

MarLIN Marine Information Network

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

Laminaria digitata and under-boulder fauna on sublittoral fringe boulders

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

Dr Heidi Tillin & Tom Stamp

2016-07-01

A report from: The Marine Life Information Network, Marine Biological Association of the United Kingdom.

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/97]. All terms and the MarESA methodology are outlined on the website (https://www.marlin.ac.uk)

This review can be cited as:

Tillin, H.M. & Stamp, T. 2016. [Laminaria digitata] and under-boulder fauna on sublittoral fringe boulders. In Tyler-Walters H. and Hiscock K. (eds) *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. DOI https://dx.doi.org/10.17031/marlinhab.97.1



The information (TEXT ONLY) provided by the Marine Life Information Network (MarLIN) is licensed under a Creative Commons Attribution-Non-Commercial-Share Alike 2.0 UK: England & Wales License. Note that images and other media featured on this page are each governed by their own terms and conditions and they may or may not be available for reuse. Permissions beyond the scope of this license are available here. Based on a work at www.marlin.ac.uk



(page left blank)



Biotope distribution data provided by **EMODnet Seabed Habitats** (www.emodnet-seabedhabitats.eu)

Researched by Dr Heidi Tillin & Tom Stamp

Refereed by Admin

Summary

UK and Ireland classification

EUNIS 2008	A3.2112	<i>Laminaria digitata</i> and under-boulder fauna on sublittoral fringe boulders
JNCC 2015	IR.MIR.KR.Ldig.Bo	<i>Laminaria digitata</i> and under-boulder fauna on sublittoral fringe boulders
JNCC 2004	IR.MIR.KR.Ldig.Bo	<i>Laminaria digitata</i> and under-boulder fauna on sublittoral fringe boulders
1997 Biotope	IR.MIR.KR.Ldig.Ldig.Bo	<i>Laminaria digitata</i> and under-boulder fauna on sublittoral fringe boulders

Description

This Laminaria digitata biotope is found on moderately exposed to sheltered boulder shores. Upper surfaces of the boulders are similar to MIR.Ldig.Ldig and are colonized by dense Laminaria digitata,

beneath which are a variety of red seaweeds including *Mastocarpus stellatus*, *Lomentaria articulata*, *Osmundea* (*Laurencia*) *pinnatifida* and *Corallina officinalis*. Where space is available beneath the boulders there may be a rich assemblage of animals. Characteristic species include the hairy porcelain crab *Porcellana platycheles*, the smooth porcelain crab *Pisidia longicornis* and juvenile edible crabs *Cancer pagurus*. Also present beneath the boulders are often high densities of the barnacle *Balanus crenatus*, the keel worm *Spirobranchus* spp., spirorbid worms, gammarid amphipods and a few small gastropods and mussels. The encrusting bryozoans *Umbonula littoralis* and *Schizoporella unicornis* and encrusting colonies of the sponges *Hymeniacidon perleve* and *Halichondria panicea* are also typical of this habitat. The richest examples also contain a variety of brittlestars, ascidians and small hydroids (JNCC, 2015).

↓ Depth range

Lower shore, 0-5 m

Additional information

-

Listed By

- none -

% Further information sources

Search on:



Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

The biotope description and information on characteristic features is taken from Connor *et al.* (2004). The upper surfaces of the boulders are colonized by *Laminaria digitata* although other kelp species or *Fucus serratus* may be present. biotopes. Surfaces below the kelp canopy are colonized by a variety of foliose red seaweeds, including *Mastocarpus stellatus*, *Palmaria palmata* and *Chondrus crispus*. Coralline algae such as *Corallina officinalis* and coralline crusts, as well as the green seaweed *Ulva lactuca*. The characterizing species define the biotope and provide complex habitats that shelter species and modify environmental conditions. The loss of the characterizing algal species, in particular *Laminaria digitata*, could lead to reclassification of the biotope, hence the sensitivity assessments focus on these species.

The species composition underneath the boulders varies considerably depending on the underlying substratum. On muddy shores, the fauna living under the boulders may be limited to a few infaunal species. Where more space is available beneath the boulders there may be a rich assemblage of animals. Also present on and beneath the boulders are the tube-forming polychaete *Spirobranchus triqueter*, spirorbid polychaetes and the topshell *Gibbula cineraria*. Encrusting colonies of the sponge *Halichondria panicea* are also typical of the undersides of boulders.

Resilience and recovery rates of habitat

No evidence for recovery rates of this specific biotope were found. The algae within the biotope can regrow damaged fronds and blades and may regrow from perennial holdfasts or crustose bases, where these remain. Where populations of animals and macroalgae are entirely removed (resistance is none) recovery will require recolonization by propagules. Adults of the mobile species present in the biotope, such as the crabs and the topshell *Gibbula cineraria* that are present under the boulders may recolonize through adult migration into the habitat from adjacent populations following disturbance or via larval recolonization. In general, the animals within the biotope, such as the barnacles and tube worms, produce high numbers of pelagic larvae which are widely distributed by water currents, supporting recolonization from surrounding populations following disturbances. Conversely, the characterizing red and brown macroalgae generally produce eggs which sink rapidly to the substratum in the vicinity of the adult plants and dispersal distances are short (Dudgeon *et al.*, 2001). Recovery of algal populations may be rapid where adults remain but prolonged where populations are entirely removed.

The available evidence indicates that the recovery of kelp biotopes, where kelp have been entirely removed, requires at least two years. Re-colonization of concrete blocks by *Laminaria digitata* was investigated by Kain (1975a) at Port Erin, Isle of Man. *Laminaria digitata* was considered re-established two years after removal, with the characterizing red foliose algae following one year later. Similarly, recovery after simulated harvesting of a standing crop of *Laminaria digitata* occurred within 18-20 months (Kain, 1979). While colonization of young *Laminaria* sporophytes may occur one year after initial substratum clearance (Kain 1979), the return of the biotope to its original mature condition is likely to lag behind this recolonization. These findings agree with previous studies which showed that when 60% of sporophytes (adult alga) were removed from a location, 18 months were required for the stand to rejuvenate (Perez, 1971), while in France, CIAM (Le Comité interprofessionel des algues marines) proposed that, regardless of collection method, the restoration of stands of laminarians took up to 18 months post harvesting (Arzel, 1998). Some disparities between reported recovery rates do exist, with cleared

plots in Helgoland taking 25 months, probably because plots were burned to ensure total removal of spores and germlings (Markham & Munda, 1980). Even after 25 months, although macroalgal density had returned to pre-clearance levels, the *Laminaria digitata* were smaller than those on undisturbed plots, suggesting full recovery needs longer than 25 months (Markham & Munda, 1980).

The seasonal timing of macroalgal removal impacts recovery rates. Engelen et al. (2011) showed that removal of 0.25 m¹ areas of Laminaria digitata forest in the spring and autumn had different recovery rates, with autumn recovery more rapid than spring (taking a minimum of 12 months). Return to conditions prior to removal took 18-24 months, with competition for space by Saccorhiza polyschides impacting recovery rates in the first year of recolonization (Engelen et al., 2011). The growth rate of Laminaria digitata changes with the seasons. Growth is rapid from February to July, slower in August to January, and occurs diffusely in the blade (Kain, 1979). This diffuse growth may enhance its resistance to potential grazers. Spores are produced at temperatures lower than 18°C with a minimum of 10 weeks a year between 5-18°C needed to ensure spore formation (Bartsch et al., 2013). Thus temperature and, by default, season impacts the level of reproductive activity. In order to maximize survival rates of mature gametophytes, gametophyte development can be delayed by the algae until optimum conditions return and the gametophyte produces gametes (Van den Hoek et al., 1995), which suggests a degree of resistance to short-term changes in temperature which may be anthropogenic in origin. However, seaweeds have been cited as being particularly sensitive to short-term warming events (Dayton & Tegner, 1984; Smale & Wernberg, 2013; Wernberg et al., 2013; Smale et al., 2013).

The red algae have complex life histories and exhibit distinct morphological stages over the reproductive life history. Alternation occurs between asexual spore producing stages (tetrasporophytes) and male and female plants producing sexually. In habitats where conditions are unfavourable e.g. low salinity habitats, asexual reproduction may maintain populations by retaining genotypes that have evolved to tolerate the prevailing habitat conditions. Life history stages can be morphologically different or very similar. The tetrasporophyte phase of Mastocarpus stellatus is known as the petrocelis and is a flat crust, capable of growing laterally and covering extensive areas. The gametophytes and tetrasporophytes of Chondrus crispus are relatively similar; the holdfasts of individual Chondrus crispus can coalesce over time and can form an extensive crust on rock (Taylor et al., 1981). Other red algae found within the biotope also have life stages that include prostrate creeping bases e.g. encrusting corallines, whereas in other species such as Palmaria palmata, the thallus or fronds arise from a small discoid holdfast. The basal crusts and crustose tetrasporophytes are perennial, tough, resistant stages that may prevent other species from occupying the rock surface and allow rapid regeneration. They may therefore provide a significant recovery mechanism. Osmundea pinnatifida turfs may also expand vegetatively where upright fronds bend over, produce rhizoids and colonize adjacent areas of bare rock by acting as stolons (Godin, 1981).

Where holdfasts and basal crusts of red algae are removed, recovery will depend on recolonization via spores. Norton (1992) reviewed dispersal by macroalgae and concluded that dispersal potential is highly variable, recruitment usually occurs on a much more local scale, typically within 10 m of the parent plant. Hence, it is expected that the algal turf would normally rely on recruitment from local individuals and that recovery of populations via spore settlement, where adults are removed, could be protracted. Minchinton *et al.* (1997) documented the recovery of *Chondrus crispus* after a rocky shore in Nova Scotia, Canada, was totally denuded by an ice scouring event. Initial recolonization was dominated by diatoms and ephemeral macroalgae, followed by fucoids and then perennial red seaweeds. After 2 years, *Chondrus crispus* had re-

established approximately 50% cover on the lower shore and after 5 years it was the dominant macroalga at this height, with approximately 100% cover. Other red algal species may colonize and spread more slowly. Observed expansion rates of *Osmundea pinnatifida* turfs are very low: 0.015 mm/month in limpet exclusion areas and 0.003 mm/month with limpets (Prathep, 2001).

Corallina officinalis was shown to settle on artificial substances within 1 week of their placement in the intertidal in New England summer (Harlin & Lindbergh, 1977). However, settlement plates laid out in the autumn were not recolonized until the next spring. In the lower rocky intertidal in southern California dominated by *Corallina officinalis* with foliose overstorey algae present, Littler & Kauker (1984) experimentally cleared plots and followed the recovery for 12 months. Some areas were scraped allowing the basal crusts to remain whereas others were completely sterilized (removal of all material and surfaces then scorched with a blow torch to remove bases). In scraped plots up to 15% cover of *Corallina officinalis* fronds returned within 3 months after removal of fronds and all other epiflora/fauna (Littler & Kauker, 1984), while in sterilized plots (all basal crusts removed) appearance of articulated fronds occurred 6 months following clearance. At the end of the 12 month observation period *Corallina officinalis* cover had increased to approximately 18% in plots where basal crusts remained and to approximately 10% in sterilized plots. Similarly, Bamber & Irving (1993) reported that new plants grew back in scraped transects within 12 months, although the resistant crustose bases were probably not removed.

Coralline crust is a generic term that in UK biotopes refers to nongeniculate (crustose) species from the family Corallinacea that could include Lithophyllum incrustans which is noted to form thick crusts in tidepools, especially in the south west (Adey & Adey, 1973). Although ubiquitous in marine coastal systems, little is understood about the taxonomy, biology and ecology of this taxa (Littler & Littler, 2013). Throughout the sensitivity assessments the term coralline crust is used to refer to the Corallinacea that occur within the biotope. Due to the lack of evidence for species the assessments are generic, although species specific information is presented where available. A number of papers by Edyvean & Ford (1984a & b, 1986, 1987) describe aspects of reproduction and growth of encrusting coralline, Lithophyllum incrustans. Studies by Edyvean & Forde (1987) on populations of Lithophyllum incrustans in Pembroke, south-west Wales, suggest that reproduction occurs on average early in the third year. Reproduction may be sexual or asexual. Populations release spores throughout the year but spore abundance varies seasonally. Spore survival is extremely low with only a tiny proportion of spores eventually recruiting to the adult population (Edyvean & Ford, 1986). Edyvean & Ford (1984a) found that the age structure of populations sampled from Orkney (Scotland), Berwick (northern England) and Devon (England) were similar. Mortality seemed highest in younger year classes with surviving individuals after the age of 10 years appear relatively long-lived (up to 30 years). In St Mary's, Northumberland, the population was dominated by the age 6-7 year classes (Edyvean & Ford, 1984a). Growth rates were highest in young plants measured at Pembroke (south-west Wales) with an approximate increase in diameter of plants of 24 mm in year class 0 and 155 mm in year 1 and slowing towards an annual average horizontal growth rate of 3 mm/year (Edyvean & Ford, 1987). Some repair of damaged encrusting coralline occurs through vegetative growth. Chamberlain (1996) observed that although Lithophyllum incrustans was quickly affected by oil during the Sea Empress spill, recovery occurred within about a year. The oil was found to have destroyed about one third of the thallus thickness but regeneration occurred from thallus filaments below the damaged area. Recolonization by propagules is an important recovery mechanism, Airoldi (2000) observed that encrusting coralline algae recruited rapidly on to experimentally cleared subtidal rock surfaces in the Mediterranean Sea, reaching up to 68% cover in 2 months. As encrusting corallines are sensitive to desiccation (Dethier, 1994) it should be noted that these subtidal habitats are probably more favourable for recruitment, growth and survival than intertidal rock pools.

The green algae associated with this biotope are classified as opportunistic species that are able to rapidly colonize newly created gaps across a range of sediment types, shore heights, wave exposures and salinity regimes. *Ulva* sp. release zoospores and gametes (collectively called swarmers) to the water column in high numbers during extended reproduction periods (Smith, 1947). Swarmers are capable of dispersal over a considerable distance, for instance, Amsler & Searles (1980) showed that swarmers of a coastal population of *Ulva* (as *Enteromorpha*) reached exposed artificial substrata on a submarine plateau 35 km away. *Ulva intestinalis* is amongst the first multicellular algae to appear on substrata that have been cleared following a disturbance after the *Torrey Canyon* oil spill in March 1967, species of the genus *Ulva* rapidly recruited to areas where oil had killed the herbivores that usually grazed on them, so that a rapid greening of the rocks (owing to a thick coating of *Ulva* spp.) was apparent by mid-May (Smith, 1968).

Gibbula cineraria, is a fast growing species with a short lifespan (Schöne *et al.*, 2007) and pelagic dispersal stages (Underwood, 1972) and is considered to recover quickly (resilience is 'High' through migration from adjacent habitats and larval recolonization from any level of impact). Recovery of the tubeworms, encrusting bryozoans and barnacles, is likely to be rapid as these are good initial colonizers of hard substrata, capable of rapid growth and reproduction (r-selected) and adapted to ephemeral habitats.

Red algae that form turfs, especially Corallina officinalis, are often highly resilient to disturbance, and can recover and reach greater abundance compared to prior disturbance conditions (Bulleri et al., 2002; Bertocci et al., 2010). Turf algae can then prevent recovery of fucoids and other species by inhibiting recruitment. Mrowicki et al. (2014) found that limpet and barnacle removal allowed ephemeral and fucoid macroalgae to establish on sheltered and wave exposed shores in Ireland. Experimental studies have shown that limpets and other grazers control the development of macroalgae by consuming microscopic phases (Jenkins et al., 2005) or the adult stages (Davies et al., 2007) and can therefore structure biotopes through feeding preferences (Underwood, 1980; Hawkins & Hartnoll, 1985). Exclusion of grazing limpets on shores in southern Britain (Swanage and Heybrook), led to the colonization of red algal turfs by *Himanthalia elongata* and *Fucus serratus* within 2 years (Boaventura et al., 2002). MacFarlane (1952) also recorded a shift to a Corallina officinalis and encrusting coralline biotope following over raking (for harvesting) of Chondrus crispus turf, in these areas gastropods had increased in abundance and prevented the recovery of Chondrus crispus by grazing. A change in the abundance of Patella vulgata or other grazers could therefore prevent or alter the recovery of this biotope. Opportunistic ephemeral green algae such as Ulva sp. can rapidly colonize gaps. These green ephemeral algae are major competitors of Fucus serratus for space colonization and nutrient uptake. Blooms of ephemeral algae facilitated by disturbance, particularly where grazers are removed may then slow the development of longerlived perennial algae, especially fucoids. On the wave exposed and scoured shores that this biotope occurs on, grazing may limit initial settlement of macroalgae but wave action will limit the presence of adults and larger species through breakage and drag effects leading to loss. Limpets and littorinids may enhance barnacle settlement by grazing and removing algae (Hawkins, 1983) or by depositing pedal mucus trails that attract barnacle larvae (Holmes et al., 2005). Barnacles may enhance survival of small limpets by moderating environmental stresses but they may also have negative effects on recruitment by occupying space and by limiting access to grazing areas (Lewis & Bowman, 1975).

Resilience assessment. Evidence from Engelen *et al.* (2011) indicated that complete recovery of *Laminaria digitata* and its associated epibiota occurs 18-24 month after complete removal of *Laminaria digitata*. Smith (1985) also suggested 24 months for the recovery of a *Laminaria*

digitata bed. Experimental evidence (Kain, 1975a, 1979; Markham & Munda, 1980) indicates that recovery where the entire community is removed (e.g. where resistance is 'None') may take longer, so that resilience is assessed as 'Medium'. Where the holdfasts and/or basal crusts of red algae remain in place then recovery by vegetative growth is likely to be rapid, although complete removal of a bed would take longer due to poor dispersal. The recovery assessments for kelp are therefore also considered applicable to the red algal turf. Recovery rates of red algae will be greatly influenced by whether the crust or holdfasts remain from which the thalli can regrow. Where the bases remain and resistance is assessed as 'Medium' (loss of <25% of individuals or cover) then recovery is assessed as 'Low' or 'None' and a high proportion of bases are lost then recovery may be more protracted. Based on recovery from ice scour (Minchinton *et al.*, 1997) recovery is assessed as 'Medium' (2-10 years). As recovery, where turfs are removed over large areas, will depend on the supply of propagules from neighbouring populations and as dispersal is limited, the recovery will depend on the supply of propagules which will be influenced site-specific factors, particularly local water transport.

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

stance Resil	ience S	Sensitivity
A: High C: High Q: High	A: High C: High	<mark>Not sensitive</mark> 2: High A: High C: High
	stance Resil High n A: High C: High Q: High	stance Resilience S High n A: High C: High Q: High A: High C: High C

Species found in the intertidal are exposed to extremes of high and low air temperatures during periods of emersion. They must also be able to cope with sharp temperature fluctuations over a short period of time during the tidal cycle. In winter, air temperatures are colder than the sea, conversely in summer air temperatures are much warmer than the sea. Species that occur in this intertidal biotope are therefore generally adapted to tolerate a range of temperatures, although the timing of site-specific factors such as low tides will influence local acclimation. For intertidal species, increased temperatures may also result in desiccation when exposed (see changes in emergence pressure). Local populations may be acclimated to the prevailing temperature regime and may, therefore, exhibit different tolerances to other populations subject to different conditions and therefore caution should be used when inferring tolerances from populations in different regions.

Laminaria digitata is distributed from Brittany to the coast of Norway, while its UK distribution encompasses the whole of the UK coast (Blight & Thompson, 2008). Its distribution suggests that the species would tolerate chronic temperature change (e.g. by 2°C for a year). However, local populations may have acclimatized to local physical conditions meaning that populations at the

extremes of the species' range are less comparable than those populations in the middle of its range. Additionally, the distribution data of this species suggests it is a northern species, as such it will be vulnerable to increases in temperature and may be out-competed at its southern limits by other kelp species.

The thermal optimum of *Laminaria digitata* is between 10-15°C, with reproductive ability impaired to 20% at 18°C (Arzel, 1998). Therefore, while the current population may not be affected, recruitment may be reduced. Spore production only occurs between 5-10°C and is the most temperature sensitive stage of reproduction in *Laminaria digitata*. Outside this temperature range, reproduction is severely reduced and the species is at risk from local extinction in the long-term. In addition, a temperature increase to 22-23°C causes cell damage and death (Sundene, 1964; Bolton & Lüning, 1982). The sensitivity of this species, therefore, relies on the current sea temperatures of the specific location (Bartsch *et al.*, 2013). A minimum of 10 weeks a year between 5-18°C is needed in order to ensure spore formation and hence reproduction (Bartsch *et al.*, 2013).

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

Littler & Kauker (1984) suggested that the crustose bases of *Corallina officinalis* are more resistant of desiccation or heating than fronds. Lüning (1990) reported that *Corallina officinalis* from Helgoland survived one week exposure to temperatures between 0°C and 28°C. Latham (2008) investigated the effects of temperature stress on *Corallina officinalis* through laboratory tests on samples collected in the autumn in Devon, (England) from rockpools. Samples were kept at 15°C for three days and then exposed to temperatures of 5°C, 15°C, 20°C, 25°C and 30°C (the normal range of temperature experienced was suggested to be between 5 and 15°C). At 35°C the *Corallina* was completely bleached after 3 days with a sample kept at 30°C beginning to bleach. After 7 days (the end of the experiment) the sample kept at 30°C was partially bleached. Samples kept at 5, 15, 20 and 25°C showed little change in chemicals produced in reaction to thermal stress and no bleaching suggesting the temperatures in that range had not induced stress reactions. Fronds of *Osmundea pinnatifida* bleach and die-back in summer, while the crustose holdfasts remain, suggesting that, as for *Corallina officinalis*, the bases are more resistant. The factors responsible for the die-back are a combination of temperature (Flores-Maya *et al.*, 1992, abstract only) desiccation and irradiance (Prathep, 2001).

In an exceptionally hot summer (1983, with an increase of between 4.8 and 8.5°C), Hawkins & Hartnoll (1985) observed no temperature bleaching of adult *Himanthalia elongata* (although some buttons were bleached) or other canopy forming species. However, understorey red algae showed more signs of damage with bleached *Corallina officinalis* observed around the edges of pools due to desiccation. Occasional damaged specimens of *Palmaria palmata*, *Osmundea pinnatifida* and *Mastocarpus stellatus* were observed. *Palmaria palmata* does well in low temperatures, with an optimum between 6 and 15°C, consistent with a distribution in northern temperate and arctic waters. This species is also found in warmer temperate waters as far south as

Portugal in Europe and with localized large populations in northern Spain (Garbary *et al.*, 2012 and references therein). Temperatures at or above 15°C may induce physiological stress (Werner & Dring, 2011; Morgan *et al.*, 1980). In tank cultures of *Palmaria palmata* at 20°C and above, all plants were dead within a week (Morgan *et al.*, 1980). Populations may be acclimated to typical conditions but it is likely that *Palmaria palmata* may be bleached or damaged by higher than usual temperatures.

Ulva spp. are characteristic of upper shore rock pools, where water and air temperatures are greatly elevated on hot days. Empirical evidence for thermal tolerance to anthropogenic increases in temperature is provided by the effects of heated effluents on rocky shore communities in Maine, USA. Ascophyllum and Fucus were eliminated from a rocky shore heated to 27-30°C by a power station whilst *Ulva intestinalis* (as *Enteromorpha intestinalis*) increased significantly near the outfall (Vadas *et al.*, 1976).

Sensitivity assessment. *Laminaria digitata* is likely to withstand an increase in temperature at the benchmark level, some of the understorey of red algae, such as *Palmaria palmata* may be lost during acute temperature increases if these occur in the summer when plants are already close to the limit of thermal tolerances. Biotope resistance is assessed as 'High' and resilience as 'High' and the biotope is considered to be 'Not sensitive'. It should be noted that the timing of acute and chronic increases would alter the degree of impact and hence sensitivity. An acute change occurring on the hottest days of the year and exceeding thermal tolerances may lead to mortality.

Temperature decreaseHigh(local)Q: High A: High C: High

igh Q: High A: High C: High

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

Many intertidal species are tolerant of freezing conditions as they are exposed to extremes of low air temperatures during periods of emersion. They must also be able to cope with sharp temperature fluctuations over a short period of time during the tidal cycle. In winter, air temperatures are colder than the sea, conversely in summer air temperatures are much warmer than the sea. Species that occur in the intertidal are therefore generally adapted to tolerate a range of temperatures, with the width of the thermal niche positively correlated with the height of the shore (Davenport & Davenport, 2005). Local populations may be acclimated to the prevailing temperature regime and may therefore exhibit different tolerances to other populations subject to different salinity conditions and therefore caution should be used when inferring tolerances from populations in different regions.

The thermal optimum of *Laminaria digitata* is between 10-15°C, with reproductive ability impaired to 20% at 18°C (Arzel, 1998). Therefore while the current population may not be affected, recruitment may be reduced. Spore production only occurs between 5-10°C and is the most temperature sensitive stage of reproduction in *Laminaria digitata*. Outside this temperature range, reproduction is severely reduced and the species is at risk from local extinction in the short-term. In additional, a temperature increase to 22-23°C causes cell damage and death (Sundene, 1964; Bolton & Lüning, 1982). During an exceptionally warm summer in Norway, Sundene (1964) reported the destruction of *Laminaria digitata* plants exposed to temperatures of 22-23°C. The sensitivity of this species, therefore, relies on the current sea temperatures of the specific location (Bartsch *et al.*, 2013). A minimum of 10 weeks a year between 5-18°C is needed in order to ensure spore formation and hence reproduction (Bartsch *et al.*, 2013).

Lüning (1990) reported that *Corallina officinalis* from Helgoland survived 0°C when exposed for one week. New Zealand specimens were found to tolerate -4°C (Frazer *et al.*, 1988). Lüning (1990)

suggested that most littoral algal species were tolerant of cold and freezing. The associated species *Mastocarpus stellatus* has a broad geographical distribution (Guiry & Guiry, 2015) and throughout its range experiences wide variation in temperatures (although local populations may be acclimated to the prevailing thermal regime). The photosynthetic rate of *Mastocarpus stellatus* higher on the shore fully recovered from 24 hrs at -20°C (Dudgeon *et al.*, 1989). Photosynthesis in *Mastocarpus stellatus* also recovered quickly after experimental freezing (Dudgeon *et al.*, 1989, 1995). *Palmaria palmata* does well in low temperatures, with an optimum between 6 and 15°C, consistent with a distribution in northern temperate and arctic waters. In the laboratory, plants only became fertile if left at temperatures between 5-7°C with a short light period (Van der Meer & Chen, 1979). Acute or chronic changes in temperature below 5°C may, therefore, reduce reproductive success although reproduction and vegetative growth in warmer months should compensate for any reduction in output. The green algae, *Ulva* spp. are eurytopic, found in a wide temperature range and in areas which frequently experience freezing conditions and are vulnerable to ice scour (Seed & Suchanek, 1992).

Sensitivity assessment. The dominant kelp *Laminaria digitata* is thought to be a northern species and likely to retreat north as a result of climate change. Therefore, it is unlikely to be sensitive to a reduction in temperature at the benchmark level. Based on the characterizing and associated species, this biotope is considered to have 'High' resistance and 'High' resilience (by default) to this pressure and is therefore considered to be 'Not sensitive'. The timing of changes and seasonal weather could result in greater impacts on species. An acute decrease in temperature coinciding with unusually low winter temperatures may exceed thermal tolerances and lead to mortalities of the associated species, although this would not alter the character of the biotope.

Salinity increase (local)

Low

Q: High A: Low C: Medium

Medium Q: High A: Low C: Medium

Medium

Q: High A: Low C: Medium

Local populations may be acclimated to the prevailing salinity regime and may, therefore, exhibit different tolerances to other populations subject to different salinity conditions and therefore caution should be used when inferring tolerances from populations in different regions. This biotope is found in full (30-35 ppt) salinity (Connor *et al.*, 2004). Biotopes found in the intertidal will naturally experience fluctuations in salinity where evaporation increases salinity and inputs of rainwater expose individuals to freshwater. Species found in the intertidal are therefore likely to have some form of behavioural or physiological adaptations to changes in salinity.

Kelps are tolerant to short-term daily fluctuation in salinity and are recorded as tolerating 5-60 psu, however, they are much less tolerant to long-term changes with growth and photosynthetic rates declining either side of 20-45 psu (Gordillo *et al.*, 2002; Karsten, 2007). Despite this tolerance, *Laminaria digitata* is considered to be a stenohaline species, and this biotope is only found in conditions of full salinity (Connor *et al.*, 2004). Therefore, other species probably outcompete *Laminaria digitata* at the limits of its salinity tolerance, meaning that despite the biotope's tolerance under conditions of no competition, under natural conditions this biotope is unlikely to occur in conditions above 40 psu.

The associated species are typically found in a range of salinities and tolerance of the red algae varied between species. *Corallina officinalis* is found in tide pools where salinities may fluctuate markedly during exposure to the air. Kinne (1971b) cites maximal growth rates for *Corallina officinalis* between 33 and 38 psu in Texan lagoons. *Chondrus crispus* is found in a range of salinities across its range and has been reported from sites with yearly salinity range 0-10 psu and 10-35 psu (Lindgren & Åberg, 1996) and sites from an average of 26-32 psu. However, at different

salinities the ratio between the abundance of the tetrasporophyte phase and the gametophyte alters (Guidone & Grace, 2010). Mathieson & Burns (1971) recorded maximum photosynthesis of *Chondrus crispus* in culture at 24 psu, but rates were comparable at 8, 16 and 32 psu. Photosynthesis continued up to 60 psu. Bird *et al.* (1979) recorded growth of Canadian *Chondrus crispus* in culture between 10 and 50 psu, with a maximum at 30 psu. *Chondrus crispus* would, therefore, appear to be euryhaline and tolerant of a range of salinities. Laboratory experiments have defined the upper and lethal lower limits for *Palmaria palmata* as 15 psu and 50 psu (Karsten *et al.*, 2003), with optimal salinity defined as 23-34 psu (Robbins, 1978).

The associated *Ulva* species can survive hypersaline conditions in supralittoral rockpools subjected to evaporation and are considered to be a very euryhaline species, tolerant of extreme salinities ranging from 0 psu to 136 psu (Reed & Russell, 1979). Some variations in salinity tolerance between populations of *Ulva intestinalis* have been found, however, suggesting that plants have some adaptation to the local salinity regime (Alströem-Rapaport *et al.*, 2010; Reed & Russell, 1979). Increased salinity is most likely to occur in the region of the littoral fringe and supralittoral zone and specimens from these areas were able to tolerate very high salinities, a significant decrease in regeneration only being recorded after exposure to concentrated seawater (102 psu and 136 psu) for >7 days (Reed & Russell, 1979).

Sensitivity assessment. Little direct evidence was found to assess sensitivity to this pressure. Although some increases in salinity may be tolerated by the associated species present, these are generally short-term and mitigated during tidal inundation. This biotope is considered, based on distribution of *Laminaria digitata* and the associated red algal species on the mid to lower shore, to be sensitive to a persistent increase in salinity to > 40 ppt. Resistance is therefore assessed as 'Low' and recovery as 'Medium' (following restoration of usual salinity). Sensitivity is therefore assessed as 'Medium'.

Salinity decrease (local)

High Q: High A: High C: High

h Q: High A: High C: High

Not sensitive

Q: High A: High C: High

Local populations may be acclimated to the prevailing salinity regime and may therefore exhibit different tolerances to other populations subject to different salinity conditions and therefore caution should be used when inferring tolerances from populations in different regions. This biotope is found in full (30-35 ppt) salinity (Connor *et al.*, 2004) and at the pressure benchmark a change to variable (18-35 ppt) or reduced (18-30 ppt) is considered. Biotopes found in the intertidal will naturally experience fluctuations in salinity where evaporation increases salinity and inputs of rainwater expose individuals to freshwater. Species found in the intertidal are therefore likely to have some form of behavioural or physiological adaptations to changes in salinity.

Birkett *et al.* (1998b) suggested that kelps are stenohaline, in that they do not tolerate wide fluctuations in salinity and require regular salinities of 30-35 psu to maintain optimum growth rates. Growth rate may be adversely affected if the kelp plant is subjected to periodic salinity stress. *Laminaria digitata* tolerates a large salinity range within a 24 hour period (5-60 psu; Karsten, 2007). At the extremes of this range, decreases in photosynthetic rates are evident, particularly at low salinities (Gordillo *et al.*, 2002). In the study by Karsten (2007), kelp thalli were kept at constant salinities for 5 days, with their photosynthetic rates measured after 2 and 5 days. The lower salinity limit for *Laminaria digitata* lies between 10 and 15 psu. On the Norwegian coast, Sundene (1964) found healthy *Laminaria digitata* plants growing between 15 and 25 psu. Axelsson & Axelsson (1987) indicated damage of the plants' plasma membranes occurs when salinity is below 20 or above 50 psu. Localized, long-term reductions in salinity to below 20 psu may result in the loss of kelp beds in affected areas (Birkett et al., 1998b).

Corallina officinalis is found in tide pools where salinities may fluctuate markedly during exposure to the air. Kinne (1971b) cites maximal growth rates for *Corallina officinalis* between 33 and 38 psu in Texan Iagoons. *Ulva* species can survive hypersaline conditions in supralittoral rockpools subjected to evaporation and is considered to be a very euryhaline species, tolerant of extreme salinities ranging from 0 psu to 136 psu (Reed & Russell, 1979).

Edyvean & Ford (1984b) suggest that populations of *Lithophyllum incrustans* are affected by temperature changes and salinity and that temperature and salinity 'shocks' induce spawning but no information on thresholds was provided (Edyvean & Ford, 1984b). Populations of *Lithophyllum incrustans* were less stable in tide pools with a smaller volume of water that were more exposed to temperature and salinity changes due to lower buffering capacity. Sexual plants (or the spores that give rise to them) were suggested to be more susceptible than asexual plants to extremes of local environmental variables (temperature, salinity etc.) as they occur with greater frequency at sites where temperature and salinity were more stable (Edyvean & Ford, 1984b).

Laboratory experiments have defined the upper and lethal lower limits for *Palmaria palmata* as 15 psu and 50 psu (Karsten *et al.*, 2003), with optimal salinity defined as 23-34 psu (Robbins, 1978). *In-situ Palmaria palmata* from the Arctic Kongsfjord (Spitsbergen) exposed for four days to salinities of 15 psu following freshwater run-off suffered high levels of mortality (Karsten *et al.*, 2003). In Danish waters where salinities are lowered by freshwater inputs, cultivation experiments found that *Palmaria palmata* growth over a seven month period was greatest at a site where mean salinity was 21±3 psu, while no growth occurred at a site where mean salinity was 17±5 psu (Bak, 2014).

A decrease in salinity may lead to replacement of more sensitive red algal turf forming species by those more tolerant of the changed conditions. *Chondrus crispus* occurs in areas of 'low' salinity. For example, the species occurs in estuaries in New Hampshire, USA, where surface water salinity varies from 16-32 psu (Mathieson & Burns, 1975). Mathieson & Burns (1971) recorded maximum photosynthesis of *Chondrus crispus* in culture at 24 psu, but rates were comparable at 8, 16 and 32 psu. Tasende & Fraga (1999) cultured *Chondrus crispus* spores from north west Spain and concluded that growth was correlated with salinity between 23 and 33 psu.

The associated *Ulva* species can survive hypersaline conditions in supralittoral rockpools subjected to evaporation and are considered to be a very euryhaline species, tolerant of extreme salinities ranging from 0 psu to 136 psu (Reed & Russell, 1979). Some variations in salinity tolerance between populations of *Ulva intestinalis* have been found, however, suggesting that plants have some adaptation to the local salinity regime (Alströem-Rapaport *et al.*, 2010; Reed & Russell, 1979). Increased salinity is most likely to occur in the region of the littoral fringe and supralittoral zone and specimens from these areas were able to tolerate very high salinities, a significant decrease in regeneration only being recorded after exposure to concentrated seawater (102 psu and 136 psu) for >7 days (Reed & Russell, 1979).

Sensitivity assessment. Prolonged reduction in salinity, e.g. from full to reduced or variable, is likely to reduce the species richness of the biotope due to loss of less tolerant red algae and some intolerant invertebrates. The sensitivity of *Palmaria palmata* for example, appears to be greater than some other turf-forming species such as *Chondrus crispus*. A change in salinity at the pressure benchmark is considered to lead to some mortality of *Palmaria palmata* although the tolerance threshold reported in laboratory and cultivation studies is slightly lower than the assessed

benchmark. Due to the variable or low salinity conditions the individual red seaweeds may not be as large as specimens found in fully marine conditions and they can lack sexually reproductive structures (JNCC, 2015). Based on changes in dominant species and reduction in habitat suitability for the characterizing species, biotope resistance is assessed as 'Low' and resilience as 'Medium' following habitat restoration. Biotope sensitivity is therefore 'Medium'.

 Water flow (tidal
 High

 current) changes (local)
 Q: High A: High C: High

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

This biotope occurs in a range of water flow conditions from moderately strong (0.5-1.5 meters /second) to weak (<0.5 m/s) (negligible) (Connor *et al.*, 2004), indicating that the characterizing species can tolerate a range of flow speeds.Moderate water movement is beneficial to seaweeds as it carries a supply of nutrients and gases to the plants and removes waste products. Propagule dispersal, fertilization, settlement, and recruitment are also influenced by water movement (Pearson & Brawley, 1996). Increased water flow can increase scour through increased sediment movement. Small life stages of macroalgae are likely to be affected by removal of new recruits from the substratum reducing successful recruitment (Devinny & Volse, 1978) (see 'siltation' pressures). A reduction in water flow can cause a thicker boundary layer resulting in lower absorption of nutrients and CO_2 by the macroalgae. Slower water movement can also cause oxygen deficiency directly impacting the fitness of algae (Olsenz, 2011). Higher water flow rates increase mechanical stress on macroalgae by increasing drag. This can result in individuals being torn off the substratum.

In Lough Ine in Ireland, *Laminaria digitata* forms dense forests in the fast flowing water of the Rapids where water speeds vary from 4-6 knots (ca 2-3 m/s) (Bassindale *et al.*, 1948). *Laminaria digitata* is also found in very strong flows (>3.87 m/s) although it is often out-competed by *Alaria esculenta*. *Laminaria digitata* partially achieves survival in a range of water flow conditions by variations in blade morphology, with fronds narrower and more digitate where water flow rates are higher (Sundene, 1964). In a laboratory study, this morphological adaptation was attributed to longitudinal stress with exposure to this stress over 6 weeks resulting in narrower blades and a significantly higher rate of cell elongation, compared to those plants that had not experienced the same stress. This plasticity would serve to decrease the risk of thallus damage in areas of greater exposure or in stormier conditions (Gerard, 1987).

As water velocity increases, algae can flex and reconfigure to reduce the size of the alga when aligned with the direction of flow, this minimizes drag and hence the risk of dislodgement (Denny *et al.*, 1998; Boller & Carrington, 2007). These characteristics allow these species to persist on shores that experience a range of flow speeds. For example, *Mastocarpus stellatus* occurs at sites in Maine, USA experiencing peak autumn flow speeds as measured by current meters of 9.2 m/s and 5.8 m/s. The habitat structure created by canopies and turfs reduce the effects of water flows on individuals by slowing and disrupting flow (Boller & Carrington, 2006), although this effect will be reduced in this biotope where *Fucus serratus* and red algae occur as scattered plants. The coralline crusts characterizing this biotope are securely attached and as these are flat are subject to little or no drag.

The crustose holdfasts of *Corallina officinalis*, the coralline crusts and the *Mastocarpus stellatus* petrocelis stage are securely attached and as these are relatively flat, are subject less drag than upright fronds and are likely to tolerate changes in water flows at the pressure benchmark. Moderate water movement is beneficial to seaweeds as it carries a supply of nutrients and gases to

the plants and removes waste products. However, if flow becomes too strong, plants may become dislodged.

Gibbula cineraria also appear to tolerate a range of wave exposures from exposed sites to those that are very sheltered (Frid & Fordham, 1994). As with *Littorina littorea*, the morphology of the shell varies according to wave exposure, allowing individuals to adapt to different conditions in the habitat in which the larvae settle(Frid & Fordham, 1994). *Gibbula cineraria* is, however, absent from areas with very strong and turbulent flow

Sensitivity assessment. Based on the available evidence the characterizing species and associated macroalgae and animals are able to occur within a range of flow flow rates and the biotope is therefore considered to be 'Not sensitive' to an increase in water flow at the pressure benchmark. A decrease in water flow may have some effects on recruitment and growth but this is not considered to be lethal at the pressure benchmark and resistance is therefore assessed as 'High' and resilience as 'High' by default, so that the biotope is considered to be 'Not sensitive'. Changes in water flow at the pressure benchmark may result in increased or decreased sediment deposition, these are not considered to alter the character of the biotope which is characterized by sediments beneath boulders (Connor *et al.*, 2004).

Emergence regime changes



igh Q: High A: Medium C: High

Medium

Q: High A: Medium C: High

Emergence regime is a key factor structuring intertidal biotopes. Changes in emergence can lead to: greater exposure to desiccation, temperature and salinity variation, reduced levels of time for filter feeding and nutrient uptake, and photosynthesising opportunities for the characterizing species. Changes in emergence can also alter competitive interactions and trophic interactions such as grazing and predation. This biotope occurs in the lower shore beneath the *Fucus serratus* zone (Fser.Bo or Fser.R) and above the *Laminaria hyperborea* zone (Lhyp). Many of the animals found under boulders in the lower shore in Fser.Bo are also found under boulders in the sublittoral fringe (Ldig.Bo), particularly the sponges and crabs. Similarly, many of the seaweeds present on the lower shore are also present in the shallow sublittoral fringe (JNCC, 2015).

This biotope occurs in the shallow sublittoral and is therefore exposed to changes in emergence. Increased emergence will expose the biotope to air for longer periods leading to drying. *Laminaria digitata* is relatively resistant to desiccation, surviving up to 40% water loss (Dring & Brown, 1982). The desiccation tolerance of *Laminaria digitata* allow beds to extend a further 2 cm into the eulittoral zone where grazing pressure is removed (Southward & Southward, 1978). When exposed to the air, kelp canopies buffer the effects of high temperatures and water loss on organisms below their fronds with substratum temperatures on average 8-10°C lower under the canopy than bare rock, additionally decreasing water loss by >45% (Bertness *et al.*, 1999).

An increase in the benchmark level for air exposure may result in the depression of the biotope's upper limit; as this species' lower limit is set by competition with *Laminaria hyperborea* (Hawkins & Harkin, 1985). The upper, landward limits of *Laminaria digitata* biotopes are generally set by competition with the brown algae *Fucus serratus* (Hawkins & Harkin, 1985). Therefore, a decrease in the benchmark level for air exposure may result in the extension of the biotope's upper limit. The main driver of competition between *Fucus serratus* and *Laminaria digitata* is based on the ability of *Fucus serratus* to control its respiration rates based on its desiccation rates, which *Laminaria digitata* is unable to do. Therefore, longer periods of emergence may result in a compression of *Laminaria digitata*'s extent as it is out-competed by *Fucus serratus* at its upper limit. The kelp is

able to resist both an increase and decrease in emergence, however, this resitance is based on the free movement of this species within its environmental optima, shifting up or down the shore.

The red algae within the biotope are likely to be sensitive to increased emergence. *Corallina officinalis* is sensitive to desiccation (Dommasnes, 1969) and is generally not found on open rock unless protected by algal canopies or where the surfaces are damp or wet. At Hinkley Point (Somerset, England), for example, seawater run-off from deep pools high in the intertidal supports dense turfs of *Corallina* spp. lower on the shore (Bamber & Irving, 1993). Fronds are highly intolerant of desiccation and do not recover from a 15% water loss, which might occur within 40-45 minutes during a spring tide in summer (Wiedemann, 1994). Bleached corallines were observed 15 months after the 1964 Alaska earthquake which elevated areas in Prince William Sound by 10 m. Similarly, increased exposure to air caused by upward movement of 15 cm due to nuclear tests at Armchitka Island, Alaska, adversely affected *Corallina pilulifera* (Johansen, 1974). During an unusually hot summer, Hawkins & Hartnoll (1985) observed damaged *Corallina officinalis* and other red algae. Littler & Kauker (1984) suggest that the basal crustose stage is adaptive, allowing individuals to survive periods of physical stress as well as physiological stress such as desiccation and heating. The basal crust stage may persist for extended periods with frond regrowth occurring when conditions are favourable.

Experimental grazer removal has allowed algae including *Palmaria palmata, Ceramium* sp. and *Osmundea* (as *Laurencia*) *pinnatifida* to grow higher on the shore (during winter and damp summers) than usual, suggesting that grazing also limits the upper shore extent of this biotope (Hawkins & Hartnoll, 1985). These observations and further grazer removal experiments by Boaventura *et al.* (2003), indicate that grazing, in combination with physiological tolerances, limits the upper shore extent of biotopes characterized by red algal turfs on moderately and more exposed shores, where grazing is greater than on sheltered shores (Hawkins & Hartnoll, 1983; Boaventura *et al.*, 2003). These results concord with other studies that show grazing and emersion stress limit the height to which red algal turfs can extend (Underwood, 1980; Boaventura, 2000).

The green algae are considered resistant to this pressure (although may be bleached at higher shore levels during periods of high temperature) as they are found throughout the intertidal including the high shore levels which may not be inundated every day.

Sensitivity assessment. This pressure is a key driver of biotope extent because the upper and lower limits of this species are set by inter-species competition. In the direct footprint of the impact resistance is therefore probably 'Low' based on loss of *Laminaria digitata* (loss of 25-75%) and likely reclassification to LR.MLR.BF.Fser.Bo. Resilience is suggested as 'High' (2-10 years) following restoration of the emergence regime. This biotope is therefore considered to have 'Medium' sensitivity to the pressure.

Wave exposure changes	<mark>High</mark>
(local)	Q: High A: High C: High

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

This biotope is found in a range of wave exposures from moderately exposed to sheltered from wave action (Connor *et al.*, 2004).

An increase in wave exposure generally leads to a decrease in macroalgae abundance and size (Lewis, 1961; Stephenson & Stephenson, 1972; Hawkins *et al.*, 1992; Jonsson *et al.*, 2006). The greatest wet weight of *Laminaria digitata* occurs at low wave exposure (mean significant wave

height <0.4 m) decreasing by a mean of 83% in medium to high wave exposures (mean significant wave height >0.4m; Gorman *et al.*, 2013). At medium to high levels of wave exposure, *Laminaria digitata* biomass has been shown to decrease by 83% in the field (Wernberg & Thomsen, 2005). In areas of high wave exposure *Laminaria digitata* may extend its upper limits into the lower eulittoral zone.

As water velocity increases the algae can flex and reconfigure to reduce the size of the alga when aligned with the direction of flow, this minimises drag and hence the risk of dislodgement (Boller & Carrington, 2007). These characteristics allow these species to persist on shores that experience a range of wave action levels. Colonies of *Lithophyllum incrustans* appear to thrive in conditions exposed to strong water movement. Irvine & Chamberlain (1994) observe that the species is best developed on wave exposed shores.

Sensitivity assessment. The natural wave exposure range of this biotope is considered to exceed changes (increases and decreases) at the pressure benchmark and this biotope is considered to have 'High' resistance and 'High' resilience (by default), to this pressure (at the benchmark). This assessment is supported by evidence for the tolerance and adaptions of the key characterizing macroalgae to different levels of wave exposure.

A Chemical Pressures

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

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

Little information was found concerning the effects of heavy metals on turf forming and encrusting coralline algae. However, Bryan (1984) suggested that the general order for heavy metal toxicity in seaweeds is: organic Hg >inorganic Hg >Cu >Ag >Zn >Cd >Pb.

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

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

Laminaria digitata is less susceptible to coating than some other seaweeds because of its preference for exposed locations where wave action will rapidly dissipate oil. The effects of oil accumulation on the thalli are mitigated by the perennial growth of kelps. No significant effects of the *Amoco Cadiz* spill were observed for *Laminaria* populations and the *World Prodigy* spill of 922 tons of oil in Narragansett Bay had no discernible effects on *Laminaria digitata* (Peckol *et al.*, 1990). Mesocosm studies in Norwegian waters showed that chronic low level oil pollution (25 µg/l) reduced growth rates in *Laminaria digitata* but only in the second and third years of growth (Bokn, 1985). Where exposed to direct contact with fresh hydrocarbons, encrusting calcareous algae have a high intolerance. The sensitivities of the faunal components of the kelp bed are not known although amphipods normally suffer high mortality in oil affected areas. Analysis of kelp holdfast fauna after the *Sea Empress* oil spill in Milford Haven illustrated decreases in number of species, diversity and abundance at sites nearest the spill (SEEEC, 1998).

Following the Torrey Canyon oil spill in 1967, oil and detergent dispersants affected high shore specimens of Corallina officinalis more than low shore specimens. Plants in deep pools were afforded some initial protection, although probably later affected by contaminated runoff. In areas of heavy spraying, however, Corallina officinalis was killed (Smith, 1968). Intolerance to hydrocarbon pollution has been assessed to be high, as key structural and important characterizing coralline algal species will be lost and the biotope not be recognized in their absence. Hydrocarbon contamination, at levels greater than the benchmark, e.g. from spills of fresh crude oil or petroleum products, may cause significant loss of Ulva spp. However, the species tends to recover very rapidly from oil pollution incidents. For instance, after the Torrey Canyon tanker oil in 1967, grazing species were killed, and a dense flush of ephemeral green algae (Ulva, Blidingia) appeared on the rocky shore within a few weeks and persisted for up to one year (Smith, 1968).

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

Not assessed (NA)

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

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

Cole et al. (1999) suggested that herbicides were (not surprisingly) very toxic to algae and macrophytes. Hoare & Hiscock (1974) noted that with the exception of Phyllophora species, all red algae including encrusting coralline forms, were excluded from the vicinity of an acidified halogenated effluent discharge in Amlwch Bay, Anglesey, and that intertidal populations of Corallina officinalis occurred in significant amounts only 600 m east of the effluent. Chamberlain (1996) observed that although Lithophyllum incrustans was quickly affected by oil during the Sea *Empress* spill, recovery occurred within about a year. The oil was found to have destroyed about one third of the thallus thickness but regeneration occurred from thallus filaments below the damaged area.

Following the Torrey Canyon oil spill in 1967, oil and detergent dispersants affected high shore specimens of Corallina officinalis more than low shore specimens. Plants in deep pools were afforded some initial protection, although probably later affected by contaminated runoff. In areas of heavy spraying, however, Corallina officinalis was killed (Smith 1968). Limpets are extremely intolerant of aromatic solvent based dispersants used in oil spill clean-up. During the clean-up response to the Torrey Canyon oil spill nearly all the limpets were killed in areas close to dispersant spraying. Viscous oil will not be readily drawn in under the edge of the shell by ciliary currents in the mantle cavity, whereas detergent, alone or diluted in seawater, would creep in much more readily and be liable to kill the limpet (Smith, 1968). A concentration of 5 ppm killed half the limpets tested in 24 hours (Southward & Southward, 1978; Hawkins & Southward, 1992). Acidified seawater affects the motility of Patella vulgata. At a pH of 5.5, motility was reduced whilst submerged but individuals recovered when returned to normal seawater. At a pH of 2.5, total inhibition of movement occurred and when returned to normal seawater half had died (Bonner et al., 1993). Reduced motility reduces time for foraging and may result in decreased survival of individuals. Acidified seawater can also change the shell composition which will lead to a decrease in its protective nature and hence survival (Bonner et al., 1993). Short periods (48 hours) are unlikely to have much effect on a population but long periods (1 year) may cause reduced grazing and an increase in algal growth. However, seawater is unlikely to reach pH 2.5 therefore intolerance to slight changes in pH will be low. Hoare & Hiscock (1974) reported that in Amlwch Bay, Patella vulgata was excluded from sites within 100-150 m of the discharge of acidified, halogenated effluent.

Date: 2016-07-01

Radionuclide contamination

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

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

No evidence.

Introduction of other substances

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

This pressure is **Not assessed**.

De-oxygenation

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

Reduced oxygen concentrations have been shown to inhibit 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).

This biotope would only be exposed to low oxygen in the water column during periods of tidal immersion. In areas of wave exposure and/or moderately strong current flow, low oxygen levels in the water are unlikely to persist for very long as oxygen levels will be recharged by the incorporation of oxygen in the air into the water column or flushing with oxygenated waters.

Reduced oxygen concentrations have been shown to inhibit 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). If levels do drop below 4 mg/l negative effects on these organisms can be expected with adverse effects occurring below 2 mg/l (Cole *et al.*, 1999). Reduced oxygen levels are likely to inhibit photosynthesis and respiration but not cause a loss of the macroalgae population directly. However, small invertebrate epifauna may be lost, causing a reduction in species richness.

Experiments have shown that thallus discs of *Ulva lactuca* plants can survive prolonged exposure to anoxia and hypoxia (Vermaat & Sand-Jensen, 1987; Corradi *et al.*, 2006). Following resumption of normal oxygen conditions gametes were produced. The associated invertebrate species also show high tolerances for reduced oxygen at levels that exceed the pressure benchmark. *Littorina littorea* can easily survive 3-6 days of anoxia (Storey *et al.*, 2013). *Semibalanus balanoides* can respire anaerobically, so they can tolerate some reduction in oxygen concentration (Newell, 1979). When placed in wet nitrogen, where oxygen stress is maximal and desiccation stress is low, *Semibalanus balanoides* have a mean survival time of 5 days (Barnes *et al.*, 1963). Limpets can also survive for a short time in anoxic seawater; Grenon & Walker (1981) found that in oxygen free water limpets could survive up to 36 hours, although Marshall & McQuaid (1989) found a lower tolerance for *Patella granularis*, which survived up to 11 hours in anoxic water. *Patella vulgata* and *Littorina littorea* are able to respire in air, mitigating the effects of this pressure during the tidal cycle.

Sensitivity assessment. As the biotope will only be exposed to this pressure when submerged during the tidal cycle and wave action will re-oxygenate waters while respiration will occur in air, biotope resistance was assessed as 'High' and resilience as 'High' (no effect to recover from), resulting in a sensitivity of 'Not sensitive'.

Nutrient enrichment

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

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

This pressure relates to increased levels of nitrogen, phosphorus and silicon in the marine environment compared to background concentrations. The benchmark is set at compliance with WFD criteria for good status, based on nitrogen concentration (UKTAG, 2014).

High levels of enrichment may stimulate algal blooms and macroalgal growth. Stimulation of fastgrowing green algae may result in smothering of boulder surfaces and lead to negative effects on both perennial algae and bases and the characterizing invertebrate hinder perennial species development or harm their recruitment. High ambient levels of phosphate and nitrogen enhance spore formation in a number of Laminaria species (Nimura et al., 2002), but will eventually inhibit spore production, particularly at the limits of temperature tolerances as seen in Saccharina latissima (studied as Laminaria saccharina; Yarish et al., 1990). Laminaria digitata seems to follow this trend with a growth peak occurring in conjunction with nutrient upwelling from deeper waters in Norway (Gévaert et al., 2001). Macroalgal growth is generally nitrogen-limited in the summer, as illustrated by the growth rates of Laminaria digitata between an oligotrophic and a eutrophic site in Abroath, Scotland (Davison et al., 1984). Laminaria digitata does not accumulate the significant internal nutrient reserves seen in some other kelp. Higher growth rates have been associated with alga situated close to sewage outfalls. However, after removal of sewage pollution in the Firth of Forth, Laminaria digitata became abundant on rocky shores from which they had previously been absent (Read et al., 1983). Enhancement of coastal nutrients is likely to favour those species with more rapid growth rates including turf forming algae (Gorgula & Connell, 2004) which could explain Laminaria digitata absence from the Firth of Forth. Additionally, epiphytic abundance and biomass on Laminaria longicruris increases under a eutrophic regime decreasing the ability to photosynthesis and withstand pressure from water movement as drag increases (Scheibling et al., 1999).

The red alga *Corallina officinalis* and the associated green algae species have been identified worldwide as species that occur in areas subject to increased nutrient input within the vicinity of sewage outfalls and at intermediately polluted sites (Bellgrove *et al.*, 2010; Littler & Murray, 1975; May, 1985; Brown *et al.*, 1990; Bellgrove *et al.*, 1997). For example, Kindig & Littler (1980) demonstrated that *Corallina officinalis* var. *chilensis* in South California showed equivalent or enhanced health indices, highest productivity and lowest mortalities (amongst the species examined) when exposed to primary or secondary sewage effluent. Grazers in the biotope may also benefit from increased availability of food resources, due to enhanced growth.

Atalah & Crowe (2010) added nutrients to rockpools occupied by a range of algae including encrusting corallines, turfs of *Mastocarpus stellatus*, *Chondrus crispus* and *Corallina officinalis* and green and red filamentous algae. The invertebrates present were mostly *Patella ulyssiponensis*, the winkle *Littorina littorea* and the flat topshell *Gibbula umbilicalis*. Nitrogen and phosphorous enhancement was via the addition of fertilizers, as either 40 g/l or 20 g/l. The treatments were applied for seven month and experimental conditions were maintained every two weeks. The experimental treatments do not directly relate to the pressure benchmark but indicate some general trends in sensitivity. Nutrients had no significant effect on the cover of *Corallina officinalis*. The cover of green filamentous algae was significantly increased both by reduced grazing and increased nutrients, although the effect size was synergistically magnified by the combined effect of grazer removal and nutrients. Nutrient enrichment caused an absolute increase in the average cover of green filamentous algae of 19% (±3.9 S.E.) respect to the control treatments while the cover of red turfing algae was not affected by nutrient addition (Atalah &

Crowe, 2010).

Sensitivity assessment. The pressure benchmark is relatively protective and may represent a reduced level of nutrient enrichment in previously polluted areas. Due to the tolerance of high levels of nutrient input demonstrated generally by red algae, including *Corallina officinalis* e.g. Bellgrove *et al.* (2010) and Atalah & Crowe (2010), resistance to this pressure is assessed as 'High' and resilience as 'High' so that the biotope is assessed as 'Not sensitive'. Grazers limit the effects of nutrient enrichment; in the absence of *Gibbula cineraria* and other grazers, significant changes in the structure of the algal assemblage could emerge following eutrophication. However, where boulders move frequently this would prevent permanent colonization by larger, perennial species and ephemeral algae could be displaced by space-occupying red algae following disturbance and the creation of gaps.

Organic enrichment

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

Not sensitive Q: High A: Medium C: High

It should be noted that biotopes occurring in tide swept or wave exposed areas are less likely to experience the effects of organic enrichment as the organic matter will be rapidly removed. Organic matter may be moved to the sediments beneath the boulders and would enhance food supply to deposit feeding infauna such as *Cirratuls cirratulus*, other polychaetes and oligochaetes. At the pressure benchmark, the input of organic carbon would represent a food subsidy leading to enrichment rather than gross pollution effects.

Organic enrichment and nutrient enrichment commonly co-occur, for example sewage deposits or outputs from fish farms may enhance nitrogen and phosphorous and organic matter. Nutrient enrichment alters the selective environment by favouring fast growing, ephemeral species such as *Ulva lactuca* and *Ulva intestinalis* (Berger *et al.*, 2004; Kraufvelin, 2007). Rohde *et al.* (2008) found that both free growing filamentous algae and epiphytic microalgae can increase in abundance with nutrient enrichment. This stimulation of annual ephemerals may accentuate the competition for light and space and hinder perennial species development or harm their recruitment (Berger *et al.*, 2003; Kraufvelin *et al.*, 2007). Bellgrove *et al.* (2010) found that coralline turfs out-competed fucoids at a site associated with organic enrichment caused by an ocean sewage outfall. Worldwide *Corallina officinalis* has been noted to increaseat the expense of canopy forming macroalgae within the vicinity of sewage outfalls and at intermediately polluted sites (Bellgrove *et al.*, 2010; Littler & Murray, 1975; May, 1985; Brown *et al.*, 1990). As turf forming algae *Corallina* spp. trap large amounts of sediment and are therefore not considered sensitive to sedimentation. The turfs host a variety of associated species and deposit feeders amongst these would be able to consume inputs of organic matter.

Sensitivity assessment. Evidence is limited but it is considered that this biotope has 'High' resistance to increased organic matter at the pressure benchmark (which represents enrichment rather than gross pollution). Resilience is therefore assessed as 'High' (no effect to recover from) and the biotope is considered to be 'Not sensitive'.

Resilience

Very Low

Q: High A: High C: High

	Resistance		
Physical loss (to land or freshwater habitat)	None		
	Q. High A. High C. High		

A Physical Pressures

Q: High A: High C: High

Sensitivity

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. Adjacent habitats and species populations may be indirectly affected where meta-population dynamics and trophic networks are disrupted and where the flow of resources e.g. sediments, prey items, loss of nursery habitat etc. is altered.

Physical change (to another seabed type)

None Q: High A: High C: High Very Low

High

Q: High A: High C: High Q: High A: High C: High

This biotope is characterized by the hard rock substratum, provided by the boulders, to which the characterizing *Laminaria digitata* and associated species such as red and green algae, barnacles and sponges can firmly attach. A change to a sedimentary substratum (without boulders) would significantly alter the character of the biotope through the loss of boulders and associated changes to the sedimentary assemblage. A biological assemblage more typical of the changed conditions would develop. A change to an artificial hard substratum could alter this biotope as it would not be equivalent to a boulder field on sediments.

Artificial hard substratum may also differ in other characteristics from natural hard substratum, so that replacement of natural surfaces with artificial may lead to changes in the biotope through changes in disturbance (Sousa, 1979), microhabitat provision (McGuinness & Underwood, 1986), changes in species composition, richness and diversity (Green *et al.*, 2012; Firth *et al.*, 2014) or the presence of non-native species (Bulleri & Airoldi, 2005).

Tests with stone panels fixed to the sublittoral, mid-tide and high-tide levels of varying roughness found that *Ulva* species settle preferentially on smother, fine grained, substratum (chalk, mottled sandstone) and *Porphyra purpurea* on rougher, granulated substratum (limestone, granite, basaltic larvae) (Luther, 1976). *Corallina officinalis* shows optimal settlement on finely rough artificial substrata (0.5 - 1 mm surface particle diameter). Although spores will settle and develop as crustose bases on smooth surfaces, fronds were only initiated on rough surfaces. *Corallina officinalis* settled on artificial substrata within one week in the field in summer months in New England (Harlin & Lindbergh 1977). Crustose coralline algae extend further to the undersides of natural, rounded boulders than experimental stone blocks (Liversage, 2015). This pattern is likely due to availability of light (Liversage, 2015).

Sensitivity assessment. A change to a soft sedimentary or artificial, stable hard substratum would remove the habitat for this biotope. Biotope resistance is assessed as 'None' and resilience as 'Very Low' as the change is considered to be permanent. Sensitivity is therefore assessed as 'High'.

Physical change (to another sediment type)

Low Q: Low A: NR C: NR



Q: Low A: Low C: Low

High

A change in sediment type below the boulders would be very likely to alter the biological assemblage as soft sediment infauna are highly sensitive to changes in sediment type. Changes in the size and shape and other characteristics of boulders would also lead to changes in the habitat. Boulders provide three microhabitats, the upper and lower surface of boulders and the substratum underneath the boulders (Cruz Motta *et al.*, 2003).

Sensitivity assessment. A change in boulder and sediment characteristics are likely to lead to changes in species composition, and shifts in abundance and distribution of species that remain. The biotope classification is unlikely to change while the species composition is relatively similar. Biotope resistance is assessed as 'Low' and resilience is Very low (the pressure is a permanent change), biotope sensitivity is, therefore, assessed as 'High'.

Habitat structure	None	Medium	Medium
substratum (extraction)	Q: Low A: NR C: NR	Q: Low A: NR C: NR	Q: Low A: Low C: Low

Removal of boulders would result in loss of this habitat. Biotope resistance is assessed as 'None' and resilience as 'Medium' following restoration of the habitat. Sensitivity is, therefore, assessed as 'Medium'.

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

The species characterizing this biotope occur on the rock and therefore have no shelter from abrasion at the surface.

Most macroalgae are very flexible but not physically robust. Brown algae are particularly intolerant of trampling, depending on intensity. Fucoid algae demonstrate a rapid (days to months) detrimental response to the effects of trampling, depending on species, which has been attributed to either the breakage of their fronds across rock surfaces (Boalch *et al.*, 1974) or their possession of small discoid holdfasts that offer little resistance to repeated impacts (Brosnan & Crumrine, 1992; Fletcher & Frid, 1996b). Foliose species such as *Mastocarpus* spp. are also likely to be intolerant of trampling (Brosnan & Crumrine, 1994). Brosnan (1993) suggested that the presence or absence of foliose algae (e.g. fucoids) could be used to indicate the level of trampling on the rocky shores of Oregon.

In the UK, Boalch *et al.* (1974) and Boalch & Jephson (1981) noted a reduction in the cover of fucoids at Wembury, south Devon, when compared to surveys conducted by Colman (1933). The size ranges of *Ascophyllum nodosum*, *Fucus vesiculosus* and *Fucus serratus* were skewed to smaller length, and the abundance of *Ascophyllum nodosum* in particular was reduced (Boalch & Jephson, 1981). It was suggested that visitor pressure, especially after the construction of a car park, was responsible for the reduced cover of fucoids (Boalch *et al.*, 1974). They suggested that the raised edges of the slatey rock severed fronds when the rocks were walked over. However, no quantitative data was provided. Conversely, algal turfs seem to be relatively tolerant of the direct effects of trampling (based on the available evidence) and some species may benefit from removal of canopy forming algae (Tyler-Walters, 2005). Their tolerance may result from their growth form as has been shown for vascular plants and corals (Liddle, 1997). Brosnan (1993) suggested that algal turf dominated areas (on shores usually dominated by fucoids) were indicative of trampling on the rocky shores of Oregon. However, tolerance is likely to vary with species and their growth form and little species specific data was found. Furthermore, algal turfs may suffer negative indirect effects where they form an understorey below canopy forming species.

Pinn & Rodgers (2005) compared a heavily visited ledge with a less visited ledge at Kimmeridge Bay, Dorset. Although the mean species richness was similar at both sites, the total number of species was greater at the less utilized site. Comparatively, the heavily utilized ledge displayed a reduction in larger, branching algal species (e.g. *Fucus serratus*) and increased abundances of ephemeral and crustose species (e.g. *Ulva linza* and *Lithothamnia* spp. respectively). Fletcher & Frid (1996a, 1996b) examined the effects of persistent trampling on two sites on the north east coast of England. The trampling treatments used were 0, 20, 80, and 160 steps per m^{II} per spring tide for 8 months between March and November. Using multivariate analysis, they noted that changes in the community dominated by fucoids (*Fucus vesiculosus, Fucus spiralis* and *Fucus serratus*) could be detected within 1 to 4 months of trampling, depending on intensity. Intensive trampling (160 steps/m^{II}/spring tide) resulted in a decrease in species richness at one site. The area of bare substratum also increased within the first two months of trampling but declined afterwards, although bare space was consistently most abundant in plots subject to the greatest trampling (Fletcher & Frid, 1996a, 1996b). The abundance of fucoids was consistently lower in trampled plots.

Fletcher & Frid (1996a, 1996b) also reported a decrease in the understorey algal community of encrusting coralline algae and red algae, which was probably an indirect effect due to increased desiccation after removal of the normally protective fucoid canopy (see Hawkins & Harkin, 1985) by trampling. They also noted that opportunistic algae (e.g. *Ulva* sp.) increased in abundance. Fletcher & Frid (1996a) noted that the species composition of the algal community was changed by as little as 20 steps per m⁰ per spring tide of continuous trampling since recolonization could not occur. A trampling intensity of 20 steps per m⁰ per spring tide could be exceeded by only five visitors taking the same route out and back again across the rocky shore in each spring tide. Both of the sites studied receive hundreds of visitors per year and damage is generally visible as existing pathways, which are sustained by continuous use (Fletcher & Frid, 1996a, 1996b). However, the impact was greatest at the site with the lower original abundance of fucoids.

Brosnan & Crumrine (1994) noted that trampling significantly reduced algal cover within 1 month of trampling. Foliose algae were particularly affected and decreased in cover from 75% to 9.1% in trampled plots. Mastocarpus papillatus decreased in abundance from 9% to 1% in trampled plots but increased in control plots. Fucus distichus decreased in the summer months only to recover in winter but in trampled plots remained in low abundance (between 1 and 3% cover). Trampling resulted in a decrease in cover of Pelvetiopsis limitata from 16% to 1.5%. Iridaea cornucopiae decreased from 38 to 14% cover within a month and continued to decline to 4-8% cover. However, after trampling ceased, recovery of algal cover including Iridaea cornucopiae and Mastocarpus papillatus was rapid (ca 12 months) (Brosnan & Crumrine, 1994). Schiel & Taylor (1999) also observed a decrease in understorey algae (erect and encrusting corallines) after 25 or more tramples, probably due to an indirect effect of increased desiccation as above. However, Schiel & Taylor (1999) did not detect any variation in other algal species due to trampling effects. Similarly, Keough & Quinn (1998) did not detect any effect of trampling on algal turf species. Littler & Littler (1984) suggest that the basal crustose stage of Corallina officinalis is adaptive to resist sand scour and wave shearing (as well as physiological stressors such as desiccation and heating). The base is much tougher than the fronds shown by experiments that demonstrate that the base has nearly twice the mechanical resistance (measured by penetration) of fronds (Littler & Kauker, 1984). In general, studies show that Corallina and other turf forming algae appear to be relatively resistant to single events and low levels of trampling. Brosnan & Crumrine (1994), for example, found that in experimentally trampled plots the cover of foliose and canopy forming species declined while turf forming algae were relatively resistant. Similarly, a comparison of rocky intertidal ledges that received different amounts of visitors in Dorset, England, found that Corallina officinalis were present on both heavily visited and less visited ledges suggesting that this species has some resistance to trampling (Pinn & Rodgers, 2005). Povey &

Keough (1991) in Mornington Peninsula, Australia, investigated the effects of sustained trampling on intertidal coralline algal mats where upright branching *Corallina* spp. formed a turf with other red algae with sand and encrusting coralline algae between turfs. The experimental strips were 2 m long and 0.5 m wide. The percentage cover of upright *Corallina* spp. was significantly affected by 25 passages of a strip per day after 12 and 33 days. The algae appeared flattened and were shorter (1-2 cm high) compared with the low intensity and control plots (3-4 cm high). However, low intensity trampling within a strip (2 passages/day) did not significantly affect the coralline turf. Brown & Taylor (1999) found that higher intensities of trampling damaged turfs. Moderate (50 steps per 0.09 m^I) or more trampling on intertidal articulated coralline algal turf in New Zealand reduced turf height by up to 50%, and weight of sand trapped within turf to about one third of controls. This resulted in declines in densities of the meiofaunal community within two days of trampling. Although the community returned to normal levels within 3 months of trampling events, it was suggested that the turf would take longer to recover its previous cover (Brown & Taylor, 1999). Similarly, Schiel & Taylor (1999) noted that trampling had a direct detrimental effect on coralline turf species on the New Zealand rocky shore. At one site coralline bases were seen to peel from the rocks (Schiel & Taylor, 1999), however, this was probably due to increased desiccation caused by loss of the algal canopy.

Schiel & Taylor (1999) reported the death of encrusting corallines one month after trampling due to removal of their protective canopy of fucoids by trampling (10 -200 tramples where one trample equals one transect walked by one person). A higher proportion of corallines died back in spring treatments presumably due to the higher levels of desiccation stress expected at this time of year. However, encrusting corallines increased within the following year and cover returned to control levels within 21 months (Schiel & Taylor, 1999). Mechanical abrasion from scuba divers was also reported to impact encrusting corallines, with cover of *Lithophyllum stictaeforme* greater in areas where diving was forbidden than visited areas (abundance, 6.36 vs 1.4; it is presumed this refers to proportion of cover, although this is not clear from the text) (Guarinieri *et al.*, 2012).

Dethier (1994) experimentally manipulated surface abrasion on a range of encrusting algae including *Lithophyllum impressum*. Crusts were brushed with either a nylon or steel brush for 1 minute a month for 24 months. Unbrushed controls grew by approximately 50% where the cover of nylon brushed crusts and steel brushed crusts decreased by approximately 25% and 40% respectively (interpreted from figures in Dethier, 1994). In laboratory tests on chips of *Lithophyllum impressum* brushing with a steel brush for 1 minute once a week for 3 weeks, resulted in no cover loss of two samples while a third 'thinned and declined' (Dethier, 1994).

Ulva spp. fronds are very thin and could be torn and damaged and individuals may be removed from the substratum, altering the biotope through changes in abundance and biomass. *Ulva* spp. cannot repair damage or reattach but torn fronds could still photosynthesize and produce gametes. Tearing and cutting of the fronds has been shown to stimulate gamete production and damaged plants would still be able to grow and reproduce.

The effects of trampling on barnacles appears to be variable with some studies not detecting significant differences between trampled and controlled areas (Tyler-Walters & Arnold, 2008). However, this variability may be related to differences in trampling intensities and abundance of populations studied. The worst case incidence was reported by Brosnan & Crumrine (1994) who found that a trampling pressure of 250 steps in a 20x20 cm plot one day a month for a period of a year significantly reduced barnacle cover (*Semibalanus glandula* and *Chthamalus dalli*) at two study sites. Barnacle cover reduced from 66% to 7% cover in 4 months at one site and from 21% to 5% within 6 months at the second site. Overall barnacles were crushed and removed by trampling.

Barnacle cover remained low until recruitment the following spring. Long *et al.* (2011) also found that heavy trampling (70 humans /km/hrs) led to reductions in barnacle cover. Single step experiments provide a clearer, quantitative indication of sensitivity to single events of direct abrasion. Povey & Keough (1991) in experiments on shores in Mornington peninsula, Victoria, Australia, found that in single step experiments 10 out of 67 barnacles (*Chthamlus antennatus* about 3 mm long) were crushed.

Sensitivity assessment. The available evidence indicates that abrasion could cause a significant loss of macroalgae cover and a reduction in species abundance and diversity. Based on the available evidence, it is concluded that the biotope is sensitive to abrasion and that resistance of characterizing and associated species (excluding *Corallina officinalis*) is 'Low' (loss of 25-75% of bed within direct impact footprint), resilience is assessed as 'Medium', resulting in a sensitivity of 'Medium'.

Penetration or	Low	Medium	Medium
disturbance of the			
substratum subsurface	Q: High A: High C: High	Q: High A: Medium C: Medium	Q: High A: Medium C: Medium

Disturbance that leads to movement and overturning of boulders is a key factor structuring the community. Disturbance can affect species numbers under boulders (McGuiness, 1987). Disturbance can also affect the pattern of algal cover on boulders (Addessi, 1994) and overturning is a key factor in determining species richness (Sousa, 1979). Boulders that are subject to high levels of disturbance and over-turning are colonized by fast growing green algae and disturbance resistance species while large boulders that are rarely over-turned host late successional communities (Sousa, 1979). The biotope IR.MIR.KR.Ldig.Bo as described (Connor *et al.*, 2004), is species rich and is unlikely to be subject to frequent disturbance. A single event of overturning, where the upper surface is turned on to the sediment is likely to lead to loss of algae as these will be smothered and damage and mortality of attached epifauna. Some under-boulder species such as amphipods and polychaetes may be able to relocate back to the underside of the boulder.

Sensitivity assessment. A single event of disturbance leading to the boulder being overturned is likely to alter species composition. Biotope resistance is assessed as 'Low' and resilience as 'Medium', biotope sensitivity is therefore 'Medium'.

Changes in suspended solids (water clarity)

Low Q: High A: Medium C: Medium

High Q: High A: High C: High Low

Q: High A: Medium C: Medium

Intertidal biotopes will only be exposed to this pressure when submerged during the tidal cycle and thus have limited exposure. Siltation, which may be associated with increased suspended solids and the subsequent deposition of these is assessed separately (see siltation pressures). In general, increased suspended particles reduce light penetration and increase scour and deposition. Changes in suspended solids may enhance food supply to filter or deposit feeders (where the particles are organic in origin) or decrease feeding efficiency (where the particles are inorganic and require greater filtration efforts). The deposit feeding infauna, such as *Cirratulus cirratulus*, that are present in the sediment below boulders and in trapped sediments amongst the algae are not likely to be directly sensitive to increased or decreased turbidity.

Light availability and water turbidity are principal factors in determining depth range at which kelp can be found (Birkett *et al.*, 1998b), an increase in suspended solids and decrease in light

penetration is, therefore, directly relevant to this biotope. Light penetration influences the maximum depth at which kelp species can grow and it has been reported that laminarians grow at depths at which the light levels are reduced to 1 percent of incident light at the surface. Maximal depth distribution of laminarians, therefore, varies from 100 m in the Mediterranean to only 6-7 m in the silt laden German Bight. In Atlantic European waters, the depth limit is typically 35 m. In very turbid waters the depth at which kelp is found may be reduced, or in some cases excluded completely (e.g. Severn Estuary), because of the alteration in light attenuation by suspended sediment (Lüning, 1990; Birkett et al., 1998b). The absence of Laminaria digitata in the Firth of Forth was suggested to be caused by the outflow from a sewage treatment plant that increased the turbidity of the water and thus decreased photosynthetic activity, although the effect of turbidity was probably coupled with increased nutrient levels (Read et al., 1983). Blue light is crucial for the gametophytic stages of Laminaria digitata, and several other congenic species (Lüning, 1980). Dissolved organic materials (yellow substance or gelbstoff) absorbs blue light (Kirk, 1976), therefore changes in riverine input or other land based runoff are likely to influence kelp density and distribution. In the silt-laden waters around Helgoland, Germany, the depth limit for Laminaria digitata growth may be reduced to between 0 m and 1.5 m (Birkett et al., 1998b). In locations where water clarity is severely decreased, Laminaria species experience a significant decrease in growth from the shading of suspended matter and/or phytoplankton (Lyngby & Mortensen, 1996; Spilmont et al., 2009).

Increases in the cover of sediment trapping, turf forming red algae at the expense of canopy forming species has been observed worldwide in temperate systems and has been linked to increased suspended solids linked to human activities worldwide (Airoldi, 2003). As turfs of *Osmundea pinnatifida* trap sediments (Prathep *et al.*, 2003), it is clear that this species has some resistance to abrasion and scour from sediment particles. *Corallina* species accumulate more sediment than any other alga (Hicks, 1985). Hence an increase in suspended sediment is likely to accumulate in the patches of *Corallina officinalis*. A significant increase may result in smothering (see siltation pressures). An accumulation of sediment within the turf may attract more sediment dwelling interstitial invertebrates such as nematodes, harpacticoids and polychaetes, although in more wave exposed locations accumulation of sediment is likely to be minimal. Increased suspended sediment may also result in increased scour, which may adversely affect *Fucus vesiculosus* and foliose red algae, and interfere with settling spores and recruitment if the factor is coincident with their major reproductive period. However, coralline algae, especially the crustose forms are thought to be resistant of sediment scour (Littler & Kauker, 1984), and will probably not be adversely affected at the benchmark level.

The biotope occurs in shallow waters where light attenuation due to increases in turbidity is probably low. Red algae and coralline algae especially are known to be shade tolerant and are common components of the understorey on seaweed dominated shores. Limited shading from suspended sediments is therefore not considered to negatively affect this genus. *Palmaria palmata* is often found under partially shaded conditions as an epiphyte on the stems of *Laminaria* spp. (Morgan *et al.* 1980) in the sublittoral zone (Lüning, 1990). In the Bay of Fundy where the tidal flux of nutrients from the marshes includes a high level of suspended sediment, *Palmaria palmata* grows well despite high turbidity. Irvine (1983) observed morphological adaptation of the plant in fairly sheltered, silty conditions; sometimes the blade divisions are wedge-shaped and finely dissected above or the blade has numerous linear divisions throughout. It is likely that this form reduces possible smothering that may result from increased siltation resulting from increased levels of suspended sediments. In the absence of nutrients, short-term increase in turbidity may affect growth and reproduction, however, as a perennial, the adults will probably survive. Other red algal species have high tolerances for high levels of

suspended solids. *Chondrus crispus* occurs in areas of sand covered rock in the subtidal biotope IR.HIR.Ksed.ProtAhn suggesting it is very resistant to high levels of turbidity and scour associated with high levels of resuspended particles.

On sites affected by high levels of resuspended colliery waste particles, Hyslop *et al.* (1997) found that *Palmaria palmata* and *Ulva* spp. Were reduced or absent, although the more tough fucoids were less affected. It is not clear how the levels of suspended solids experienced by these sites relate to the pressure benchmark.

Experiments have shown that *Ulva* is a shade tolerant genus and can compensate for reduced irradiance by increasing chlorophyll concentration and light absorption at low light levels. *Ulva* spp. Were able to survive over two months in darkness and to begin photosynthesising immediately when returned to the light (Vermaat & Sand-Jensen, 1987). Limited shading from suspended sediments is therefore not considered to negatively affect this genus.

Sensitivity assessment. The exposure of this biotope to suspended sediments in the water column will be limited to immersion periods, and wave action will reduce accumulation. The biotope is considered to be 'Not sensitive' to a reduction in suspended solids, although this may reduce food supply to barnacles and other filter and deposit feeders that occur in this biotope. An increase in suspended solids may lead to some sub-lethal abrasion of fronds and some reduction in photosynthesis while submerged with some effects on recruitment. Evidence globally indicates that increase suspended solids favour the turf-forming algae that occur within this biotope (Airoldi, 2003). Resistance is therefore assessed as 'Low' and resilience as 'High' so that sensitivity of the biotope is considered to be 'Low'. An increase in suspended solids above the pressure benchmark may result in a change in species composition with an increase in species seen in very turbid, silty environments e.g. *Ahnfeltia plicata, Rhodothamniella floridula, Polyides rotunda* and *Furcellaria lumbricalis*.

Smothering and siltation	Medium	<mark>High</mark>	Low
rate changes (light)	Q: High A: High C: Medium	Q: High A: Low C: Medium	Q: High A: Low C: Medium

Sedimentation can directly affect assemblages inhabiting rocky shores in different ways, but the main direct effects are burial/smothering and scour/abrasion of organisms. The degree of smothering experienced by the characterizing species will be influenced by the size and shape of the boulders. In areas with greater water flow or wave action, excess sediments will be removed from the rock surface within a few tidal cycles and may be redeposited on the sediments below the boulders, although scour patterns around boulders will determine the movement and removal of sediments.

The state of the tide will mediate the degree of impact on macroalgae. If smothering occurs at low tide when the algae is lying flat on the substratum, then most of the organism as well as the associated community will be covered by the deposition of fine material at the level of the benchmark. Smothering will prevent photosynthesis resulting in reduced growth and eventually death. If, however, smothering occurs whilst the alga is submerged standing upright then the photosynthetic surfaces of adult plants could be left uncovered. The resistance of this biotope to the given pressure may vary with time of day. Germlings, however, are likely to be smothered and killed in both scenarios and are inherently most susceptible to this pressure. Indeed early life stages are smaller in size than adults and are thus most vulnerable to this pressure as even a small load of added sediment will lead to the complete burial. In general, propagules, early post-settlement stages and juveniles suffer severe stress and mortality from sediments (Devinny &

Volse, 1978; Eriksson & Johansson, 2003; Berger *et al.*, 2003; Vadas *et al.*, 1992; Airoldi, 2003). Moss *et al.* (1973), for example, found that growth of zygotes of *Himanthalia elongata* were inhibited by a layer of silt 1-2 mm thick and that attachment on silt was insecure.

Increased abundance of algal turfs worldwide has been linked to sediment perturbations although not all the pathways and mechanisms of these effects are clear (see review by Airoldi, 2003). However, even the most tolerant of organisms would eventually suffer from inhibition and mortality following smothering although the thresholds for these effects have has not been identified (Airoldi, 2003). Corallina officinalis and others within the genus (e.g. Corallina pinnatifolia and Corallina vancouveriensis) are found on shores subject to high rates of sedimentation that are periodically disturbed by sand burial and scour (Stewart, 1989). Coralline turfs also trap sediments within the turf. The amount of sediment present and the associated fauna varies naturally depending on local conditions such as wave exposure (Dommasnes, 1969). On intertidal shores in southern California the amount of sediment trapped within turfs of Corallina spp. varied seasonally from <5 mm to >4.5 cm and was closely related to species composition and the structure of the turf. Airoldi (2003) identified a number of morphological, physiological and life history traits that conferred high levels of tolerance to sedimentation. Those shared by Corallina spp. are the regeneration of upright fronds from a perennial basal crust resistant to burial and scour, calcified thalli, apical meristems, large reproductive ouptuts, lateral vegetative growth and slow growth rates (Airoldi, 2003). Experimental deposition of sand on coralline turfs and maintained at 3 cm or 6 cm for one month via daily top-ups did not remove the turfs but did lead to rapid (within 1 hours) changes in the invertebrate species as highly mobile species moved away from the turf with later colonization by sand adapted species (Huff & Jarett, 2007). The community had recovered one month after sand deposition ceased (Huff & Jarett, 2007).

In a review of the effects of sedimentation on rocky coast assemblages, Airoldi (2003) outlined the evidence for the sensitivity of coralline algae to sedimentation. The reported results are contradictory with some authors suggesting that coralline algae are negatively affected by sediments while others report that encrusting corallines are often abundant or even dominant in a variety of sediment impacted habitats (Airoldi, 2003 and references therein). Crustose corallines have been reported to survive under a turf of filamentous algae and sediment for 58 days (the duration of experiment) in the Galapagos (species not identified, Kendrick, 1991). The crustose coralline *Hydrolithon reinboldii* has also been reported to survive deposition of silty sediments on subtidal reefs off Hawaii (Littler, 1973).

Atalah & Crowe (2010) added sediment to rockpools in controlled experiments that appear to be very similar to this biotope. The rockpools were occupied by a range of algae including encrusting corallines, turfs of *Mastocarpus stellatus*, *Chondrus crispus* and *Corallina officinalis* and green and red filamentous algae. The invertebrates present were mostly *Patella ulyssiponensis*, the winkle *Littorina littorea* and the flat topshell *Gibbula umbilicalis*. Sediment treatment involved the addition of a mixture of coarse and fine sand of either 300 mg/cml/month or 600 mg/cml every 15 days (the depth of sediment was not reported). The experimental treatments do not directly relate to the pressure benchmark but indicate some general trends in sensitivity. In the pools, the chronic addition of both levels of sediment led to a significant decrease in grazers and crustose coralline algae (*Ulva* sp.) but led to an increase in the mean cover of red turfing algae (*Mastocarpus stellatus* and *Chondrus crispus* and *Corallina officinalis*) from 11.7% (±1.0 S.E.) in controls to 26.1% (±4.7 S.E.) in sedimented assemblages, but there were no differences between the two levels of sedimentation. The cover of red filamentous algae (*Ceramium* spp.) and *Gelidium* spp.) was also

significantly increased in the sedimentation experiments. The experimental results support the general trend of greater sensitivity of grazers and encrusting corallines to sedimentation than turf-forming algae.

Observations and experiments indicate that *Ulva* spp. have relatively high tolerances for the stresses induced by burial such as darkness, hypoxia and exposure to sulphides (Vermaat & Sand-Jensen, 1987; Corradi *et al.*, 2006; Kamermans *et al.*, 1998). *Ulva lactuca* is a dominant species on sand-affected rocky shores in New Hampshire (Daly & Mathieson, 1977), although Littler *et al.* (1983) suggest that *Ulva* sp. are present in areas periodically subject to sand deposition not because they are able to withstand burial but because they are able to rapidly colonize sand-scoured areas. *Ulva* spp. have, however, been reported to form turfs that trap sediments (Airoldi, 2003, references therein) suggesting that resistance to chronic rather than acute siltation events may be higher.

Sensitivity assessment. Deposition of 5 cm of fine material (see benchmark) in a single incident is unlikely to result in significant mortality before sediments are removed by current and wave action. Burial will lower survival and germination rates of spores and cause some mortality in early life stages of *Laminaria digitata* and foliose red algae. Adults are more resistant but will experience a decrease in growth and photosynthetic rates. Mortality will be reduced, and possibly avoided, where the smothering sediment is removed due to wave action or tidal streams, depending on how long the sediment remains. Resistance has been assessed as 'Medium' as boulders are likely to project above the sediment surface and deposited sediments may be removed rapidly. Resilience is assessed as 'High'. Overall the biotope has a 'Low' sensitivity to smothering at the level of the benchmark.

Smothering and siltation Low rate changes (heavy) Q: Low A:

Low Q: Low A: NR C: NR Medium Q: High A: Low C: Medium Medium Q: Low A: Low C: Low

Sensitivity to this pressure will be mediated by site-specific hydrodynamic conditions and the footprint of the impact. Where a large area is covered, sediments may be shifted by wave and tides rather than removed. However, mortality will depend on the duration of smothering, where wave action rapidly mobilizes and removes fine sediments, survival may be much greater. No evidence was found to assess this pressure at the benchmark. The degree to which boulders are smothered will depend on the size and shape. Where boulders are large they may project above the deposit although sediment re-suspension and scour during the tidal cycle will impact the epifauana and flora. A deposit at the pressure benchmark would cover sediments with a thick layer of fine materials and scour patterns around boulders will influence the time for the sediment to be removed.

Sensitivity assessment. At the level of the benchmark (30 cm of fine material added to the seabed in a single event) smothering is likely to result in mortalities of the *Laminaria digitata* understorey algae and invertebrates present on the boulders and within the sediments underlying the boulders. Resistance is assessed as 'Low' as many individuals exposed to siltation at the benchmark level are predicted to die and resilience is assessed as 'Medium'. Overall the biotope is assessed as having 'Medium' sensitivity to siltation, at the pressure benchmark.

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

Increased levels of diffuse irradiation correlate with increased growth in macroalgae (Aguilera *et al.*, 1999). Macroalgae require light to photosynthesize, so that changes in light intensity are likely to affect photosynthesis, growth, competition and survival. Chapman (1995) noted that too little or too much light are likely to be stressors. There is considerable literature on the light compensation point of marine algae (see Lüning, 1990) but it is difficult to correlate such evidence with 'shading', as light saturation and compensation points depend on light availability, light quality, season and turbidity. As *Laminaria digitata is* out-competed by *Laminaria hyperborea* in deeper waters, it is likely that permanent shading would affect their growth and allow them to be out-competed by other, more shade tolerant species, within the affected area.

Corallina officinalis and other red algae are shade tolerant, often occurring under a macroalgal canopy that reduces light penetration. In areas of higher light levels, the fronds and bases may be lighter in colour due to bleaching (Colhart & Johansen, 1973). Other red algae in the biotope are flexible with regard to light levels. Canopy removal experiments in a rocky subtidal habitat in Nova Scotia, Canada, by Schmidt & Scheibling (2007) did not find a shift in understorey macroalgal turfs (dominated by *Corallina officinalis, Chondrus crispus* and *Mastocarpus stellatus*) to more light-adapted species over 18 months. Coralline crusts and *Corallina officinalis* are shade tolerant algae, often occurring under a macralgal canopy that reduces light penetration. These species can acclimate to different levels of light intensity and quality and encrusting corallines can occur in deeper water than other algae where light penetration is limited. Samples of *Lithophyllum impressum* suspended from a raft and shaded (50-75% light reduction) continued to grow over two years (Dethier, 1994).

Sensitivity assessment. As *Laminaria digitata* are out-competed in sublittoral conditions, it is likely that permanent shading would affect their growth and allow them to be out-competed by other, more shade tolerant species, such as red algae within the affected area, therefore a biotope resistance of 'Low' is suggested, with low confidence. Resilience is assessed as 'High' so that sensitivity is 'Low'.

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

No direct evidence was found to assess this pressure. The associated macroalgae (with the exception of *Ulva* spp.) have limited dispersal, barriers and changes in tidal excursion are not

considered relevant to these species as dispersal is limited.

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' to seat abrasion'.	ed habitats. NB. Collision	by grounding vessels is ac	ldressed under 'surface	
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'.				
Siological Pressures				
	Resistance	Resilience	Sensitivity	

			e en
Genetic modification &	Not relevant (NR)	Not relevant (NR)	Not relevant (NR)
indigenous species	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

No information was found on current production of *Mastocarpus stellatus*, *Chondrus crispus* or other turf forming red seaweeds in the UK and it is understood that wild harvesting rather than cultivation is the method of production. No evidence was found for the effects of gene flow between cultivated species and wild populations. *Palmaria palmata* may be cultivated for use as biofilters and/or food. Experiments by Van der Meer (1987) found that the hybrids of *Palmaria palmata* crosses from Canada and Ireland had vigorous growth and normal morphology, however, the tetraspores had lower viability and those that germinated produced abnormal sporelings. It was concluded that populations from Ireland and Canada represent the same species that is in the process of splitting into sibling species. Populations around the UK express different haplotypes (Provan *et al.*, 2005) indicating some genetic variation between populations. Although cultivation of different genotypes may lead to gene flow between wild and cultivated populations, the limited dispersal may reduce exposure. Some negative effects may arise from hybridization between very geographically separated populations but there is no evidence to suggest that gene flow between different UK haplotypes would lead to negative effects.

Sensitivity assessment. The pressure is considered to be 'Not relevant'.



Invasive Non-Indigenous Species (INIS) that can alter habitats (ecological engineers), or outcompete the native species for space and other resources such as light and nutrients, are the most likely species to negatively affect this biotope. Space pre-emption by *Laminaria digitata* and the turf and crustose bases of the red macroalgae, as well as the trapped sediment within the turf, may prevent settlement of INIS until disturbance events, such as boulder movement, create gaps for invasion. Not all species require bare patches, however, and in the Mediterranean, crustose corallines and algal turfs facilitate attachment of *Caulerpa racemosa* by providing a more complex substratum than bare rock (Bulleri & Benedetti-Cecchi, 2008).

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

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

In New Zealand, Thompson & Schiel (2012) observed that intertidal fucoids could outcompete *Undaria pinnatifida* and re-dominate the substratum. However, Thompson & Schiel (2012) suggested the fucoid recovery was partially due to an annual *Undaria pinnatifida* die back, which as noted by Heiser *et al.* (2014) does not occur in Plymouth sound, UK. *Undaria pinnatifida* was successfully eradicated on a sunken ship in Clatham Islands, New Zealand, by applying a heat treatment of 70°C (Wotton *et al.*, 2004), however, numerous other eradication attempts have failed, and as noted by Fletcher & Farrell (1998) once established, *Undaria pinnatifida* resists most attempts of long term removal. The biotope is unlikely to fully recover until *Undaria pinnatifida* is fully removed from the habitat, which as stated above is unlikely to occur.

The red seaweeds Heterosiphonia japonica and Neosiphonia harveyi may also occur in this biotope but again no impacts have been reported. The tunicates Didemnum vexillum and Asterocarpa humilis, the hydroid Schizoporella japonica and the bryozoan Watersipora subatra (Bishop, 2012c; Bishop, 2015a and b; Wood, 2015) are currently only recorded from artificial hard substratum in the UK and it is not clear what their established range and impacts in the UK would be.

A significant potential INIS is the Pacific oyster *Magallana gigas*, as its distribution and environmental tolerances are considered to overlap with this biotope and this reef forming species can alter habitat structure. It is found from the mid-littoral to the upper subtidal, and grows on hard substrata but also on other bivalves (e.g. blue mussels) and polychaete reefs (Padilla, 2010). Diederich (2005, 2006) examined settlement, recruitment and growth of *Magallana gigas* (as *Crassostrea gigas*) in the northern Wadden Sea. Recruitment of *Magallana gigas* was significantly higher in the intertidal than the shallow subtidal and the survival of adult oysters in the subtidal was limited by predation. *Magallana gigas* prefer to settle on conspecifics, so that it can build massive oyster reefs.

The non-native crab Hemigrapsus sanguineus has recently been recorded in the UK (Sweet & Sewell,

2014) and has the potential to be a significant predator of intertidal invertebrates. Significant reductions in common shore crab abundance and mussel density have been reported where the crab has achieved high densities in mainland Europe (Sweet & Sewell, 2014). In Rye, New York, declines of approximately 80% of *Littorina littorea* in the intertidal were reported to coincide with an expansion of the *Hemigrapsus sanguineus* population (Kraemer *et al.*, 2007). This crab occurs on exposed shores and may therefore occur in this biotope when established. If predation of littorinids was significantly increased this could impact the algal composition and abundance of this biotope by altering the level of grazing pressure.

Sensitivity assessment. Little evidence was found to assess the impact of INIS on this biotope and much of the evidence comes from intertidal habitats in other countries. The conversion of this biotope to a *Magallana gigas* reef would represent a significantly negative impact. Replacement of red algal turfs by other similar species may lead to some subtle effects on local ecology but at low abundances the biotope would still be recognizable from the description. Based on conversion to a *Sargassum muticum* or *Undaria pinnatifida* or *Crassostrea gigas* dominated biotope, resistance to this pressure is assessed as 'Low'. The biotope will only recover if these species are removed, either through active management or natural processes. To recognize that recovery may be prolonged, resilience is assessed as 'Very Low' and sensitivity is therefore assessed as 'High'.

Introduction of microbial	High	<mark>High</mark>
pathogens	Q: High A: High C: Medium	Q: High A: High C: High

Not sensitive

Q: High A: High C: Medium

Symptoms of disease are regularly seen on *Laminaria* species, however, little evidence in the literature is apparent. Infection of *Laminaria japonica* sporophytes by *Pseudoalteromonas*, *Vibrio* and *Halomonas* results in the characteristic symptoms of hole-rotten disease (Wang *et al.*, 2008). Additionally, red spot disease may be caused by bacteria of the genus *Alteromonas* (Sawabe *et al.*, 1998). Hyperplasia or gall growths are often seen as dark spots on *Laminaria digitata* and have been associated with endophytic brown filamentous algae. It can be inferred from these observations that microbial pathogens may impact growth rates of individuals. There is no evidence in the literature that infection by microbial pathogens results in mass death

of *Laminaria* populations and the kelp themselves are known to regulate bacterial infections through iodine metabolism (Cosse *et al.*, 2009).

Several coralline and non-coralline species are epiphytic on *Corallina officinalis*. Irvine & Chamberlain (1994) cite tissue destruction caused by *Titanoderma corallinae*. However, no information on pathogenic organisms in the UK was found. *Corallina officinalis*, like many other algal species has been demonstrated to produce antibacterial substances (Taskin *et al.*, 2007). No evidence was found for pathogens of the other red algae which may be present in this biotope. The fungal pathogen, *Petersenia palmaria* n. sp (Oomycetes) which infects *Palmaria mollis*, does not affect *Palmaria palmata* (Meer & Pueschel, 1985).

Other species associated with this biotope may experience low levels of infestation by pathogens but mass-mortalities have not been recorded. Barnacles are parasitized by a variety of organisms and, in particular, the cryptoniscid isopod *Hemioniscus balani*, in which heavy infestation can cause castration of the barnacle. At usual levels of infestation these are not considered to lead to high levels of mortality.

Diseased encrusting corallines were first observed in the tropics in the early 1990's when the bacterial pathogen Coralline Lethal Orange Disease (CLOD) was discovered (Littler & Littler, 1995). All species of articulated and crustose species tested to date are easily infected by CLOD

and it has been increasing in occurrence at sites where first observed and spreading through the tropics. Another bacterial pathogen causing a similar CLOD disease has been observed with a greater distribution and a black fungal pathogen first discovered in American Samoa has been dispersing (Littler & Littler, 1998). An unknown pathogen has also been reported to lead to white 'target-shaped' marks on corallines, again in the tropic (Littler *et al.*, 2007). No evidence was found that these are impacting temperate coralline habitats.

Sensitivity assessment. No evidence was found that outbreaks of microbial pathogens significantly impact populations of the key characterizing *Laminaria digitata* and other associated algal species. Biotope resistance is, therefore, assessed as 'High' and resilience as 'High', so that the biotope is considered to be 'Not sensitive'.

Removal of target species

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

Q: High A: Medium C: Medium

Direct, physical impacts from harvesting are assessed through the abrasion and penetration of the seabed pressures. The sensitivity assessment for this pressure considers any biological/ecological effects resulting from the removal of target species on this biotope. Many of the algal species characterizing or associated with this biotope may be targeted by either recreational or commercial harvesters.

Traditionally *Laminaria digitata* was added to agricultural lands as fertilizers; now *Laminaria* species are used in a range of different products, with its alginates used in the cosmetic, pharmaceutical and agri-food industries (Kervarec *et al.*, 1999; McHugh, 2003). In France, *Laminaria digitata* is harvested with a 'Scoubidou' (a curved iron hook which is mechanically operated). This device is considered to be selective; only harvesting individuals older than 2 years (Arzel, 2002). France reportedly harvests 75,000t kelp, mainly consisting of *Laminaria digitata* annually (FAO, 2007). Davoult *et al.* (2011) suggested that the maintenance of a sustainable crop of *Laminaria digitata* was possible if the industry continues employing small vessels evenly dispersed along the coastline. This would protect against habitat fragmentation and buffer over exploitation (Davoult *et al.*, 2011). A fallow period of 18-24 months has been suggested for *Laminaria digitata* and *Saccorhiza polyschides* was indicated as a threat to the continued harvesting effort of *Laminaria digitata* and *Saccorhiza polyschides* was indicated as a threat to the continued harvesting effort of *Laminaria digitata* (Engelen *et al.*, 2011). If *Laminaria digitata*, the key characterizing and structuring species of this biotope is removed then the biotope, is considered lost due to the significant alteration to the biotope classification and character of the habitat is likely.

Canopy removal of *Laminaria digitata* has been shown to reduce shading, resulting in the bleaching of sub-canopy algae (Hawkins & Harkin, 1985). Harvesting may also result in habitat fragmentation, a major threat to this biotope's ecosystem functioning (Valero *et al.*, 2011). In the UK, harvesting of *Laminaria digitata* is currently restricted to manual removal and farming on small scales.

Red algae within the biotope may also be subject to hand gathering. *Mastocarpus stellatus* is harvested commercially in Scotland and Ireland to produce carrageen, the stipe is removed but the base is left intact to allow the algae to re-grow. *Palmaria palmata* and *Osmundea pinnatifida* are also collected by hand commercially and recreationally for consumption. *Corallina officinalis* is collected for medical purposes; the fronds are dried and converted to hydroxyapatite and used as bone forming material (Ewers *et al.*, 1987). It is also sold as a powder for use in the cosmetic industry.

Sensitivity assessment. As the macroalgae species that are harvested in this biotope are attached and conspicuous, a single event of targeted harvesting could efficiently remove individuals and resistance is assessed as 'Low'. Resilience of *Laminaria digitata and* the turf forming red seaweeds is assessed as 'High' (based on evidence for recovery from harvesting that did not damage the algal bases, although see caveats in the resilience section) and biotope sensitivity is assessed as 'Low'. This assessment refers to a single collection event, long-term harvesting over wide spatial scales will lead to greater impacts, with lower resistance and longer recovery times.

Removal of non-target species

Low Q: Low A: NR C: NR Medium Q: High A: Low C: Medium

Medium

Q: Low A: Low C: Low

Direct, physical impacts are assessed through the abrasion and penetration of the seabed pressures, while this pressure considers the ecological or biological effects of incidental removal of species. Removal of a large proportion of the brown and red macroalgae would substantially alter the character of the biotope. Loss of the characterizing and associated species would also alter ecosystem functions, such as rates of production and the provision of a structurally complex habitat.

Sensitivity assessment. Removal of species as by-catch would remove the biological assemblage that defines the biotope, hence the biotope is considered to have 'Low' resistance to this pressure and to have 'Medium' resilience. Biotope sensitivity is therefore 'Medium'.

Bibliography

Addessi, L., 1994. Human Disturbance and Long-Term Changes on a Rocky Intertidal Community. *Ecological Applications*, **4**, 786-797.

Adey, W.H. & Adey, P.J., 1973. Studies on the biosystematics and ecology of the epilithic crustose corallinacea of the British Isles. *British Phycological Journal*, **8**, 343-407.

Aguilera, J., Karsten, U., Lippert, H., Voegele, B., Philipp, E., Hanelt, D. & Wiencke, C., 1999. Effects of solar radiation on growth, photosynthesis and respiration of marine macroalgae from the Arctic. *Marine Ecology Progress Series*, **191**, 109-119.

Airoldi, L., 2003. The effects of sedimentation on rocky coast assemblages. *Oceanography and Marine Biology: An Annual Review*, **41**,161-236

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.

Alströem-Rapaport, C., Leskinen, E. & Pamilo, P., 2010. Seasonal variation in the mode of reproduction of *Ulva intestinalis* in a brackish water environment. *Aquatic Botany*, **93** (4), 244-249.

Amsler, C.D. & Searles, R.B., 1980. Vertical distribution of seaweed spores in a water column off shore of North Carolina. *Journal of Phycology*, **16**, 617-619.

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

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

Atalah, J. & Crowe, T.P., 2010. Combined effects of nutrient enrichment, sedimentation and grazer loss on rock pool assemblages. *Journal of Experimental Marine Biology and Ecology*, **388** (1), 51-57.

Axelsson, B. & Axelsson, L., 1987. A rapid and reliable method to quantify environmental effects on *Laminaria* based on measurements of ion leakage. *Botanica Marina*, **30**, 55-61.

Bak, U.G., 2014. Suitable cultivation areas for *Palmaria palmata* (Rhodophyta) and *Saccharina latissima* (Phaeophyceae) in the inner Danish waters in relation to variations in light, temperature and salinity. Roskilde University. MSc thesis

Bamber, R.N. & Irving, P.W., 1993. The Corallina run-offs of Bridgewater Bay. Porcupine Newsletter, 5, 190-197.

Barnes, H., Finlayson, D.M. & Piatigorsky, J., 1963. The effect of desiccation and anaerobic conditions on the behaviour, survival and general metabolism of three common cirripedes. *Journal of Animal Ecology*, **32**, 233-252.

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.

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

Beer, S., Björk, M. & Beardall, J., 2014. Photosynthesis in the Marine Environment. John Wiley & Sons.

Bellgrove, A., Clayton, M.N. & Quinn, G., 1997. Effects of secondarily treated sewage effluent on intertidal macroalgal recruitment processes. *Marine and Freshwater Research*, **48** (2), 137-146.

Bellgrove, A., McKenzie, P.F., McKenzie, J.L. & Sfiligoj, B.J., 2010. Restoration of the habitat-forming fucoid alga *Hormosira banksii* at effluent-affected sites: competitive exclusion by coralline turfs. *Marine Ecology Progress Series*, **419**, 47-56.

Berger, R., Bergström, L., Granéli, E. & Kautsky, L., 2004. How does eutrophication affect different life stages of *Fucus vesiculosus* in the Baltic Sea? - a conceptual model. *Hydrobiologia*, **514** (1-3), 243-248.

Berger, R., Henriksson, E., Kautsky, L. & Malm, T., 2003. Effects of filamentous algae and deposited matter on the survival of *Fucus* vesiculosus L. germlings in the Baltic Sea. *Aquatic Ecology*, **37** (1), 1-11.

Bertness, M.D., Leonard, G.H., Levine, J.M., Schmidt, P.R. & Ingraham, A.O., 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology*, **80** (8), 2711-27

Bertocci, I., Arenas, F., Matias, M., Vaselli, S., Araújo, R., Abreu, H., Pereira, R., Vieira, R. & Sousa-Pinto, I., 2010. Canopy-forming species mediate the effects of disturbance on macroalgal assemblages on Portuguese rocky shores. *Marine Ecology Progress Series*, **414**, 107-116.

Bird, N.L., Chen, L.C.-M. & McLachlan, J., 1979. Effects of temperature, light and salinity of growth in culture of *Chondrus crispus*, *Furcellaria lumbricalis, Gracilaria tikvahiae* (Gigartinales, Rhodophyta), and *Fucus serratus* (Fucales, Phaeophyta). *Botanica Marina*, **22**, 521-527.

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, J. 2012c. Carpet Sea-squirt, *Didemnum vexillum.Great Britain Non-native Species Secretariat* [On-line]. [cited 30/10/2018]. Available from: http://www.nonnativespecies.org/factsheet/factsheet.cfm?speciesId=1209

Bishop, J. 2015a. Compass sea squirt, Asterocarpa humilis. Great Britain Non-native Species Secretariat. [On-line] [cited 16/06/2015].

Available from: < http://www.nonnativespecies.org

Bishop, J. 2015b. Watersipora subatra. Great Britain Non-native Species Secretariat. [On-line][cited 16/06/2015]. Available from: http://www.nonnativespecies.org

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

Boalch, G.T. & Jephson, N.A., 1981. A re-examination of the seaweeds on Colman's traverses at Wembury. *Proceedings of the International Seaweed Symposium*, **8**, 290-293.

Boalch, G.T., Holme, N.A., Jephson, N.A. & Sidwell, J.M.C., 1974. A resurvey of Colman's intertidal traverses at Wembury, South Devon. *Journal of the Marine Biological Association of the United Kingdom*, **5**, 551-553.

Boaventura, D., 2000. Patterns of distribution in intertidal rocky shores: the role of grazing and competition in structuring communities. Tese de Doutoramento, Universidade do Algarve.

Boaventura, D., Alexander, M., Della Santina, P., Smith, N.D., Re, P., da Fonseca, L.C. & Hawkins, S.J., 2002. The effects of grazing on the distribution and composition of low-shore algal communities on the central coast of Portugal and on the southern coast of Britain. *Journal of Experimental Marine Biology and Ecology*, **267** (2), 185-206.

Boaventura, D., Da Fonseca, L.C. & Hawkins, S.J., 2003. Size matters: competition within populations of the limpet Patella depressa. *Journal of Animal Ecology*, **72** (3), 435-446.

Bokn, T., 1985. Effects of diesel oil on commercial benthic algae in Norway. In *Proceedings of 1985 Oil Spill Conference*, (ed. American Petroleum Institute), pp. 491-496. Washington, D.C.: American Petroleum Institute.

Boller, M.L. & Carrington, E., 2006. In situ measurements of hydrodynamic forces imposed on *Chondrus crispus* Stackhouse. *Journal of Experimental Marine Biology and Ecology*, **337** (2), 159-170.

Boller, M.L. & Carrington, E., 2007. Interspecific comparison of hydrodynamic performance and structural properties among intertidal macroalgae. *Journal of Experimental Biology*, **210** (11), 1874-1884.

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.

Bonner, T. M., Pyatt, F. B. & Storey, D. M., 1993. Studies on the motility of the limpet *Patella vulgata* in acidified sea-water. *International Journal of Environmental Studies*, **43**, 313-320.

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

Brosnan, D.M., 1993. The effect of human trampling on biodiversity of rocky shores: monitoring and management strategies. *Recent Advances in Marine Science and Technology*, **1992**, 333-341.

Brosnan, D.M. & Crumrine, L.L., 1992. Human impact and a management strategy for Yaquina Head Outstanding Natural Area (summary only). A report to the Bureau of Land Management, Department of the Interior, Salem, Oregon.

Brosnan, D.M. & Crumrine, L.L., 1994. Effects of human trampling on marine rocky shore communities. *Journal of Experimental Marine Biology and Ecology*, **177**, 79-97.

Brown, P.J. & Taylor, R.B., 1999. Effects of trampling by humans on animals inhabiting coralline algal turf in the rocky intertidal. *Journal of Experimental Marine Biology and Ecology*, **235**, 45-53.

Brown, V., Davies, S. & Synnot, R., 1990. Long-term monitoring of the effects of treated sewage effluent on the intertidal macroalgal community near Cape Schanck, Victoria, Australia. *Botanica Marina*, **33** (1), 85-98.

Bryan, G.W., 1984. Pollution due to heavy metals and their compounds. In *Marine Ecology: A Comprehensive, Integrated Treatise on Life in the Oceans and Coastal Waters*, vol. 5. *Ocean Management*, part 3, (ed. O. Kinne), pp.1289-1431. New York: John Wiley & Sons.

Bryan, G.W., Langston, W.J., Hummerstone, L.G., Burt, G.R. & Ho, Y.B., 1983. An assessment of the gastropod Littorina littorea (L.) as an indicator of heavy metal contamination in United Kingdom estuaries. *Journal of the Marine Biological Association of the United Kingdom*, **63**, 327-345.

Bulleri, F. & Airoldi, L., 2005. Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea. *Journal of Applied Ecology*, **42** (6), 1063-1072.

Bulleri, F. & Benedetti-Cecchi, L., 2008. Facilitation of the introduced green alga *Caulerpa racemosa* by resident algal turfs: experimental evaluation of underlying mechanisms. *Marine Ecology Progress Series*, **364**, 77-86.

Bulleri, F., Benedetti-Cecchi, L., Acunto, S., Cinelli, F. & Hawkins, S.J., 2002. The influence of canopy algae on vertical patterns of distribution of low-shore assemblages on rocky coasts in the northwest Mediterranean. *Journal of Experimental Marine Biology and Ecology*, **267** (1), 89-106.

Chamberlain, Y.M., 1996. Lithophylloid Corallinaceae (Rhodophycota) of the genera Lithophyllum and Titausderma from southern Africa. *Phycologia*, **35**, 204-221.

Chapman, A.R.O. (1995). Functional ecology of fucoid algae: twenty-three years of progress. Phycologia, 34(1), 1-32.

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/

Colhart, B.J., & Johanssen, H.W., 1973. Growth rates of *Corallina officinalis* (Rhodophyta) at different temperatures. *Marine Biology*, **18**, 46-49.

Colman, J., 1933. The nature of the intertidal zonation of plants and animals. *Journal of the Marine Biological Association of the United Kingdom*, **18**, 435-476.

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 1861075618. 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/

Corradi, M.G., Gorbi, G. & Zanni, C., 2006. Hypoxia and sulphide influence gamete production in *Ulva* sp. *Aquatic Botany*, **84** (2), 144-150.

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.

Cruz Motta, J.C., Underwood, A., Chapman, M. & Rossi, F., 2003. Benthic assemblages in sediments associated with intertidal boulder-fields. *Journal of Experimental Marine Biology and Ecology*, **285**, 383-401.

Daly, M.A. & Mathieson, A.C., 1977. The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, USA. *Marine Biology*, **43**, 45-55.

Davenport, J. & Davenport, J.L., 2005. Effects of shore height, wave exposure and geographical distance on thermal niche width of intertidal fauna. *Marine Ecology Progress Series*, **292**, 41-50.

Davies, A.J., Johnson, M.P. & Maggs, C.A., 2007. Limpet grazing and loss of *Ascophyllum nodosum* canopies on decadal time scales. *Marine Ecology Progress Series*, **339**, 131-141.

Davison, I.R., Andrews, M. & Stewart, W.D.P., 1984. Regulation of growth in *Laminaria digitata*: use of in-vivo nitrate reductase activities as an indicator of nitrogen limitation in field populations of *Laminaria* spp. *Marine Biology*, **84**, 207-217.

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

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

Denny, M., Gaylord, B., Helmuth, B. & Daniel, T., 1998. The menace of momentum: dynamic forces on flexible organisms. *Limnology* and Oceanography, **43** (5), 955-968.

Dethier, M.N., 1994. The ecology of intertidal algal crusts: variation within a functional group. *Journal of Experimental Marine Biology and Ecology*, **177** (1), 37-71.

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

Diederich, S., 2005. Differential recruitment of introduced Pacific oysters and native mussels at the North Sea coast: coexistence possible? *Journal of Sea Research*, **53** (4), 269-281.

Diederich, S., 2006. High survival and growth rates of introduced Pacific oysters may cause restrictions on habitat use by native mussels in the Wadden Sea. *Journal of Experimental Marine Biology and Ecology*, **328** (2), 211-227.

Dommasnes, A., 1969. On the fauna of Corallina officinalis L. in western Norway. Sarsia, 38, 71-86.

Dring, M.J. & Brown, F.A., 1982. Photosynthesis of intertidal brown algae during and after periods of emersion: a renewed search for physiological causes of zonation. *Marine Ecology Progress Series*, **8**, 301-308.

Dudgeon, S. R., Davison. L R. & Vadas, R. L., 1989. Effect of freezing on photosynthesis of intertidal macroalgae relative tolerance of *Chondrus crispus* and *Mastocarpus stellatus* (Rhodophyta). *Marine Biology*, **101**, 107-114

Dudgeon, S., Kübler, J., Wright, W., Vadas Sr, R. & Petraitis, P.S., 2001. Natural variability in zygote dispersal of Ascophyllum nodosum at small spatial scales. *Functional Ecology*, **15** (5), 595-604.

Dudgeon, S.R., Kuebler, J.E., Vadas, R.L. & Davison, I.R., 1995. Physiological responses to environmental variation in intertidal red algae: does thallus morphology matter? *Marine Ecology Progress Series*, **117**, 193-206.

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., 1984b. Population biology of the crustose red alga *Lithophyllum incrustans* Phil. 3. The effects of local environmental variables. *Biological Journal of the Linnean Society*, **23**, 365-374.

Edyvean, R.G.J. & Ford, H., 1986. Population structure of *Lithophyllum incrustans* (Philippi) (Corallinales Rhodophyta) from southwest Wales. *Field Studies*, **6**, 397-405.

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

Eriksson, B.K. & Johansson, G., 2003. Sedimentation reduces recruitment success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic

Sea. European Journal of Phycology, **38** (3), 217-222.

Ewers, R., Kasperk, C. & Simmons, B., 1987. Biologishes Knochenimplantat aus Meeresalgen. Zahnaerztliche Praxis, **38**, 318-320.

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

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

Firth, L., Thompson, R., Bohn, K., Abbiati, M., Airoldi, L., Bouma, T., Bozzeda, F., Ceccherelli, V., Colangelo, M. & Evans, A., 2014. Between a rock and a hard place: Environmental and engineering considerations when designing coastal defence structures. *Coastal Engineering*, **87**, 122-135.

Fletcher, H. & Frid, C.L.J., 1996b. The response of an inter-tidal algal community to persistent trampling and the implications for rocky shore management. In Jones, P.S., Healy, M.G. & Williams, A.T. (ed.) Studies in European coastal management., Cardigan, Wales: Samara Publishing

Fletcher, H. & Frid, C.L.J., 1996a. Impact and management of visitor pressure on rocky intertidal algal communities. Aquatic Conservation: Marine and Freshwater Ecosystems, **6**, 287-297.

Fletcher, R. & Farrell, P., 1998. Introduced brown algae in the North East Atlantic, with particular respect to Undaria pinnatifida (Harvey) Suringar. *Helgolander Meeresuntersuchungen*, **52** (3-4), 259-275.

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

Flores-Moya, A., Fernandez-Garcia, J.A. & Niell, F.X., 1992. Influences of lightintensity and temperature on the summer disappearance of *Laurencia pinnatifida* (Ceramiales Rhodophyta). *Cryptogamic Botany*, **2** (4), 345-350.

Frazer, A.W.J., Brown, M.T. & Bannister, P., 1988. The frost resistance of some littoral and sub-littoral algae from southern New Zealand. *Botanica Marina*, **31**, 461-464.

Frid, C.L.J. & Fordham, E., 1994. The morphology of the sub-littoral gastropod *Gibula cineraria* (L) along a gradient of wave action. *Ophelia*, **40** (2), 135-146.

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.

Garbary, D.J., Beveridge, L.F., Flynn, A.D. & White, K.L., 2012. Population ecology of *Palmaria palmata* (Palmariales, Rhodophyta) from harvested and non-harvested shores on Digby Neck, Nova Scotia, Canada. *Algae*, **27** (1), 33-42.

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.

Gevaert, F., Davoult, D., Creach, A., Kling, R., Janquin, M.-A., Seuront, L. & Lemoine, Y., 2001. Carbon and nitrogen content of *Laminaria saccarina* in the eastern English Channel: Biometrics an dseasonal variations. *Journal of the Marine Biological Association* of the United Kingdom, **81**, 727-734.

Godin, J., 1981. Modalités de la fixation et de la dispersion du Laurencia pinnatifida (Hudson) Lamouroux (Rhodophycée, Céramiale) sur les substrats rocheux de mode battu. *Botanica Marina*, **24**(5), 245-250.

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

Gorgula, S.K. & Connell, S.D., 2004. Expansive covers of turf-forming algae on human-dominated coast: the relative effects of increasing nutrient and sediment loads. *Marine Biology*, **145** (3), 613-619.

Gorman, D., Bajjouk, T., Populus, J., Vasquez, M. & Ehrhold, A., 2013. Modeling kelp forest distribution and biomass along temperate rocky coastlines. *Marine Biology*, **160** (2), 309-325.

Green, D., Chapman, M. & Blockley, D., 2012. Ecological consequences of the type of rock used in the construction of artificial boulder-fields. *Ecological Engineering*, **46**, 1-10.

Grenon, J.F. & Walker, G., 1981. The tenacity of the limpet, *Patella vulgata* L.: an experimental approach. *Journal of Experimental Marine Biology and Ecology*, **54**, 277-308.

Guarnieri, G., Terlizzi, A., Bevilacqua, S. & Fraschetti, S., 2012. Increasing heterogeneity of sensitive assemblages as a consequence of human impact in submarine caves. *Marine Biology*, **159** (5), 1155-1164.

Guidone, M. & Grace, S., 2010. The ratio of gametophytes to tetrasporophytes of intertidal *Chondrus crispus* (Gigartinaceae) across a salinity gradient. *Rhodora*, **112** (949), 80-84.

Guiry, M.D. & Guiry, G.M. 2015. AlgaeBase [Online], National University of Ireland, Galway [cited 30/6/2015]. Available from: http://www.algaebase.org/

Harlin, M.M., & Lindbergh, J.M., 1977. Selection of substrata by seaweed: optimal surface relief. *Marine Biology*, **40**, 33-40.

Hawkins, S., 1983. Interactions of *Patella* and macroalgae with settling *Semibalanus balanoides* (L.). *Journal of Experimental Marine Biology and Ecology*, **71** (1), 55-72.

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

Hawkins, S.J. & Hartnoll, R.G., 1983. Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology: an Annual Review*, **21**, 195-282.

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

Hawkins, S.J. & Southward, A.J., 1992. The Torrey Canyon oil spill: recovery of rocky shore communities. In Restoring the Nations Marine Environment, (ed. G.W. Thorpe), Chapter 13, pp. 583-631. Maryland, USA: Maryland Sea Grant College.

Hawkins, S.J., Hartnoll, R.G., Kain, J.M. & Norton, T.A., 1992. Plant-animal interactions on hard substrata in the north-east Atlantic. In *Plant-animal interactions in the marine benthos* (ed. D.M. John, S.J. Hawkins & J.H. Price), pp. 1-32. Oxford: Clarendon Press. [Systematics Association Special Volume, no. 46.]

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

Hicks, G.R.F., 1985. Meiofauna associated with rocky shore algae. In *The Ecology of Rocky Coasts: essays presented to J.R. Lewis*, D.Sc., (ed. P.G. Moore & R. Seed, ed.). pp. 36-56. London: Hodder & Stoughton Ltd.

Hiscock, K., 1984. Rocky shore surveys of the Isles of Scilly. March 27th to April 1st and July 7th to 15th 1983. Peterborough: Nature Conservancy Council, CSD Report, No. 509.

Hoare, R. & Hiscock, K., 1974. An ecological survey of the rocky coast adjacent to the effluent of a bromine extraction plant. *Estuarine and Coastal Marine Science*, **2** (4), 329-348.

Holmes, S.P., Walker, G. & van der Meer, J., 2005. Barnacles, limpets and periwinkles: the effects of direct and indirect interactions on cyprid settlement and success. *Journal of Sea Research*, **53** (3), 181-204.

Huff, T.M. & Jarett, J.K., 2007. Sand addition alters the invertebrate community of intertidal coralline turf. *Marine Ecology Progress* Series, 345, 75-82.

Hyslop, B.T., Davies, M.S., Arthur, W., Gazey, N.J. & Holroyd, S., 1997. Effects of colliery waste on littoral communities in northeast England. *Environmental Pollution*, **96** (3), 383-400.

Irvine, L. M. & Chamberlain, Y. M., 1994. Seaweeds of the British Isles, vol. 1. Rhodophyta, Part 2B Corallinales, Hildenbrandiales. London: Her Majesty's Stationery Office.

Irvine, L.M., 1983. Seaweeds of the British Isles vol. 1. Rhodophyta Part 2A. Cryptonemiales (sensu stricto), Palmariales, Rhodymeniales. London: British Museum (Natural History).

Jenkins, S., Aberg, P., Cervin, G., Coleman, R., Delany, J., Hawkins, S., Hyder, K., Myers, A., Paula, J. & Power, A., 2001. Population dynamics of the intertidal barnacle *Semibalanus balanoides* at three European locations: spatial scales of variability. *Marine Ecology Progress Series*, **217**, 207-217.

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

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

Johansen, W.H., 1974. Articulated coralline algae. Oceanography and Marine Biology: an Annual Review, **12**, 77-127.

Jonsson, P.R., Granhag, L., Moschella, P.S., Åberg, P., Hawkins, S.J. & Thompson, R.C., 2006. Interactions between wave action and grazing control the distribution of intertidal macroalgae. *Ecology*, **87** (5), 1169-1178.

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

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

Kamermans, P., Malta, E.-j., Verschuure, J.M., Lentz, L.F. & Schrijvers, L., 1998. Role of cold resistance and burial for winter survival and spring initiation of an *Ulva* spp.(Chlorophyta) bloom in a eutrophic lagoon (Veerse Meer lagoon, The Netherlands). *Marine Biology*, **131** (1), 45-51.

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

Karsten, U., Dummermuth, A., Hoyer, K. & Wiencke, C., 2003. Interactive effects of ultraviolet radiation and salinity on the ecophysiology of two Arctic red algae from shallow waters. *Polar Biology*, **26** (4), 249-258.

Kendrick, G.A., 1991. Recruitment of coralline crusts and filamentous turf algae in the Galapagos archipelago: effect of simulated scour, erosion and accretion. *Journal of Experimental Marine Biology and Ecology*, **147** (1), 47-63

Keough, M.J. & Quinn, G.P., 1998. Effects of periodic disturbances from trampling on rocky intertidal algal beds. *Ecological Applications*, **8** (1), 141-161.

Kervarec, F., Arzel, P. & Guyader, O., 1999. Fisher Behaviour and Economic Interactions Between Fisheries: Examining Seaweed and Scallop Fisheries of the Brest District (Western Brittany, France). *The XIth Annual Conference of the European Association of Fisheries Economists.* 6th-10th April 1999, Dublin, pp.

Kindig, A.C., & Littler, M.M., 1980. Growth and primary productivity of marine macrophytes exposed to domestic sewage effluents. *Marine Environmental Research*, **3**, 81-100.

Kinne, O., 1971b. Salinity - invertebrates. In Marine Ecology: A Comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters. Vol. 1 Environmental Factors, Part 2, pp. 821-995. London: John Wiley & Sons.

Kinne, O., 1977. International Helgoland Symposium "Ecosystem research": summary, conclusions and closing. Helgoländer

Wissenschaftliche Meeresuntersuchungen, 30(1-4), 709-727.

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

Kraemer, G.P., Sellberg, M., Gordon, A. & Main, J., 2007. Eight-year record of *Hemigrapsus sanguineus* (Asian shore crab) invasion in western Long Island sound estuary. *Northeastern Naturalist*, **14** (2), 207-224.

Kraufvelin, P., 2007. Responses to nutrient enrichment, wave action and disturbance in rocky shore communities. *Aquatic Botany*, **87** (4), 262-274.

Kraufvelin, P., Moy, F.E., Christie, H. & Bokn, T.L., 2006. Nutrient addition to experimental rocky shore communities revisited: delayed responses, rapid recovery. *Ecosystems*, **9** (7), 1076-1093.

Kraufvelin, P., Ruuskanen, A., Nappu, N. & Kiirikki, M., 2007. Winter colonisation and succession of filamentous algae and possible relationships to *Fucus vesiculosus* settlement in early summer. *Estuarine Coastal and Shelf Science*, **72**, 665-674.

Latham, H., 2008. Temperature stress-induced bleaching of the coralline alga *Corallina officinalis*: a role for the enzyme bromoperoxidase. *Bioscience Horizons*, 1-10

Lewis, J., 1961. The Littoral Zone on Rocky Shores: A Biological or Physical Entity? Oikos, 12 (2), 280-301.

Lewis, J. & Bowman, R.S., 1975. Local habitat-induced variations in the population dynamics of *Patella vulgata* L. *Journal of Experimental Marine Biology and Ecology*, **17** (2), 165-203.

Liddle, M.J., 1997. Recreational ecology. The ecological impact of outdoor recreation and ecotourism. London: Chapman & Hall.

Lindgren, A. & Åberg, P., 1996. Proportion of life cycle stages of *Chondrus crispus* and its population structure: a comparison between a marine and an estuarine environment. *Botanica Marina*, **39** (1-6), 263-268.

Littler, M. & Littler, D., 1998. An undescribed fungal pathogen of reef-forming crustose corraline algae discovered in American Samoa. *Coral Reefs*, **17** (2), 144-144.

Littler, M. & Littler, D.S. 2013. The nature of crustose coralline algae and their interactions on reefs. *Smithsonian Contributions to the Marine Sciences*, **39**, 199-212

Littler, M. & Murray, S., 1975. Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. *Marine Biology*, **30** (4), 277-291.

Littler, M. M., & Littler, D. S. 1984. Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. *Journal of Experimental Marine Biology and Ecology*, **74**(1), 13-34.

Littler, M.M., 1973. The population and community structure of Hawaiian fringing-reef crustose Corallinaceae (Rhodophyta, Cryptonemiales). *Journal of Experimental Marine Biology and Ecology*, **11** (2), 103-120.

Littler, M.M. & Littler, D.S., 1995. Impact of CLOD pathogen on Pacific coral reefs. *Science*, **267**, 1356-1356.

Littler, M.M., & Kauker, B.J., 1984. Heterotrichy and survival strategies in the red alga *Corallina officinalis* L. *Botanica Marina*, **27**, 37-44.

Littler, M.M., Littler, D.S. & Brooks, B.L. 2007. Target phenomena on south Pacific reefs: strip harvesting by prudent pathogens? *Reef Encounter*, **34**, 23-24

Littler, M.M., Martz, D.R. & Littler, D.S., 1983. Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. *Marine Ecology Progress Series.* **11** (2), 129-139.

Liversage, K., 2015. The influence of boulder shape on the spatial distribution of crustose coralline algae (Corallinales, Rhodophyta). *Marine Ecology*, **37**, 459-462.

Long, J.D., Cochrane, E. & Dolecal, R., 2011. Previous disturbance enhances the negative effects of trampling on barnacles. *Marine Ecology Progress Series*, **437**, 165-173.

 $\label{eq:linear} L"uning, K., 1990. Seaweeds: their environment, biogeography, and ecophysiology: John Wiley \& Sons.$

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

Luther, G., 1976. Bewuchsuntersuchungen auf Natursteinsubstraten im Gezeitenbereich des Nordsylter Wattenmeeres: Algen. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, 28 (3-4), 318-351.

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

MacFarlane, C.I., 1952. A survey of certain seaweeds of commercial importance in southwest Nova Scotia. *Canadian Journal of Botany*, **30**, 78-97.

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

Marshall, D.J. & McQuaid, C.D., 1989. The influence of respiratory responses on the tolerance to sand inundation of the limpets *Patella granularis* L.(Prosobranchia) and *Siphonaria capensis* Q. et G.(Pulmonata). *Journal of Experimental Marine Biology and Ecology*, **128** (3), 191-201.

Mathieson, A.C. & Burns, R.L., 1971. Ecological studies of economic red algae. 1. Photosynthesis and respiration of *Chondrus crispus* (Stackhouse) and *Gigartina stellata* (Stackhouse) Batters. *Journal of Experimental Marine Biology and Ecology*, **7**, 197-206.

Mathieson, A.C. & Burns, R.L., 1975. Ecological studies of economic red algae. 5. Growth and reproduction of natural and

harvested populations of *Chondrus crispus* Stackhouse in New Hampshire. *Journal of Experimental Marine Biology and Ecology*, **17**, 137-156.

May, V., 1985. Observations on algal floras close to two sewerage outlets. Cunninghamia, 1, 385-394.

MBA (Marine Biological Association), 1957. *Plymouth Marine Fauna*. Plymouth: Marine Biological Association of the United Kingdom.

McGuinness, K., 1987. Disturbance and organisms on boulders. II. Causes of patterns in diversity and abundance. *Oecologia*, **71**, 420-430

McGuinness, K. & Underwood, A., 1986. Habitat structure and the nature of communities on intertidal boulders. *Journal of Experimental Marine Biology and Ecology*, **104** (1-3), 97-123.

McHugh, D.J., 2003. A guide to the seaweed industry: Food and Agriculture Organization of the United Nations Rome.

Van der Meer, J., 1987. Experimental hybridization of *Palmaria palmata* (Rhodophyta) from the northeast and northwest Atlantic Ocean. *Canadian Journal of Botany*, **65** (7), 1451-1458.

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

Minchinton, T.E., Schiebling, R.E. & Hunt, H.L., 1997. Recovery of an intertidal assemblage following a rare occurrence of scouring by sea ice in Nova Scotia, Canada. *Botanica Marina*, **40**, 139-148.

Morgan, K.C., Shacklock, P.F. & Simpson, F.J., 1980. Some aspects of the culture of *Palmaria palmata* in greenhouse tanks. *Botanica Marina*, 23, 765-770.

Moss, B., Mercer, S., & Sheader, A., 1973. Factors Affecting the Distribution of *Himanthalia elongata* (L.) S.F. Gray on the North-east Coast of England. *Estuarine and Coastal Marine Science*, **1**, 233-243.

Mrowicki, R.J., Maggs, C.A. & O'Connor, N.E., 2014. Does wave exposure determine the interactive effects of losing key grazers and ecosystem engineers? *Journal of Experimental Marine Biology and Ecology*, **461** (0), 416-424.

Newell, R.C., 1979. Biology of intertidal animals. Faversham: Marine Ecological Surveys Ltd.

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

Olsenz, J.L., 2011. Stress ecology in Fucus: abiotic, biotic and genetic interactions. Advances in Marine Biology, 59 (57), 37.

Padilla, D.K., 2010. Context-dependent impacts of a non-native ecosystem engineer, the Pacific Oyster Crassostrea gigas. Integrative and Comparative Biology, **50** (2), 213-225.

Pearson, G.A. & Brawley, S.H., 1996. Reproductive ecology of *Fucus distichus* (Phaeophyceae): an intertidal alga with successful external fertilization. *Marine Ecology Progress Series*. Oldendorf, **143** (1), 211-223.

Peckol, P., Levings, S.C. & Garrity, S.D., 1990. Kelp response following the World Prodigy oil spill. Marine Pollution Bulletin, **21**, 473-476.

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

Pinn, E.H. & Rodgers, M., 2005. The influence of visitors on intertidal biodiversity. *Journal of the Marine Biological Association of the United Kingdom*, **85** (02), 263-268.

Povey, A. & Keough, M.J., 1991. Effects of trampling on plant and animal populations on rocky shores. Oikos, 61: 355-368.

Prathep, A. 2001. Population ecology of a turf-forming red alga, *Osmundea pinnatifida* from the Isle of Man, British Isles. Ph.D. thesis. University of Liverpool.

Prathep, A., Marrs, R. & Norton, T., 2003. Spatial and temporal variations in sediment accumulation in an algal turf and their impact on associated fauna. *Marine Biology*, **142** (2), 381-390.

Provan, J., Murphy, S. & Maggs, C.A., 2005. Tracking the invasive history of the green alga *Codium fragile* ssp. tomentosoides. *Molecular Ecology*, **14**, 189-194.

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

Read, P.A., Anderson, K.J., Matthews, J.E., Watson, P.G., Halliday, M.C. & Shiells, G.M., 1983. Effects of pollution on the benthos of the Firth of Forth. *Marine Pollution Bulletin*, **14**, 12-16.

Reed, R.H. & Russell, G., 1979. Adaptation to salinity stress in populations of *Enteromorpha intestinalis* (L.) Link. Estuarine and *Coastal Marine Science*, **8**, 251-258.

Robbins, J.V., 1978. Effects of physical and chemical factors on photosynthetic and respiratory rates of *Palmaria palmata* (Florideophyceae), In *Proceedings of the ninth International Seaweed Symposium, Santa Barbara, California, USA, 20-27 August 1977,* (ed. Jensen, A. & Stein, J.R.), 273-283. Science Press, Princeton, NJ, USA.

Rohde, S., Hiebenthal, C., Wahl, M., Karez, R. & Bischof, K., 2008. Decreased depth distribution of *Fucus vesiculosus* (Phaeophyceae) in the Western Baltic: effects of light deficiency and epibionts on growth and photosynthesis. *European Journal of Phycology*, **43** (2), 143-150.

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

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

Schöne, B.R., Rodland, D.L., Wehrmann, A., Heidel, B., Oschmann, W., Zhang, Z.J., Fiebig, J. & Beck, L., 2007. Combined sclerochronologic and oxygen isotope analysis of gastropod shells (*Gibbula cineraria*, North Sea): life-history traits and utility as a high-resolution environmental archive for kelp forests. *Marine Biology*, **150** (6), 1237-1252.

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

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

Schiel, D.R. & Taylor, D.I., 1999. Effects of trampling on a rocky intertidal algal assemblage in southern New Zealand. *Journal of Experimental Marine Biology and Ecology*, **235**, 213-235.

Schmidt, A.L. & Scheibling, R.E., 2007. Effects of native and invasive macroalgal canopies on composition and abundance of mobile benthic macrofauna and turf-forming algae. *Journal of Experimental Marine Biology and Ecology*, **341** (1), 110-130.

Seed, R. & Suchanek, T.H., 1992. Population and community ecology of *Mytilus*. In *The mussel* Mytilus: *ecology*, *physiology*, *genetics and culture*, (ed. E.M. Gosling), pp. 87-169. Amsterdam: Elsevier Science Publ. [Developments in Aquaculture and Fisheries Science, no. 25.]

SEEEC (Sea Empress Environmental Evaluation Committee), 1998. The environmental impact of the Sea Empress oil spill. Final Report of the Sea Empress Environmental Evaluation Committee, 135 pp., London: HMSO.

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.

Smale, D.A., Wernberg, T., Yunnie, A.L. & Vance, T., 2014. The rise of *Laminaria ochroleuca* in the Western English Channel (UK) and comparisons with its competitor and assemblage dominant *Laminaria hyperborea*. *Marine ecology*.

Smith, B.D., 1985. Recovery following experimental harvesting of *Laminaria longicruris* and *Laminaria digitata* in Southwestern Nova Scotia. *Helgolander Meeresuntersuchungen*, **39**(1), 83-101.

Smith, G.M., 1947. On the reproduction of some Pacific coast species of Ulva. American Journal of Botany, 34, 80-87.

Smith, J.E. (ed.), 1968. 'Torrey Canyon'. Pollution and marine life. Cambridge: Cambridge University Press.

Sousa, W.P., 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs*, **49** (3), 227-254.

Sousa, W.P., 1985. Disturbance and patch dynamics on rocky intertidal shores. In *The ecology of natural disturbance and patch dynamics* (ed. S.T.A. Pickett and P.S. White), pp. 101-124. New York: Academic Press.

Southward, A.J. & Southward, E.C., 1978. Recolonisation of rocky shores in Cornwall after use of toxic dispersants to clean up the *Torrey Canyon* spill. *Journal of the Fisheries Research Board of Canada*, **35**, 682-706.

Spilmont, N., Denis, L., Artigas, L.F., Caloin, F., Courcot, L., Creach, A., Desroy, N., Gevaert, F., Hacquebart, P., Hubas, C., Janquin, M.-A., Lemoine, Y., Luczak, C., Migne, A., Rauch, M. & Davoult, D., 2009. Impact of the *Phaeocystis globosa* spring bloom on the intertidal benthic compartment in the eastern English Channel: A synthesis. *Marine Pollution Bulletin*, **58** (1), 55-63.

Stæhr, P.A., Pedersen, M.F., Thomsen, M.S., Wernberg, T. & Krause-Jensen, D., 2000. Invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. *Marine Ecology Progress Series*, **207**, 79-88.

Stephenson, T.A. & Stephenson, A., 1972. Life between tidemarks on rocky shores. *Journal of Animal Ecology*, **43** (2), 606-608.

Stewart, J.G., 1989. Establishment, persistence and dominance of *Corallina* (Rhodophyta) in algal turf. *Journal of Phycology*, **25** (3), 436-446.

Storey, K.B., Lant, B., Anozie, O.O. & Storey, J.M., 2013. Metabolic mechanisms for anoxia tolerance and freezing survival in the intertidal gastropod, *Littorina littorea*. *Comparative Biochemistry and Physiology Part A*: *Molecular & Integrative Physiology*, **165** (4), 448-459.

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

Sweet, N.S. & Sewell, J. 2014. Asian shore crab, *Hemigrapsus sanguineus*. *Great Britain Non-native Species Secretariat*. [cited 16/06/2015]. Available from: http://www.nonnativespecies.org

Tasende, M.G. & Fraga, M.I., 1999. The growth of *Chondrus crispus* Stackhouse (Rhodophyta, Gigartinaceae) in laboratory culture. *Ophelia*, **51**, 203-213.

Taskin, E., Ozturk, M. & Kurt, O., 2007. Antibacterial activities of some marine algae from the Aegean Sea (Turkey). African Journal of Biotechnology, **6** (24), 2746-2751.

Taylor, A. R. A., Chen, L. C. M., Smith, B. D., & Staples, L. S. 1981. Chondrus holdfasts in natural populations and in culture. In *Proceedings of the International Seaweed Symposium* **8**, 140-145.

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

Tyler-Walters, H., 2005. *Laminaria hyperborea* with dense foliose red seaweeds on exposed infralittoral rock. *Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme [on-line]*: Plymouth: Marine Biological Association of the United Kingdom. 2015(20/05/2015). http://www.marlin.ac.uk/habitatsbasicinfo.php?habitatid=171&code=1997

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

UKTAG, 2014. UK Technical Advisory Group on the Water Framework Directive [online]. Available from: http://www.wfduk.org

Underwood, A.J., 1972. Observations on the reproductive cycles of *Monodonta lineata*, *Gibbula umbilicalis* and *G. cineraria*. *Marine Biology*, **17**, 333-340.

Underwood, A.J., 1980. The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. *Oecologia*, **46**, 210-213.

Vadas, R.L., Johnson, S. & Norton, T.A., 1992. Recruitment and mortality of early post-settlement stages of benthic algae. *British Phycological Journal*, **27**, 331-351.

Vadas, R.L., Keser, M. & Rusanowski, P.C., 1976. Influence of thermal loading on the ecology of intertidal algae. In *Thermal Ecology II*, (eds. G.W. Esch & R.W. McFarlane), ERDA Symposium Series (Conf-750425, NTIS), Augusta, GA, pp. 202-212.

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

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

Van der Meer, J. & Pueschel, C.M., 1985. Petersenia palmariae n. sp.(Oomycetes): a pathogenic parasite of the red alga Palmaria mollis (Rhodophyceae). Canadian Journal of Botany, 63 (3), 404-408.

Van der Meer, J.P. & Chen, C-M., 1979. Evidence for sexual reproduction in the red algae Palmaria palmata and Halosaccion ramentaceum.

Vermaat J.E. & Sand-Jensen, K., 1987. Survival, metabolism and growth of *Ulva lactuca* under winter conditions: a laboratory study of bottlenecks in the life cycle. *Marine Biology*, **95** (1), 55-61.

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

Wernberg, T. & Thomsen, S., 2005. Miniview: What affects the forces required to break or dislodge macroalgae? *European Journal of Phycology*, **40** (2), 139-148.

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.

Werner, A. & Dring, M., 2011. Cultivating Palmaria palmata. Aquaculture Explained, 27, Bord Iascaigh Mhara (BIM).

Wiedemann, T., 1994. Oekologische Untersuchungen in Gezeitentuempeln des Helgolaender Nord-Ost Felswatts., Diploma thesis, University of Kiel, Germany.

Wood, C., 2015. The red ripple bryozoan *Watersipora subatra*. *Great Britain Non-native Species Secretariat*. [On-line][cited 16/06/2015]. Available from: http://www.nonnativespecies.org/factsheet/factsheet.cfm?speciesId=3748

Wotton, D.M., O'Brien, C., Stuart, M.D. & Fergus, D.J., 2004. Eradication success down under: heat treatment of a sunken trawler to kill the invasive seaweed *Undaria pinnatifida*. *Marine Pollution Bulletin*, **49** (9), 844-849.

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