *et al.* (2000) suggested that the abundance, biomass and production of epifaunal assemblages decreased with increasing fishing effort suggesting that, resistance and recovery of the biotope's species are likely to vary with pressure intensity. Resistance and resilience will therefore be lower (and hence sensitivity greater) to repeated abrasion events.

**Penetration or disturbance of the substratum subsurface**

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 characterizing this biotope group are epifauna or epiflora occurring on rock, which is resistant to subsurface penetration. The assessment for abrasion at the surface only is considered to equally represent sensitivity to this pressure. This pressure is not thought relevant to hard rock biotopes.

**Changes in suspended solids (water clarity)**

Medium

Q: High A: Medium C: Medium

Medium

Q: High A: High C: Medium

Medium

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 the biotope (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 alga 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 congeneric 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) absorb 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* 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 adaptation, so that growth is reduced if daily irradiances exceeding an average of 20 E (radiant flux) /m<sup>2</sup>/day. The resistance of a particular population to this pressure, therefore, varies with location..

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*, which would result 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 sub surface light attenuation (Kd) (Devlin *et al.*, 2008). Laminarians 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). Due to 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.

Moore (1977) suggested that *Echinus esculentus* was unaffected by turbid conditions. *Echinus esculentus* is an important grazer of red macro-algae in this biotope. Increased turbidity and resultant reduced light penetration is likely to negatively affect algal growth. However, *Echinus esculentus* can feed on alternative prey, detritus or dissolved organic material (Lawrence, 1975, Comely & Ansell, 1988).

**Sensitivity Assessment:** The evidence presented suggests that an increase in suspended organic matter may be beneficial to the filter feeding brittlestar species by providing increased food material. While for *Saccharina latissima* and other algae an increase in suspended solids will decrease light availability, and consequently lead to a reduction in the suitability of some of the habitat. The opposite is true for a decrease in suspended sediment. From the evidence available it is unlikely that a change in the pressure at the benchmark will have an effect on *Echinus esculentus*. At the benchmark a change in suspended solids may see a change in abundance of algae and

brittlestars. Consequently, resistance is assessed as 'Medium' and resilience as 'Medium', so that the biotope is assessed as 'Medium' sensitivity to a change in turbidity at the pressure benchmark.

### Smothering and siltation rate changes (light)

**High**  
Q: High A: Medium C: Medium

**High**  
Q: High A: High C: Medium

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

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 seven 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, in 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 (Devanny & Volve, 1978, Norton, 1978; Bartsch *et al.*, 2008).

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.

Comely & Ansell (1988) recorded large *Echinus esculentus* from kelp beds on the west coast of Scotland in which the substratum was seasonally covered with "high levels" of silt. This suggests that *Echinus esculentus* is unlikely to be killed by smothering, however, smaller specimens and juveniles may be less resistant. A layer of sediment may interfere with larval settlement. If retained within the biotope for extended periods a layer of 5 cm of the sediment may negatively affect successive recruitment events.

**Sensitivity assessment.** Where smothering is short-term (less than seven days), then the characterizing species, and therefore the biotope, should be relatively resistant to this pressure at the benchmark. As 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. Therefore, 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 rate changes (heavy)

**Low**  
Q: High A: Medium C: Medium

**Medium**  
Q: High A: High C: Medium

**Medium**  
Q: High A: Medium C: Medium

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 seven 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, in 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.** The level of sediment deposition and the amount of time that it might take for the sediment to be removed from the habitat mean that there is likely to be a considerable amount of mortality of the characterizing species, and resistance has been assessed as 'Low'. Resilience is assessed as 'Medium', and takes into consideration the amount of time it might take for the sediment to be removed from the habitat. Therefore, the overall sensitivity of the biotope is assessed as 'Medium'.

## 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.

## Electromagnetic changes

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.

## Underwater noise changes

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

Species characterizing this habitat do not have hearing perception but vibrations may cause an impact, however, no studies exist to support an assessment.

## Introduction of light or shading

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

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). Light availability is very important to this photosynthesising organism. However, there is no information on how unnatural light sources may affect *Saccharina latissima*.

There is a lack of evidence relating to the effect of light on *Echinus esculentus*. Although some brittlestar species are able to perceive differences in light and dark, visual perception is limited (Tillin & Tyler-Walters, 2014) and this suggests that the brittlestars are unlikely to be directly affected by change in light.

**Sensitivity assessment.** Due to the lack of evidence regarding all of the characterizing species within this biotope an assessment of 'No evidence' is given.

#### 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. Physical and hydrographic barriers may limit propagule dispersal. However, propagule dispersal is not considered under the pressure definition and benchmark.

#### Death or injury by collision

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. Physical and hydrographic barriers may limit propagule dispersal. However, propagule dispersal is not considered under the pressure definition and benchmark.

#### Visual disturbance

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.

### Biological Pressures

Resistance

Resilience

Sensitivity

#### Genetic modification & translocation of indigenous species

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

*Echinus esculentus* was identified by Kelly & Pantazis (2001) as a species suitable for culture for the urchin roe industry. However, no evidence was found to suggest that significant *Echinus esculentus* mariculture was present in the UK. If industrially cultivated, it is feasible that *Echinus esculentus* individuals could be translocated. Translocation also has the potential to transport pathogens to uninfected areas (see pressure 'introduction of microbial pathogens'). The sensitivity of the 'donor' population to harvesting to supply stock for translocation is assessed for the pressure 'removal of target species'. No evidence can be found regarding the cultivation of either *Saccharina latissima* or brittlestars within the British Isles at the time of writing

**Sensitivity assessment.** Due to the lack of evidence regarding the cultivation of any of the characterizing species from this biotope the pressure is considered 'Not relevant'.

## Introduction or spread of invasive non-indigenous species

High

Q: High A: Medium C: Medium

High

Q: High A: High C: Medium

Not sensitive

Q: High A: Medium C: Medium

The effects of invasive species on *Saccharina latissima* appear to be limited, or not 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,. 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 the kelp was undetermined its presence illustrated the resistance 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 recolonization and recovery of *Saccharina latissima* beds in the Skagerrak area (Andersen *et al.*, 2011). If an invasion of ephemeral turf algae is coupled with a large scale disturbance event (e.g. a storm) *Saccharina latissima* is likely to be vulnerable, and consequently the whole biotope could be at risk (O'Brien *et al.*, 2015).

There is no evidence on the presence of non-indigenous species or impacts of non-indigenous species on either *Echinus esculentus* or the brittlestar species within this biotope.

**Sensitivity assessment.** At present there is little evidence to suggest that this biotope would be at significant risk of any known INIS. Therefore, the resistance and resilience are assessed as 'High' and the biotope is considered 'Not sensitive' at the pressure benchmark. However, due to the constant threat of further species being introduced to British Isles a search for new evidence should be made regularly.

## Introduction of microbial pathogens

High

Q: High A: Medium C: Medium

High

Q: High A: High C: Medium

Not sensitive

Q: High A: Medium C: Medium

*Saccharina latissima* (studied as *Laminaria saccharina*) may be infected by the microscopic brown alga *Streblonema aecidioides* that may manifest to different degrees from dark spots to heavy deformations, crippled thalli, and reduce growth rates. Infection rates have been recorded as 87% ( $\pm 13\%$ ) 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 two algal pathogens, *Pseudoalteromonas elyakovii* and *Algicola bacteriolytica*. *Pseudomonads* produces antibiotics that prevent *Saccharina latissima*'s infection, suggesting that this biotope's resistance to disease is population and location specific (Nagel *et al.*, 2012).

There is no evidence in the literature that infection by microbial pathogens results in mass death of kelp 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.

*Echinus esculentus* is susceptible to 'Bald-sea-urchin disease', which causes lesions, loss of spines, tube feet, pedicellariae, destruction of the upper layer of skeletal tissue and death. It is thought to be caused by the bacteria *Vibrio anguillarum* and *Aeromonas salmonicida*. Bald sea-urchin disease was recorded from *Echinus esculentus* on the Brittany Coast. Although associated with mass mortalities of *Strongylocentrotus franciscanus* in California and *Paracentrotus lividus* in the French Mediterranean it is not known if the disease induces mass mortality (Bower, 1996).

**Sensitivity assessment.** There are no recorded mass mortalities of the characterizing species within this biotope through infection by microbial pathogens. This suggests that although the species are affected by pathogens the danger that they cause to the biotope are low, especially where certain species such as *Saccharina latissima* can self-regulate bacterial infection. Based on the available evidence the biotope is judged to have 'High' resistance and resilience that results in the biotope being classed as 'Not sensitive'.

### Removal of target species

**None**

Q: High A: Medium C: Medium

**Medium**

Q: High A: Medium C: Medium

**Medium**

Q: High A: Medium C: Medium

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, so that the impact of harvesting is localised. Mechanical harvesting of *Saccharina latissima* occurs 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 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.

Apex predators (in particular fin fish) have been overfished in UK and Irish waters for centuries. This has resulted in habitats dominated by invertebrates and commercially undesirable fish such as the lesser spotted cat shark (Molfese *et al.*, 2014). It has also caused an ecosystem level shift in the way these food webs function. The urchin barrens recorded off the coast of Norway and in the north west Atlantic are not common to UK waters. The deforestation by urchins is restricted and patchy (although some have been noted in Scotland; Smale *et al.*, 2013) but could be a result of a shift in apex predators, and a temporary more stable, less dynamic biotope.

No information could be found on the commercial harvest of *Echinus esculentus* in the British Isles. Kelly *et al.* (2001) investigated the commercial potential of *Echinus esculentus* and found that the wild capture of this urchin for commercial gain would be 'impractical economically'.

**Sensitivity assessment.** Due to the methods of harvesting used for *Saccharina latissima*, with the emphasis on aquaculture rather than wild harvesting, little evidence for the resilience of this biotope to harvesting exist. It is not though that *Echinus esculentus* is harvested in the British Isles, as wild capture is not economically viable. The removal of *Saccharina latissima* from this biotope would remove the main source of food for the other characterizing species, *Echinus esculentus*. Therefore, the removal of *Saccharina latissima* is likely to cause a loss of the biotope. Resistance is regarded as 'None' as the pressure is defined as the removal of key characterizing species from the biotope. Nevertheless, resilience is probably 'Medium', so that sensitivity to this pressure is assessed as 'Medium'.

**Removal of non-target species****Low**

Q: High A: Medium C: Medium

**Medium**

Q: High A: High C: Medium

**Medium**

Q: High A: Medium C: Medium

Direct, physical impacts from harvesting are assessed through the abrasion and penetration of the seabed pressures. The characterizing species within n this biotope could easily be incidentally removed from this biotope as by-catch when other species are being targeted. The loss of these species and other associated species would decrease species richness and negatively impact on the ecosystem function.

**Sensitivity assessment.** Removal of a large percentage of the characterizing species would alter the character of the biotope. The resistance to removal is 'Low' due to the easy accessibility of the biotopes location and the inability of these species to evade collection. The resilience is 'Medium', with recovery only being able to begin when the harvesting pressure is removed altogether. This gives an overall sensitivity score of 'Medium'.

## Bibliography

- Airoldi, L., 2000. Responses of algae with different life histories to temporal and spatial variability of disturbance in subtidal reefs. *Marine Ecology Progress Series*, **195** (8), 81-92.
- 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.
- Aronson, R.B., 1989. Brittlestar beds: low-predation anachronisms in the British Isles. *Ecology*, **70**, 856-865.
- Aronson, R.B., 1992. Biology of a scale-independent predator-prey relationship. *Marine Ecology Progress Series*, **89**, 1-13.
- Ball, B.J., Costelloe, J., Könnecker, G. & Keegan, B.F., 1995. The rocky subtidal assemblages of Kinsale Harbour (south coast of Ireland). In *Proceedings of the 28th European Marine Biology Symposium, Institute of Marine Biology of Crete, Iraklio, Crete, 1993. Biology and Ecology of Shallow Coastal Waters* (ed. A. Eleftheriou, A.D. Ansell & C.J. Smith), pp.293-302. Fredensborg: Olsen & Olsen.
- 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.
- 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.
- 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>
- Bishop, G.M. & Earll, R., 1984. Studies on the populations of *Echinus esculentus* at the St Abbs and Skomer voluntary Marine Nature Reserves. *Progress in Underwater Science*, **9**, 53-66.
- Bishop, G.M., 1985. *Aspects of the reproductive ecology of the sea urchin Echinus esculentus* L. Ph.D. thesis, University of Exeter, UK.
- Bolton, J.J. & Lüning, K.A.F., 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.
- Booolootian, R.A., 1966. *Physiology of Echinodermata*. (Ed. R.A. Booolootian), pp. 822-822. New York: John Wiley & Sons.
- 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.
- Bower, S.M., 1996. *Synopsis of Infectious Diseases and Parasites of Commercially Exploited Shellfish: Bald-sea-urchin Disease*. [On-line]. Fisheries and Oceans Canada. [cited 26/01/16]. Available from: <http://www.dfo-mpo.gc.ca/science/aah-saa/diseases-maladies/bsudsu-eng.html>
- 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.
- Bradshaw, C., Veale, L.O., Hill, A.S. & Brand, A.R., 2002. The role of scallop-dredge disturbance in long-term changes in Irish Sea benthic communities: a re-analysis of an historical dataset. *Journal of Sea Research*, **47**, 161-184.
- Bricker, S.B., Clement, C.G., Pirhalla, D.E., Orlando, S.P. & Farrow, D.R., 1999. National estuarine eutrophication assessment: effects of nutrient enrichment in the nation's estuaries. NOAA, National Ocean Service, Special Projects Office and the National Centers for Coastal Ocean Science, Silver Spring, MD, 71 pp.
- Bricker, S.B., Longstaff, B., Dennison, W., Jones, A., Boicourt, K., Wicks, C. & Woerner, J., 2008. Effects of nutrient enrichment in the nation's estuaries: a decade of change. *Harmful Algae*, **8** (1), 21-32.
- Broom, D.M., 1975. Aggregation behaviour of the brittle star *Ophiothrix fragilis*. *Journal of the Marine Biological Association of the United Kingdom*, **55**, 191-197.
- Brun, E., 1969. Aggregation of *Ophiothrix fragilis* (Abildgaard)(Echinodermata: Ophiuroidea). *Nytt Magasin Zoologi*, **17** (2), 153-160.
- 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.
- Castège, I., Milon, E. & Pautrizel, F., 2014. Response of benthic macrofauna to an oil pollution: Lessons from the "Prestige" oil spill on the rocky shore of Guéthary (south of the Bay of Biscay, France). *Deep Sea Research Part II: Topical Studies in Oceanography*, **106**, 192-197.
- Chamberlain, Y.M., 1996. Lithophylloid Corallinaceae (Rhodophycota) of the genera *Lithophyllum* and *Titauserma* from southern Africa. *Phycologia*, **35**, 204-221.
- 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/>
- Comely, C.A. & Ansell, A.D., 1988. Invertebrate associates of the sea urchin, *Echinus esculentus* L., from the Scottish west coast. *Ophelia*, **28**, 111-137.
- Comely, C.A. & Ansell, A.D., 1989. The occurrence of black necrotic disease in crab species from the west of Scotland. *Ophelia*, **30**, 95-112.
- 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., 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, D., & Gounin, F., 1995. Suspension feeding activity of a dense *Ophiothrix fragilis* (Abildgaard) population at the water-sediment interface: Time coupling of food availability and feeding behaviour of the species. *Estuarine, Coastal and Shelf Science*, **41**, 567-577.
- Davoult, D., Gounin, F. & Richard, A., 1990. Dynamique et reproduction de la population d'*Ophiothrix fragilis* (Abildgaard) du détroit du Pas de Calais (Manche orientale). *Journal of Experimental Marine Biology and Ecology*, **138**, 201-216.
- 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.
- Devlin, J. & Volsse, 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., Sivyver, 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.
- Diaz, R.J. & Rosenberg, R., 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology: an Annual Review*, **33**, 245-303.
- 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.
- Edyvean, R.G.J. & Ford, H., 1987. Growth rates of *Lithophyllum incrustans* (Corallinales, Rhodophyta) from south west Wales. *British Phycological Journal*, **22** (2), 139-146.
- Edyvean, R.G.J. & Ford, H., 1984a. Population biology of the crustose red alga *Lithophyllum incrustans* Phil. 2. A comparison of populations from three areas of Britain. *Biological Journal of the Linnean Society*, **23** (4), 353-363.
- Edyvean, R.G.J. & Ford, H., 1986. Population structure of *Lithophyllum incrustans* (Philippi) (Corallinales Rhodophyta) from south-west Wales. *Field Studies*, **6**, 397-405.
- 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.
- 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.
- Gage, J.D., 1990. Skeletal growth bands in brittle stars: Microstructure and significance as age markers. *Journal of the Marine Biological Association of the United Kingdom*, **70**, 209-224.
- Gage, J.D., 1992a. Growth bands in the sea urchin *Echinus esculentus*: results from tetracycline mark/recapture. *Journal of the Marine Biological Association of the United Kingdom*, **72**, 257-260.
- Gage, J.D., 1992b. Natural growth bands and growth variability in the sea urchin *Echinus esculentus*: results from tetracycline tagging. *Marine Biology*, **114**, 607-616.
- 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**.
- George, C.L. & Warwick, R.M., 1985. Annual macrofauna production in a hard-bottom reef community. *Journal of the Marine Biological Association of the United Kingdom*, **65**, 713-735.
- 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 longicuris* (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.
- 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.
- Gorzula, S., 1977. A study of growth in the brittle-star *Ophiocoma nigra*. *Western Naturalist*, **6**, 13-33.
- Groenewold, S. & Fonds, M., 2000. Effects on benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea. *ICES Journal of Marine Science*, **57** (5), 1395-1406.
- Gunnill, F., 1985. Population fluctuations of seven macroalgae in southern California during 1981-1983 including effects of severe storms and an El Niño. *Journal of Experimental Marine Biology and Ecology*, **85**, 149-164.
- Hall-Spencer, J.M. & Moore, P.G., 2000c. Scallop dredging has profound, long-term impacts on maerl habitats. *ICES Journal of Marine Science*, **57**, 1407-1415.
- Hansson, H., 1998. NEAT (North East Atlantic Taxa): South Scandinavian marine Echinodermata Check-List. *Tjärnö Marine Biological Association* [On-line] [cited 26/01/16]. Available from: [http://www.tmbi.gu.se/libdb/taxon/neat\\_pdf/NEAT\\*Echinodermata.pdf](http://www.tmbi.gu.se/libdb/taxon/neat_pdf/NEAT*Echinodermata.pdf)
- Hayward, P.J. & Ryland, J.S. (ed.) 1995b. *Handbook of the marine fauna of North-West Europe*. Oxford: Oxford University Press.
- 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.
- Herreid, C.F., 1980. Hypoxia in invertebrates. *Comparative Biochemistry and Physiology Part A: Physiology*, **67** (3), 311-320.
- Hill, J.M., 2001. *Ophiothrix fragilis* and/or *Ophiocoma nigra* beds on slightly tide-swept circalittoral rock or mixed substrata. In *Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme* [on-line], 2014 Plymouth: Marine Biological Association of the United Kingdom.
- Hily, C., 1991. Is the activity of benthic suspension feeders a factor controlling water quality in the Bay of Brest? *Marine Ecology Progress Series*, **69**, 179-188.
- Hiscock, K., 1983. Water movement. In *Sublittoral ecology. The ecology of shallow sublittoral benthos* (ed. R. Earll & D.G. Erwin), pp. 58-96. Oxford: Clarendon Press.
- Hobson, A., 1930. Regeneration of the Spines in Sea-Urchins. *Nature*, **125**, 168.
- Holme, N.A., 1984. Fluctuations of *Ophiothrix fragilis* in the western English Channel. *Journal of the Marine Biological Association of the United Kingdom*, **64**, 351-378.
- Hughes, D.J., 1998b. Subtidal brittlestar beds. An overview of dynamics and sensitivity characteristics for conservation management of marine SACs. *Natura 2000 report prepared for Scottish Association of Marine Science (SAMS) for the UK Marine SACs Project.*, Scottish Association for Marine Science. (UK Marine SACs Project, Vol. 3). Available from: <http://www.ukmarinesac.org.uk/pdfs/britstar.pdf>
- 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.
- Jenkins, S.R., Beukers-Stewart, B.D. & Brand, A.R., 2001. Impact of scallop dredging on benthic megafauna: a comparison of

- damage levels in captured and non-captured organisms. *Marine Ecology Progress Series*, **215**, 297-301.
- Jennings, S. & Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. *Advances in Marine Biology*, **34**, 201-352.
- 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.
- Johnston, E.L. & Roberts, D.A., 2009. Contaminants reduce the richness and evenness of marine communities: a review and meta-analysis. *Environmental Pollution*, **157** (6), 1745-1752.
- Jones, L.A., Hiscock, K. & Connor, D.W., 2000. Marine habitat reviews. A summary of ecological requirements and sensitivity characteristics for the conservation and management of marine SACs. *Joint Nature Conservation Committee, Peterborough. (UK Marine SACs Project report.)*. Available from: <http://www.ukmarinesac.org.uk/pdfs/marine-habitats-review.pdf>
- 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., 1975b. The biology of *Laminaria hyperborea* VII Reproduction of the sporophyte. *Journal of the Marine Biological Association of the United Kingdom*, **55**, 567-582.
- Kain, J.M., 1979. A view of the genus *Laminaria*. *Oceanography and Marine Biology: an Annual Review*, **17**, 101-161.
- Kaiser, M.J., Ramsay, K., Richardson, C.A., Spence, F.E. & Brand, A.R., 2000. Chronic fishing disturbance has changed shelf sea benthic community structure. *Journal of Animal Ecology*, **69**, 494-503.
- Karsten, U., 2007. Research note: salinity tolerance of Arctic kelps from Spitsbergen. *Phycological Research*, **55** (4), 257-262.
- Kelly, M., Owen, P. & Pantazis, P., 2001. The commercial potential of the common sea urchin *Echinus esculentus* from the west coast of Scotland. *Hydrobiologia*, **465** (1-3), 85-94.
- 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.
- Lüning, K., 1979. Growth strategy of three *Laminaria* species (Phaeophyceae) inhabiting different depth zones in the sublittoral region of Helgoland (North Sea). *Marine Ecological Progress Series*, **1**, 195-207.
- 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.
- Lawrence, J.M., 1975. On the relationships between marine plants and sea urchins. *Oceanography and Marine Biology: An Annual Review*, **13**, 213-286.
- 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.
- Leewis, R.J., Waardenburg, H.W. & van der Tol, M.W.M., 1994. Biomass and standing stock on sublittoral hard substrates in the Oosterschelde estuary (SW Netherlands). *Hydrobiologia*, **282/283**, 397-412.
- 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., 1979a. Colonization of an artificial reef by the sea-urchin *Echinus esculentus*. *Progress in Underwater Science*, **4**, 189-195.
- 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.
- Lüning, K., 1990. *Seaweeds: their environment, biogeography, and ecophysiology*: John Wiley & Sons.
- 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., 1988. Photoperiodic control of sorus formation in the brown alga *Laminaria saccharina*. *Marine Ecology Progress Series*,

45, 137-144.

Lynby, J.E. & Mortensen, S.M., 1996. Effects of dredging activities on growth of *Laminaria saccharina*. *Marine Ecology, Pubblicazioni 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.

MacBride, E.W., 1914. *Textbook of Embryology, Vol. I, Invertebrata*. London: MacMillan & Co.

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.

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).

Moore, P.G., 1977a. Inorganic particulate suspensions in the sea and their effects on marine animals. *Oceanography and Marine Biology: An Annual Review*, **15**, 225-363.

Morton, B., 1977. The tidal rhythm of feeding and digestion in the Pacific oyster, *Crassostrea gigas* (Thunberg). *Journal of Experimental Marine Biology and Ecology*, **26** (2), 135-151.

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).

Newton, L.C. & McKenzie, J.D., 1995. Echinoderms and oil pollution: a potential stress assay using bacterial symbionts. *Marine Pollution Bulletin*, **31**, 453-456.

Nichols, D., 1979. A nationwide survey of the British Sea Urchin *Echinus esculentus*. *Progress in Underwater Science*, **4**, 161-187.

Nichols, D., 1984. An investigation of the population dynamics of the common edible sea urchin (*Echinus esculentus* L.) in relation to species conservation management. *Report to Department of the Environment and Nature Conservancy Council from the Department of Biological Sciences, University of Exeter*.

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.

Pagett, R.M., 1981. The penetration of brackish-water by the Echinodermata. In *Feeding and Survival Strategies of Estuarine Organisms* (ed. N.V. Jones & W.J. Wolff), **15**, 135-151. New York: Plenum Press.

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 Pêches 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.

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., Isaksson, I., Wennhage, H. & Moksnes, P.-O., 1995. Recent increase of filamentous algae in shallow Swedish bays: effects on the community structure of epibenthic fauna and fish. *Netherlands Journal of Aquatic Ecology*, **29** (3-4), 349-358.

Pihl, L., Wennhage, H. & Nilsson, S., 1994. Fish assemblage structure in relation to macrophytes and filamentous epiphytes in shallow non-tidal rocky-and soft-bottom habitats. *Environmental Biology of Fishes*, **39** (3), 271-288.

Pingree, R.D. & Maddock, L., 1977. Tidal residuals in the English Channel *Journal of the Marine Biological Association of the United*

Kingdom, **57**, 339-354.

Raymont, J.E.G., 1950. A fish cultivation experiment in an arm of a sea loch. IV. The bottom fauna of Kyle Scotnish. *Proceedings of the Royal Society of Edinburgh (B)*, **64**, 65-108.

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

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.

Rosenberg, R., Hellman, B. & Johansson, B., 1991. Hypoxic tolerance of marine benthic fauna. *Marine Ecology Progress Series*, **79**, 127-131.

Russell, M., 2013. Echinoderm Responses to Variation in Salinity. *Advances in Marine Biology*, **66**, 171-212.

Saier, B. & Chapman, A.S., 2004. Crusts of the alien bryozoan *Membranipora membranacea* can negatively impact spore output from native kelps (*Laminaria longicuris*). *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.

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.

Sherk Jr, J.A. & Cronin, L.E., 1970. The effects of suspended and deposited sediments on estuarine organisms. *Literature summary and research needs, Contr. 443*, Natural Resources Institute, University of Maryland.

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

Sköld, M., 1998. Escape responses in four epibenthic brittle stars (Ophiuroidea: Echinodermata). *Ophelia*, **49**, 163-179.

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.

Smith, J., 1940. The reproductive system and associated organs of the brittle-star *Ophiothrix fragilis*. *Quarterly Journal of Microscopical Science*, **82**, 267-309.

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.

Stachowitsch, M., 1984. Mass mortality in the Gulf of Trieste: the course of community destruction. *Marine Ecology, Pubblicazione della Stazione Zoologica di Napoli*, **5**, 243-264.

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.

Stickle, W.B. & Diehl, W.J., 1987. Effects of salinity on echinoderms. In *Echinoderm Studies, Vol. 2* (ed. M. Jangoux & J.M. Lawrence), pp. 235-285. A.A. Balkema: Rotterdam.

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.

Taylor, A., 1958. Studies on the biology of the offshore species of Manx Ophiuroidea. Master of Science-thesis. University of Liverpool. Marine Biological Station. Port Erin. Isle of Man, 59.

Tillin, H. & Tyler-Walters, H., 2014. Assessing the sensitivity of subtidal sedimentary habitats to pressures associated with marine activities. Phase 2 Report – Literature review and sensitivity assessments for ecological groups for circalittoral and offshore Level 5 biotopes. *JNCC Report No. 512B*, 260 pp. Available from: [www.marlin.ac.uk/publications](http://www.marlin.ac.uk/publications)

Tyler, P.A. & Young, C.M., 1998. Temperature and pressures tolerances in dispersal stages of the genus *Echinus* (Echinodermata: Echinoidea): prerequisites for deep sea invasion and speciation. *Deep Sea Research II*, **45**, 253-277

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](http://www.marlin.ac.uk/publications)

Ursin, E., 1960. A quantitative investigation of the echinoderm fauna of the central North Sea. *Meddelelser fra Danmark Fiskeri-og-Havundersogelser*, **2** (24), pp. 204.

- 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.
- Veale, L.O., Hill, A.S., Hawkins, S.J. & Brand, A.R., 2000. Effects of long term physical disturbance by scallop fishing on subtidal epifaunal assemblages and habitats. *Marine Biology*, **137**, 325-337.
- 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.
- Warner, G.F. & Woodley, J.D., 1975. Suspension feeding in the brittle star *Ophiothrix fragilis*. *Journal of the Marine Biological Association of the United Kingdom*, **55**, 199-210.
- Warner, G.F., 1971. On the ecology of a dense bed of the brittle star *Ophiothrix fragilis*. *Journal of the Marine Biological Association of the United Kingdom*, **51**, 267-282.
- 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 Simplicies section of *Laminaria*. *Bot. gothoburg.*, **3**, 247-256.
- Wolff, W.J., 1968. The Echinodermata of the estuarine region of the rivers Rhine, Meuse and Scheldt, with a list of species occurring in the coastal waters of the Netherlands. *The Netherlands Journal of Sea Research*, **4**, 59-85.
- Yarish, C., Penniman, C.A. & Egan, B., 1990. Growth and reproductive responses of *Laminaria longicuris* (*Laminariales*, *Phaeophyta*) to nutrient enrichment. *Hydrobiologia*, **204**, 505-511.