Ascophyllum nodosum on very sheltered mid eulittoral rock

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

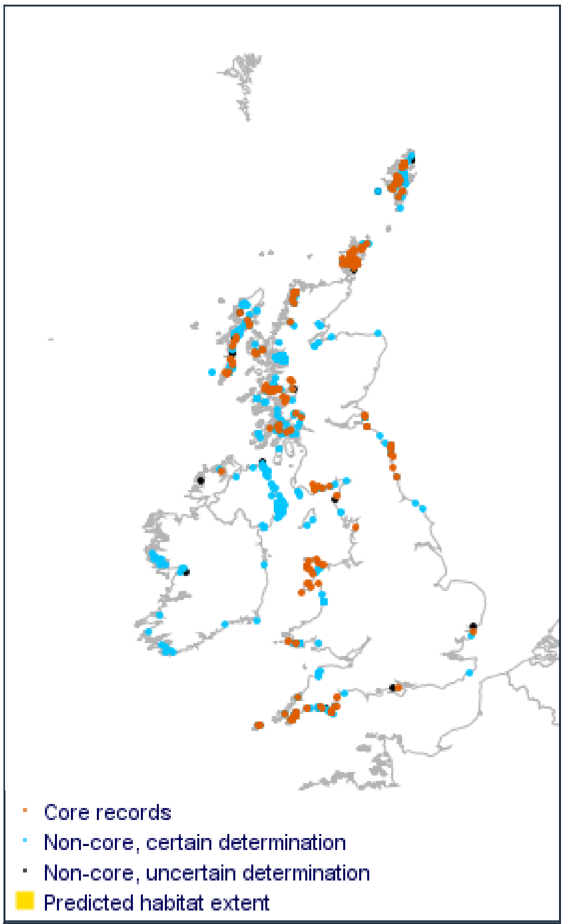
Frances Perry & Jacqueline Hill

2015-09-30

This review can be cited as:
Perry, F. & Hill, J.M., 2015. [Ascophyllum nodosum] on very sheltered mid eulittoral rock. 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.4.1

(page left blank)

***Ascophyllum nodosum* on very sheltered mid eulittoral rock**
Photographer: David Connor
Copyright: Joint Nature Conservation Committee (JNCC)



17-09-2018
Biotope distribution data provided by EMODnet Seabed Habitats (www.emodnet-seabedhabitats.eu)

Researched by Frances Perry & Jacqueline Hill **Refereed by** This information is not refereed.

Summary

UK and Ireland classification

EUNIS 2008	A1.314	*Ascophyllum nodosum* on very sheltered mid eulittoral rock
JNCC 2015	LR.LLR.F.Asc	*Ascophyllum nodosum* on very sheltered mid eulittoral rock
JNCC 2004	LR.LLR.F.Asc	*Ascophyllum nodosum* on very sheltered mid eulittoral rock
1997 Biotope	LR.SLR.F.Asc	*Ascophyllum nodosum* on very sheltered mid eulittoral rock

Description

Sheltered to extremely sheltered mid eulittoral rock with the wrack *Ascophyllum nodosum*. The red seaweed *Polysiphonia lanosa* is often found growing as an epiphyte on the *Ascophyllum nodosum* fronds while disturbed areas among the *Ascophyllum nodosum* is colonized by the wrack *Fucus vesiculosus* and the green seaweed *Ulva intestinalis*, barnacle *Semibalanus balanoides*, the limpet *Patella vulgata* and *Littorina littorea* can all be found on the bedrock underneath the *Ascophyllum nodosum* canopy along with coralline crusts. The whelk *Nucella lapillus* can be found preying on the barnacles and limpets. Two variants of the LR.LLR.F.Asc biotope are described. These are the full salinity (Asc.FS) and mixed substrata (Asc.X) biotopes. Similar biotopes have been identified as tide-swept (AscT) and variable salinity (AscVS). The unique loose lying growth form *Ascophyllum nodosum* ecad *mackayi* is found on very sheltered shores (Asc.mac).

This biotope is usually found between the wrack *Fucus spiralis* (Fspi) and *Fucus serratus* dominated biotopes (Fserr), although on some shores a narrow zone of *Fucus vesiculosus* (Fves) may occur immediately above the *Ascophyllum nodosum*. With increasing wave exposure the *Ascophyllum nodosum* canopy is replaced by F. vesiculosus (FvesB; Fves). LR.LLR.F.Asc can occur on more exposed shores, where there is localised shelter. *Ascophyllum nodosum* communities are generally very stable communities with individual plants reaching ages of more than 25 years on shores with little wave-action. (Information adapted from Connor *et al*., 2004; JNCC, 2015).

Depth range

Mid shore, Lower shore

Additional information

-

Listed By

- none -

Further information sources

Search on:

JNCC

Habitat review

Ecology

Ecological and functional relationships

While physical factors, especially the degree of exposure to wave action and amount of emersion, clearly influence the distribution and abundance of species on rocky shores, biological factors are especially described here.

- *Ascophyllum nodosum* is of great ecological importance in the North Atlantic because of its high abundance on most sheltered rocky shores, where it must be a major contributor to the oxygen budget of shallow waters to a wide range of intertidal animals (Stengel & Dring, 1997). The species, and other macroalgae, increase the amount of space available for attachment, provide shelter from wave action, desiccation and heat, and may be an important food source.
- Sheltered conditions favour the growth of fucoid algae and allow the maintenance of a more or less total and permanent canopy (Hartnoll & Hawkins, 1985). Communities on sheltered shores are much more stable than those of moderately exposed shores where a mosaic of patches of fucoid cover, dense barnacles and limpets are subject to small scale temporal variations. The biotope may also be present on sheltered areas of more exposed shores.
- *Patella* are absent in New England and it is possible that this allows *Ascophyllum nodosum* to extend into more exposed conditions. The exclusion of fucoids from exposed shores, and hence the presence of dense beds of fucoids on sheltered shores, results from grazing pressure on exposed shores. A dynamic balance probably exists between fucoids and limpets plus barnacles, and is mediated by wave action. In sheltered conditions the balance shifts in favour of the fucoids and in exposure the balance shifts towards limpets, barnacles and mussels. Limpet grazing normally prevents fucoids from extending onto exposed headlands, but how fucoids maintain their dominance on sheltered shores and what stops barnacles and limpets extending into sheltered conditions is unknown (Raffaelli & Hawkins, 1996).
- The presence of a dense fucoid canopy inhibits the settlement of barnacles by blocking larval recruitment mainly by 'sweeping' the rock of colonizers.
- There is a close association between *Ascophyllum nodosum* and the snail *Littorina obtusata*. The snail grazes away some epiphytes, thereby reducing the hydrodynamic loadings on plants and decreasing the detachment rate during storms. Although the snail also consumes the algal thallus, this does not appear to affect the performance of the plant. *Ascophyllum* produces noxious secondary chemical (polyphenols) which deter most grazers, but which attract *L. obtusata*. It is one of the few grazers to actually consume the thallus tissue, others feed on epiphytes (Norton *et al.*, 1990 cited in Raffaelli & Hawkins, 1996). *Littorina littorea* may be an important grazer of small fucoid plants and germlings and where it occurs in high abundance may delay colonization of fucoids (Lewis, 1964).
- Grazing on rocky shores can exert significant controlling influences on the algal vegetation, particularly by patellid limpets and littorinid snails which are usually the most prominent grazers. There are probably also significant effects caused by 'mesograzers' - amphipods such as *Hyale prevostii* and isopods, which are much smaller but may occur in high densities.

Seasonal and longer term change

Sheltered conditions favour the growth of fucoid algae and allow the maintenance of a more or less total and permanent canopy (Hartnoll & Hawkins, 1985) so that communities on sheltered rocky shores tend to have a high level of stability both seasonally and in the longer term. *Ascophyllum nodosum* has a very long lifespan where individual fronds can survive for 10-15 years and the holdfast for several decades which also contributes to the stability of the biotope. Other fucoid plants found in the biotope, such as *Fucus vesiculosus*, have lifespans in the order of 3-5 years. However, growth rates do show seasonal changes. For example, in Strangford Lough in Northern Ireland, Stengel & Dring (1997) observed the growth of *Ascophyllum nodosum* to be highly seasonal with low growth rates during November and December, and highest growth rates in late spring and early summer. A decline in growth in mid-summer was observed at all shore levels. Of the animal species present, *Hyale prevostii* may increase in numbers during the reproductive period when juveniles are released from brood pouches of the females, whilst littorinids are unlikely to show significant seasonal change. Although present in small numbers in the biotope, barnacles are likely to show increased abundance after settlement in the spring.

Habitat structure and complexity

Fucoid shores provide a variety of habitats and refugia for other species. The dense beds of *Ascophyllum nodosum* and the other fucoids in the biotope increases the structural complexity of the habitat providing a variety of resources that are not available on bare rock. Fronds provide space for attachment of encrusting or sessile epifauna and epiphytic algae and provide shelter from wave action, desiccation and heat for invertebrates. For example, the immediate effects of the removal of *Ascophyllum* plants are to: destroy the epifauna and flora; increase desiccation; increase predation; increase erosion and aid the settlement of other species (Boaden & Dring, 1980). Crevices in the bedrock and overhangs on fucoid rocky shores also increase habitat complexity by providing refugia for a variety of species.

Productivity

Rocky shore communities are highly productive and are an important source of food and nutrients for members of neighbouring terrestrial and marine ecosystems (Hill *et al*., 1998). Production rates of *Ascophyllum nodosum* in Nova Scotia were estimated to be between 0.61 and 2.82 kg/m2; (Cousens, 1984). Only about 10% of the primary production is directly cropped by herbivores (Raffaelli & Hawkins, 1999). Macroalgae, such as *Ascophyllum nodosum* and other fucoids, exude considerable amounts of dissolved organic carbon which are taken up readily by bacteria and may even be taken up directly by some larger invertebrates. Dissolved organic carbon, algal fragments and microbial film organisms are continually removed by the sea. This may enter the food chain of local, subtidal ecosystems, or be exported further offshore. Rocky shores make a contribution to the food of many marine species through the production of planktonic larvae and propagules which contribute to pelagic food chains.

Recruitment processes

Many rocky shore species, plant and animal, possess a planktonic stage: gamete, spore or larvae which float in the plankton before settling and metamorphosing into adult form. This strategy allows species to rapidly colonize new areas that become available such as gaps created by storms. For these organisms it has long been evident that recruitment from the pelagic phase is important in governing the density of populations on the shore (Little & Kitching, 1996). Both the demographic structure of populations and the composition of assemblages may be profoundly affected by variation in recruitment rates.

- *Ascophyllum nodosum* is recruited from pelagic sporelings, but recruitment is generally poor and few germlings are found on the shore. The species is extremely fertile every year and Printz (1959) suggests it must be assumed that some special combination of climatic or environmental conditions is needed for an effective colonization.
- Recruitment of *Patella vulgata* fluctuates from year to year and from place to place. Fertilization is external and the larvae is pelagic for up to two weeks before settling on rock at a shell length of about 0.2mm. Winter breeding occurs only in southern England, in the north of Scotland it breeds in August and in north-east England in September.
- Barnacle recruitment can be very variable because it is dependent on a suite of environmental and biological factors, such as wind direction and success depends on settlement being followed by a period of favourable weather. Long-term surveys have produced clear evidence of barnacle populations responding to climatic changes. During warm periods *Chthamalus* spp. predominate, whilst *Semibalanus balanoides* does better during colder spells (Hawkins *et al*., 1994). Release of *Semibalanus balanoides* larvae takes place between February and April with peak settlement between April and June. Release of larvae of *Chthamalus montagui* takes place later in the year, between May and August.

Some of the species living in the biotope do not have pelagic larvae, but instead have direct development of larvae producing their offspring as 'miniature adults'. For example, *Nucella lapillus* and some winkles do this, as do all amphipods. Adult populations of these species are governed by conditions on the shore and will generally have a much smaller dispersal range.

Time for community to reach maturity

The time for an *Ascophyllum nodosum* community to reach maturity is likely to be many years because the species has very poor recruitment and is very slow growing. The species does not reach sexual maturity until about 5 years of age and individual fronds can live to be up to 15 years old and whole plants for several decades. In their work on fucoid recolonization of cleared areas at Port Erin, Knight and Parke (1950) observed that even eight years after the original clearance there was still no sign of the establishment of an *Ascophyllum nodosum* population. There is a long-recognised shortage of sporelings (David, 1943) and the failure of the species to recolonize denuded areas for decades. However, the species is extremely fertile every year and Printz (1959) suggests it must be assumed that some special combination of climatic or environmental conditions is needed for an effective recolonization. If plants are not removed completely *Ascophyllum nodosum* plants cut within 10-15cm of the base recover fully in 4-5 years (Printz, 1959).

Additional information

-

Preferences & Distribution

Habitat preferences

Depth Range	Mid shore, Lower shore

Water clarity preferences	High clarity / Low turbidity, Medium clarity / Medium turbidity, No preference
Limiting Nutrients	Nitrogen (nitrates), Phosphorus (phosphates)
Salinity preferences	Full (30-40 psu), Variable (18-40 psu)
Physiographic preferences	Enclosed coast / Embayment
Biological zone preferences	Mid eulittoral
Substratum/habitat preferences	Bedrock, Large to very large boulders, Small boulders
Tidal strength preferences	Moderately Strong 1 to 3 knots (0.5-1.5 m/sec.), Strong 3 to 6 knots (1.5-3 m/sec.), Very Weak (negligible), Weak < 1 knot (<0.5 m/sec.)
Wave exposure preferences	Extremely sheltered, Sheltered, Very sheltered
Other preferences	

Additional Information

Species composition

Species found especially in this biotope

- *Ascophyllum nodosum*

Rare or scarce species associated with this biotope

-

Additional information

Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

This biotope is characterized by a dense canopy of *Ascophyllum nodosum.* The fucoid *Fucus vesiculosus* is also common within this biotope. The red seaweed *Polysiphonia lanosa* is a common epiphyte on *Ascophyllum nodosum.* The sheltered nature of this biotope allows *Ascophyllum nodosum* ecad *mackayi* to form on rare occasions. The barnacle *Semibalanus balanoides* is found on the rock surfaces beneath the canopy, along with the limpet species *Patella vulgata.* Both of these species are important in the structuring of the biological community on rocky intertidal ecosystems (Hawkins, 1983). A number of littorinids are found within this biotope and are important grazers. The crab *Carcinus maenas* and the dog whelk *Nucella lapillus* are dominant predators.

Ascophyllum nodosum is the key structuring species of this biotope. This species acts as an ecosystem engineer and the canopy that their fronds create modify habitat conditions. Although *Fucus vesiculosus* is important to this biotope, its loss from the biotope would not result in loss of the biotope. The fucoid canopy provides protection from desiccation for the various underlying seaweeds in addition to providing a substratum for epifauna and being the primary food resource for grazers. This can facilitate the existence and survival of other intertidal species and, therefore, strongly influences the structure and function of intertidal ecosystems (Jenkins *et al*., 2008). Therefore, the sensitivity assessment is based on the key structuring species *Ascophyllum nodosum*, although the sensitivity of other species is addressed where relevant.

Resilience and recovery rates of habitat

Ascophyllum nodosum has been reported to survive for over 100 years in areas free from ice scour (Åberg 1992). However, individual fronds are more likely to last for 15 -20 years, after which they break off and new fronds regenerate from the holdfast. The average age within populations of *Ascophyllum nodosum* is high, and there is little population turn over (Schiel & Foster, 2006). *Ascophyllum nodosum* takes five years to become sexually mature (Sundene, 1973). As many as 10^9 eggs m^2/year may be produced in a mature stand of *Ascophyllum nodosum* (Åberg & Pavia 1997). However, Dudgeon & Petraitis (2005) estimated that it could take a minimum of 13 years for an individual to replace itself. This is due to high mortality rates of germlings. Lazo *et al.* (1994) found that predation by grazers can reduce annual recruit survival rates to 0.01%. Other factors that affect the survival rates of recruited *Ascophyllum nodosum* include; their susceptibility to sedimentation (Airoldi, 2003); inability to tolerate desiccation at low tide (Brawley & Johnson, 1991), and inter and intraspecific density-dependent competition of germlings (Choi & Norton, 2005).

Choi & Norton (2005) examined the competitive interactions between the germlings of *Ascophyllum nodosum* and *Fucus vesiculosus.* Experiments undertaken on the Isle of Man and in the laboratory found that growth rates of both species decreased as the density of germlings increased. Of the two species, *Ascophyllum nodosum* germlings grew slower and were least competitive in mixed cultures. This finding was mirrored in earlier experiments undertaken by Sundene (1973). Sundene (1973) noted that the production of sexual cells in *Ascophyllum nodosum* was as rapid as it was in *Fucus vesiculosus.* It was the growth rate of *Ascophyllum nodosum* that led to *Fucus vesiculosus* being more competitive on the shore. However, Choi & Norton (2005) found that the presence of *Fucus vesiculosus* increased the survival of *Ascophyllum nodosum* when exposed to desiccation stress. This showed that the presence of a mixed culture could either facilitate germling survival or lead to competitive exclusion under different environmental conditions (Choi & Norton, 2005). Competition is reversed in mature ecosystems where *Ascophyllum nodosum* plants can out-compete fucoids (Keser *et al.*, 1981).

Lamote & Johnson (2008) studied temporal and spatial variation in recruitment of fucoid algae (including *Ascophyllum nodosum*). They found that recruitment to artificial substrata located in different micro-habitats along a semi-exposed shore was noticeably different. Under the fucoid canopy in the study area, recruitment was 10-50 times greater than it was on exposed surfaces and in tide pools. To determine if this difference was due to lower levels of mortality under the canopy or to restricted distribution capacity, newly settled recruits from under the canopy were relocated to alternative microhabitats. Mortality rates of the relocated germlings were higher in the more exposed locations. However, the difference was not great enough to explain the observed difference in the number of germlings within the two different microhabitats. Lamote & Johnson (2008) concluded that the number of recruits was greater from under the fucoid canopy because of restricted distribution abilities.

Ascophyllum nodosum has a low dispersal capacity that suggests re-colonization of a shore after a mass mortality event can be extremely slow. It can also limit the speed at which the species recovers from partial die back. *Ascophyllum nodosum's* poor dispersal ability has been widely acknowledged and the reasons behind it have been well studied. Experiments on the effect of wave action on *Ascophyllum nodosum* showed that a low-velocity wave can remove 99% of 15 minute old zygotes from experimental tiles (Vadas *et al.*, 1990). Further investigation with the use of refuges found that 75-90% of zygotes as old as four hours could be removed by a single wave. The attachment success of *Ascophyllum nodosum was* very poor at current speeds of over 20 cm/s^{-1} (Vadas *et al.*, 1992). Therefore, calm conditions are required for successful recruitment in *Ascophyllum nodosum.*

Keser *et al.* (1981) recorded the levels of re-growth exhibited by *Ascophyllum nodosum* and *Fucus vesiculosus* after harvesting in Maine. Harvesting was simulated by cutting fronds to three different lengths, that is, frond removed to the holdfast, to 15 cm from the holdfast and to 25 cm from the holdfast. Subsequent harvesting was repeated annually for three years. The experiment was carried out at eight sites, six of which were in sheltered areas. Re-growth of *Ascophyllum nodosum* was found to be dependent on a number of variables. These included; the age structure of the population; the extent and pattern of branching with a clump; the presence or absence of grazers (importantly *Littorina littorea*), and the environmental conditions. Recovery was found to be more rapid in estuaries (Keser *et al.*, 1981). Of the fronds which that were cut back to the holdfast, only those within sheltered, estuarine and grazer free conditions showed any re-growth. More mature *Ascophyllum nodosum* fronds cut back to 15 cm and 25 cm within a sheltered site showed some re-growth, however, there were high rates of mortality. The lack of re-growth was suggested to be caused by a lack of functional growing points found towards the bottom of the frond in older individuals. Almost all (95%) of young *Ascophyllum nodosum* individuals cut back to 15 cm and 25 cm regrew. In almost all populations measured within the experiment, repeat harvests resulted in lower biomass yields (Keser *et al.*, 1981).

Baardseth (1970) also reported slow re-growth of *Ascophyllum nodosum* after harvesting from the holdfast. Harvesting was found to destroy beds for extended periods of time where *Ascophyllum nodosum* was harvested from the bed by scrapping it from the substratum. On shores where *Ascophyllum nodosum* had been removed, re-colonization was dominated by *Fucus vesiculosus*, with very little recovery of *Ascophyllum nodosum*. When artificial substrata, such as sea walls, are introduced into an intertidal area *Ascophyllum nodosum* can take many years to colonize. *Fucus* *vesiculosus* and *Fucus spiralis* were the first species to colonize a breakwater built in Norway (Baardseth, 1970). It took two years for occasional *Ascophyllum nodosum* individuals to appear on the breakwater, and after eight years there was still no distinct *Ascophyllum nodosum* zone. Another breakwater studied had an established *Ascophyllum nodosum* zone after 30 years (Knight & Parke, 1950).

Printz (1959) also carried out harvesting experiments where fronds were cut back to 25 cm, 15 cm and 5 cm from the holdfast. Individuals that had been cut back to 25 cm had an 'abundance of new shoots' and had grown to 30-35 cm in length after a year. Individuals that had been trimmed back to 5 cm showed almost no change a year after the harvesting event. When the 5 cm individuals where re-visited three years after the harvesting event they were still almost unaltered. The reasons for the lack of re-growth were attributed to the lack of regenerative tissue found in the older flesh further down the thallus (Printz, 1959).

Mass mortality events caused by changes in the physical environment have been observed in *Ascophyllum nodosum.* A total mortality event of an *Ascophyllum nodosum* population occurred within the Long Island Sound in 1984 caused by water temperatures from two power plant thermal discharge pipes exceeding 28°C (Keser *et al*., 2005). From 1984 onwards temperatures at the site fluctuated with the opening of a third thermal discharge pipe and the closing and reopening of the pipes all three pipes. However, there was no recovery of the population in the 18 years since the mortality event and the end of Keser *et al.'s* (2005) study. Keser *et al.* (2005) reported that similar mortality events have been observed near other power plant thermal discharge pipes in Maine (Vadas *et al*., 1978) and Massachusetts (Wilce *et al*., 1978).

Printz (1959) indicated that a number of other studies (unreferenced in the paper) reported similar findings. Other studies have concluded that *Ascophyllum nodosum* takes long periods of time to recover from removal include Bertness *et al.* (2002), Jenkins *et al*. (1999, 2004) and Petraitis & Dudgeon (2005). Ingólfsson & Hawkins (2008) sum up the findings from previous studies on *Ascophyllum nodosum* re-colonization times within their discussion where they state 'the partial recovery of the *Ascophyllum nodosum* canopy after a 12 year period is consistent with some very early studies'. The twenty-year study untaken by Ingólfsson & Hawkins (2008) found that after removing an *Ascophyllum nodosum* community, the canopy could return within the study time period, yet the understorey communities had still not recovered after 20 years. There is a considerable evidence to suggest that if *Ascophyllum nodosum* fronds are cut higher up the thallus recovery times are reduced considerably to two to three years (Ang *et al*., 1996; Fegley, 2001; Keser *et al*., 1981; Sharp, 1987; Ugarte *et al*., 2006) (taken from Phillipi *et al*., 2014). However, the effect of this kind of canopy removal on the understory community is not known and neither is the recovery time.

Svensson *et al.* (2009) compared the population growth of *Ascophyllum nodosum* from two shores, one on the Isle of Man and one from Sweden. Although there were significant differences in the demography and appearance of the two populations, the phenotypic plasticity and sensitivities of the two populations were very similar. This is curious as the poor dispersal abilities of *Ascophyllum nodosum* means that minimal recruitment would occur between the two study populations. In addition, the geographical locations of the two shores mean that the environmental factors are significantly different and provide different selective pressures. It was suggested that the combination of different selective pressures and lack of genetic crossover could lead some level of allopatric speciation. However, this was not the case, which suggests that *Ascophyllum nodosum* has significant life history plasticity and can able to withstand 'very large environmental variation' (Svensson *et al*., 2009). The results from Svensson *et al.* (2009) also suggest that pressures that affect the survival or growth of large sexually reproductive *Ascophyllum nodosum* could have severe negative effects on regional abundance and biomass of the species.

The high levels of water movement within this biotope make it a suitable habitat for a number of filter feeders. Although their presence is mediated by the presence of *Ascophyllum nodosum*, the resistance and resilience of these species are important when considering how long it would take for the biotope community to recover. The average life expectancy of *Halichondria panicea* is three years (Fish & Fish, 1996) with individuals reaching sexual maturity within their first year. Wapstra & van Soest (1987) found that oocytes were present in the hermaphroditic *Halichondria panicea* year round. Maturation of these oocytes and the present of embryos were present from May to August when water temperatures increased. New *Halichondria panicea* recruits can become apparent on the shore a year after they were spawned (Vethaak, 1982). The sea squirt *Ascidiella scabra* is a highly fecund species (Lindsay & Thompson, 1930). Age at maturity is thought to be 6 months with a lifespan of 2-5 years. *Semibalanus balanoides* are often quick to colonize available gaps on intertidal rocky shores. Bennell (1981) observed that barnacles that were removed when the surface rock was scraped off in a barge accident at Amlwch, North Wales returned to pre-accident levels within 3 years. Petraitis & Dudgeon (2005) also found that *Semibalanus balanoides* quickly recruited (present a year after and increasing in density) to experimentally cleared areas within the Gulf of Maine, that had been dominated by *Ascophyllum nodosum* previously. However, barnacles are gregarious and larvae settle within areas where adults are present (Knight-Jones & Stevenson, 1950). Re-colonization of *Patella vulgata* on rocky shores is rapid as seen by the appearance of limpet spat 6 months after the *Torrey Canyon* oil spill reaching peak numbers 4-5 years after the spill. However, although re-colonization was rapid, the alteration to the population structure (size and age class) persisted for about 15 years because of the complex cycles of dominance involving limpets, barnacles and algae (Hawkins & Southward, 1992; Lewis & Bowman, 1975). The ability of these species to recolonize a habitat after the negative effects of a pressure varies. However, *Ascophyllum nodosum* takes the longest to recover and, therefore, it is this species on which the recovery of this biotope hinges.

Resilience assessment. *Ascophyllum nodosum* has low dispersal ability, high juvenile mortality rates and can take in excess of five years to reach reproductive maturity. If a pressure causes a mass mortality event on a shore an *Ascophyllum nodosum* canopy can take 12 years to recover. This recovery depends on mature populations of the macroalgae in the vicinity from which to recruit. If partial damage occurs to the frond but 15 cm – 25 cm remain, then recovery of an individual can occur within two to three years. Evidence suggests that even after the recovery of an *Ascophyllum nodosum* population after a mass mortality event the understory communities of the area can take in excess of 20 years to return (Jenkins *et al.*, 2004). This biotope has a diverse associated community, some of the species within which can recover relatively quickly, so recovery times scales may vary. In conclusion, if only partial damage is done to the characteristic macroalgae within his biotope then recovery could take between two to ten years, giving a resilience of **'Medium'**. However, if a pressure causes significant mortality of the characterizing species, *Ascophyllum nodosum*, the resilience is probably **'Low'.**

Note. 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 recognisable as the initial habitat of interest. It should be noted that the recovery rates are only indicative of the recovery potential.

Hydrological Pressures

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

Schonbeck & Norton (1979) demonstrated that fucoids can increase tolerance in response to a gradual change in temperature through a process known as 'drought hardening'. However, acute changes in temperatures may cause damage to macroalgae and other species. Temperature ranges of species may not accurately describe their ability to withstand localized changes in temperature. However, they will display the limits of the species genetic ability to acclimatize to temperatures. The juvenile life stages of organisms can be less tolerant of environmental conditions than more mature stages.

Ascophyllum nodosum is found in the middle of its range in the British Isles, with populations in the North East Atlantic as far south as Portugal and extending north to the White Sea. *Ascophyllum nodosum* is unlikely to be affected by a short-term change of 5°C, as it was not damaged during the unusually hot summer of 1983 when the average temperature was 8.3°C higher than normal (Hawkins & Hartnoll, 1985). *Ascophyllum nodosum* can tolerate certain levels of exposure as they are regularly exposed to rapid and short-term variations in temperature. Both exposure at low tide or rising tide on a sun-heated shore involves considerable temperature changes, and during winter the air temperature may be far below freezing point. The growth of *Ascophyllum nodosum* has been measured between 2.5 and 35°C with an optimum between 10 and 17°C (Strömgren, 1977). *Ascophyllum nodosum* can be damaged by thermal pollution if the water temperature remains above 24°C for several weeks (Lobban & Harrison, 1997), and temperatures exceeding 27°C cause direct mortality (Keser *et al*., 2005). Water temperature is an excellent predictor of gamete release in *Ascophyllum* (Bacon & Vadas, 1991). Consequently, changes in temperatures could impact on gamete release. Investigations into the tolerance of *Ascophyllum nodosum* germlings from Norway, to temperatures between 7°C -17°C found that there was no difference in survival rates within the given range (Steen & Rueness, 2004). Germination of *Ascophyllum nodosum* has been recorded between the temperatures of 4°C -23°C.

Other species found within this biotope are probably tolerant of temperature changes at the benchmark level as they are widely distributed in the UK. The balance of interactions between fucoids and barnacles changes with geographical location. Warmer conditions further south than the British Isles favour greater penetration of barnacles into sheltered locations (Ballantine, 1961 cited in Raffaelli & Hawkins, 1996). Warmer conditions are also likely to favour *Chthamalus* spp. rather than *Semibalanus balanoides* although a change of species will not alter the function of the biotope. Those species which are mobile, such as the littorinids and *Carcinus maenas* have the opportunity to move away from areas if physical conditions become too harsh

Sensitivity assessment. The characterizing species *Ascophyllum nodosum* is found in the middle of its habitat range in the British Isles. Although the range of these species can extend down to Portugal if the temperature changes are acute and occur over a short period leaving no time for acclimation then there could be some damage caused to the microalgae's. However, if the changes are more gradual then the algae may have time to acclimate which would not produce any significant negative impact. The benchmark scenario which is likely to cause the most stress to this biotope is an increase of 5°C for one month. Therefore, resistance and resilience are assessed as **'Medium'** so that sensitivity is assessed as a **'Medium'** at the benchmark.

Temperature decrease (local)	Medium Q: High A: High C: Medium	Medium Q: High A: Medium C: Medium	Medium Q: High A: Medium C: Medium

Schonbeck & Norton (1979) demonstrated that fucoids can increase tolerance in response to a gradual change in temperature through a process known as 'drought hardening'. However acute changes in temperatures may cause damage to macroalgae and other species. Temperature ranges of species may not accurately describe their ability to withstand localized changes in temperature. However, they will display the limits of the species genetic ability to acclimatize to temperatures. The juvenile life stages of organisms can be less tolerant of environmental conditions than more mature stages.

Ascophyllum nodosum is found in the middle of its range in the British Isles, with populations in the North East Atlantic as far south as Portugal and extending north to the White Sea. The growth of *Ascophyllum nodosum* has been measured between 2.5 and 35°C with an optimum between 10 and 17°C (Strömgren, 1977). Water temperature is an excellent predictor of gamete release in *Ascophyllum* (Bacon & Vadas, 1991). Consequently, changes in temperatures could impact on gamete release. Investigations into the tolerance of *Ascophyllum nodosum* germlings from Norway, to temperatures between 7°C -17°C found that there was no difference in survival rates within the given range (Steen & Rueness, 2004). Germination of *Ascophyllum nodosum* has been recorded between the temperatures of 4°C - 23°C.

A large number of the species found within this biotope are found throughout the British Isles and are not on the edge of their range. Therefore it is unlikely that a decrease in temperature is going to cause significant mortalities. In addition to this those species which are mobile, such as the littorinids, *Nucella lapillus* and *Carcinus maenas* have the opportunity to move away from areas if physical conditions become too harsh. Hence, these species may decrease in abundance.

Sensitivity assessment. The characterizing species *Ascophyllum nodosum* is found in the middle of its habitat range in the British Isles. Although the range of this species can extend up to the White Sea if the temperature changes are acute and occur over a short period leaving no time for acclimation then there could be some damage caused to the macroalgae. However, if the changes are more gradual then the algae may have time to acclimate which would not produce any significant negative impact. The benchmark scenario that is likely to cause the most stress to this biotope is a decrease of 5°C for one month. Therefore, resistance and resilience are assessed as **'Medium'** and sensitivity as **'Medium'** to this pressure at the benchmark.

Salinity increase (local)	Low Q: High A: High C: Medium	Low Q: High A: Medium C: Medium	High Q: High A: Medium C: Medium

Intertidal macroalgae often experience large but short-term changes in salinities (Lobban & Harrison, 1997). Salinities within these habitats vary due to weather conditions such as rainfall at low tide and evaporation from rock pools causing hypersaline conditions on hot days. Intertidal shores within estuarine environments can also experience considerable short-term changes in salinities. However intertidal macroalgae tolerances to longer-term changes in salinities can be minimal and can quickly reduce photosynthetic abilities and cause mortality.

This biotope is recorded from variable (18 – 35 ppt) and fully saline conditions (30 -40 ppt) (Connor *et al*., 2004). Consequently, an increase in salinity could make the conditions hypersaline. Little empirical evidence was found to assess how an increase in salinity at this benchmark would affect *Ascophyllum nodosum*. Baardseth, 1970 noted that *Ascophyllum nodosum* is euryhaline with a salinity tolerance of about 15 to 37 psu. Studies undertaken by Chock & Mathieson (1979) found *Ascophyllum nodosum* plants in the laboratory photosynthesised at salinities from 0 to 40 psu although the long-term effects within this range were not evaluated. No information could be found on the effects of an increase in salinity on the reproductive cycle of *Ascophyllum nodosum*.

A number of the species associated with this biotope can also be found within rockpools where hypersaline conditions can be found for short periods of time (Newell, 1979). Consequently, an increase in salinity within the benchmark of this pressure may not cause negative impacts for a short period of time. *Semibalanus balanoides* can tolerate salinities between 12 and 50 psu; below and above this cirral activity ceases (Foster, 1970). The littorinids, *Nucella lapillus* and *Carcinus maenas* are mobile species and have the ability to move to suitable conditions on the shore.

Sensitivity assessment. This biotope is found in both fully and variable salinity conditions (Connor *et al*., 2004). Therefore the pressure at this benchmark would create hyper-saline conditions. Although many species within this biotope would be able to cope with a short-term increase in salinity, long-term hypersaline conditions could cause mass mortalities of the biological community within this biotope. Both the resistance and resilience of this biotope to pressure at the stated benchmark has been assessed as 'Low'. Overall the biotope has a 'High' sensitivity to changes in emergence regime at the pressure benchmark.

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

Intertidal macroalgae often experience large but short-term changes in salinities (Lobban & Harrison, 1994). Salinities within these habitats vary due to weather conditions such as rainfall at low tide and evaporation from rock pools causing hypersaline conditions on hot days. Intertidal shores within estuarine environments can also experience considerable short-term changes in salinities. However intertidal macroalgae tolerances to longer-term changes in salinities are minimal and can quickly reduce photosynthetic abilities and cause mortality.

Ascophyllum nodosum is euryhaline with a salinity tolerance of about 15 to 37 psu (Baardseth, 1970). The species can also withstand periodic emersion in freshwater (Baardseth, 1970) and frequently inhabits estuaries where salinity is variable. Doty & Newhouse (1954) reported *Ascophyllum nodosum* from estuarine waters with a maximum salinity of 17.3 psu and a minimum of 0 psu. Chock & Mathieson (1979) found *Ascophyllum nodosum* plants in the laboratory photosynthesised at salinities from 0 to 40 psu although the long-term effects within this range were not evaluated. In the Teign Estuary in South Devon *Ascophyllum nodosum* inhabits areas subject to salinities as low as 8psu (Laffoley & Hiscock, 1993). Investigations into the salinity tolerance of *Ascophyllum nodosum* in laboratory controlled conditions found that the photosynthetic capabilities of this species decreased with reduced salinities. *Ascophyllum nodosum* tolerated 7 days at salinities of 5, and all samples died after 15 days at salinities of 5 (Connan & Stengel, 2011). There is some evidence to suggest that reduced salinities can influence the rate of receptacle maturation in fucoids (Munda, 1964). The rate of fructification in *Ascophyllum nodosum* has been measured to increase in diluted seawater (Munda, 1964).

A number of the other species within the biotope can also be found within rockpools where hyposaline conditions can be found for short periods of time (Newell, 1979). Consequently, a decrease in salinity within the benchmark of this pressure would not cause any significant mortalities. For example, *Semibalanus balanoides* can tolerate salinities between 12 and 50 psu, below and above this cirral activity ceases (Foster, 1970). Both *Ascidiella scabra* and *Halichondria panicea* can be found in habitats with variable salinity and would, therefore, tolerate a decrease in the salinity within this biotope. The littorinids, *Nucella lapillus* and *Carcinus maenas* are mobile species and have the ability to move to suitable conditions on the shore.

Sensitivity assessment. This biotope is recorded from both variable (18 – 40 ppt) and fully saline conditions (30 -40 ppt) (Connor *et al*., 2004). A decrease in salinity at the given benchmark could create a reduced salinity regime. With a change in the salinity at the benchmark the species within this biotope including the characterizing species would be able to withstand these reductions in salinities; however, there are likely to be reductions in the reproductive success and growth rates and consequently the abundances. Both the resistance and resilience of this biotope is assessed as **'Medium'** so that the sensitivity is assessed as **'Medium'.**

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

Water motion is a key determinant of marine macroalgal ecology, influencing physiological rates and community structure (Hurd, 2000). Higher water flow rates increase mechanical stress on macroalgae by increasing drag. Fucoids are highly flexible but not physically robust and an increase in water flow could cause mechanical damage, breaking fronds or even dislodging whole algae from the substratum. Fucoids are however highly flexible and are able to re-orientate their position in the water column to become more streamlined. This ability allows fucoids to reduce the relative velocity between algae and the surrounding water, thereby reducing drag and lift (Denny *et al*., 1998). Fucoids are permanently attached to the substratum and would not be able to re-attach if removed. Organisms living on the fronds and holdfasts will be washed away with the algae whereas free-living community components could find new habitat in surrounding areas. Wave exposure has been shown to limit the size of fucoids (Blanchette, 1997) as smaller individuals create less resistance to water movement, it is likely that water flow exerts a very similar pressure on fucoids. This biotope can be found in tidal currents ranging from 1 - 3 knots (0.5 – 1.5 m/s) (Connor *et al*., 2004).

Fucus vesiculosus individuals of 10cm or larger have been recorded to be completely removed at 7-8m/s (Jonsson *et al*., 2006). Flow rates at which adult *Ascophyllum nodosum* are removed are not known. However, Thompson & Wernberg (2005) provide strong evidence that with an increase in thallus size there is an increase in the break force required to remove algae. Consequently, the force required to remove *Ascophyllum nodosum* from the shore is likely to be comparable to that of *Fucus vesiculosus* as both are large macroalgae with similar thallus sizes. The upper limit of the tidal flows within this biotope is >1.5 m/s (Connor *et al*., 2004). An increase in the current flow of 0.2 m/s is unlikely to have an impact on many examples of this biotope except for those which are at the upper limit of water flow tolerance.

Propagule dispersal, fertilization, settlement, and recruitment are also influenced by water movement (Pearson & Brawley, 1996). An increase in water flow could have negative impacts on the reproductive success of *Ascophyllum nodosum*. Experiments on the effect of wave action on *Ascophyllum nodosum* showed that a low-velocity wave can remove 99% of 15 minute old zygotes from experimental tiles Vadas *et al.* (1990). Further investigation with the use of refuges found that 75-90% of zygotes as old as four hours could be removed by a single wave. Current speeds of over 20 cm s^{-1} make attachment success of *Ascophyllum nodosum* very poor (Vadas *et al.*, 1992). These studies show the need for periods of calm conditions for successful recruitment for *Ascophyllum nodosum.* An increase in the mean water flow will reduce the time during which attachment is possible. In addition, greater water flow can increase scour through increased sediment movement. Small life stages of macroalgae are likely to be affected by removing new recruits from the substratum and hence reducing successful recruitment (Devinny & Volse, 1978) (see 'siltation' pressures). Changes in water motion can thus strongly influence local distribution patterns of *Fucus* spp. (Ladah *et al.*, 2008).

Sensitivity assessment. This is not a tidally swept biotope. Hence, the abundance of filter feeders and epifauna is not dependent on the high water flow. This biotope is present in negligible water flows, therefore, a decrease in water flow is unlikely to have an impact. An increase in the level of water flow at the benchmark (0.1-0.2 m/s) is unlikely to have a significant effect. Therefore, resistance and resilience have been assessed as 'High' and the biotope is assessed as 'Not Sensitive' at the benchmark level.

Emergence regime changes	Low Q: High A: High C: High	Low Q: High A: Medium C: Medium	High Q: High A: Medium C: Medium

Within the British Isles populations of *Ascophyllum nodosum* can suffer from bleaching and consequent mortality during exceptionally hot weather (Schonbeck & Norton, 1978, Hawkins & Hartnoll, 1985, Norton, 1985). However, these mortality events do not occur every year and tend to occur when the effects of unusually hot conditions combine with periods of rapid change, which do not allow for macroalgae to acclimate (Raffaelli & Hawkins, 1996).

Stengel & Dring (1997) reported that growth rates in *Ascophyllum nodosum* decreased with height on the shore, correlating with an increase in environmental severity. *Ascophyllum nodosum* productivity is affected by desiccation when water loss exceeds 50% (Brinkhuis *et al.*, 1976). Higher temperatures can increase the rate of desiccation and consequently lead to a loss of productivity, and eventually mortality (Keser *et al.*, 1981).

When Stengel & Dring (1997) transplanted *Ascophyllum nodosum* from the lower shore to the upper shore, 80% of the transplants died within 3 months. In contrast, 100% of the individuals from the upper shore transplanted to the lower shore survived, as did all of the controls. The plants which survived transplantation to the upper shore acclimated to the conditions on the upper shore, yet their survival was determined by thallus morphology a predetermined genetic attribute which may be fixed (Stengel & Dring, 1997). Choi & Norton (2005) also carried out transplantation experiments and found that the growth rates of *Ascophyllum nodosum* decreased dramatically from the lower shore to the upper shore.

The southern and northern range limits of a number of intertidal macroalgae fall within Portugal. Lima *et al.* (2007) mapped the re-adjustment of 129 macroalgal ranges in relation to the change in air and sea temperatures observed within the north-eastern Atlantic over the past 50 years. Significant differences in distributions of algae were found, yet there was a disparity in the level of change found in the ranges of those of warm and cold adapted species. The species that were at the northern limit of their range in Portugal showed a greater change in distribution than the cold adapted species. Roughly half of the cold adapted species, including *Ascophyllum nodosum*, showed no significant change in their distribution. Lima *et al.*, (2007) suggested that the cold adapted species had greater tolerance to adverse conditions for longer periods of time than the warm adapted species.

Information regarding the effect of changes in the level of exposure on *Ascophyllum nodosum* germlings is not available. Germlings will be protected from desiccation stresses to a certain extent because of the protection provided to them by the fucoid canopy. Increases in temperature will be one of the effects changes in exposure will have on germlings. For further information refer to temperature pressure.

Dense aggregations of algae can reduce the effect of more severe physical conditions such as those experienced with greater levels of exposure. Clumping enables organisms to retain moisture and reduce heat stress (Scrosati & DeWreede, 1998, Stafford & Davies, 2005).

Sensitivity assessment. Desiccation and the associated osmotic stress, especially when combined with high temperatures can cause mortalities (Pearson *et al*., 2009). The sensitivity of the characterizing species to emersion pressure will depend on the health and demography of individual populations, with germlings being most vulnerable life stage to this pressure.

Ascophyllum nodosum has a level of resistance to an increase in emersion. However, at the level of the benchmark, there is likely to be a change in the biotope, with the top of the biotope being most sensitive to change as it is already at the upper tolerance limits. The change in this pressure at the benchmark is likely to see all of the biotopes on the shore shifting downwards. *Ascophyllum nodosum* can take as many as twelve years to recover, with the return of ecosystem functioning taking considerably longer. The resistance of this biotope to pressure at the stated benchmark has been assessed as 'Low' and resilience as 'Low'. Overall, the biotope is assessed as 'High' sensitivity to changes in emergence regime at the pressure benchmark.

Wave exposure changes (local)	Medium	Medium	Medium
	Q: Medium A: Medium C: Medium	Q: High A: Medium C: Medium	Q: Medium A: Medium C: Medium

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). Fucoids are highly flexible but not physically robust and an increase in wave exposure can cause mechanical damage, breaking fronds or even dislodging whole algae from the substratum. *Ascophyllum nodosum* is permanently attached to the substratum and would not be able to re-attach if removed. Organisms living on the fronds and holdfasts will be washed away with the algae whereas free-living community components could find new habitat in surrounding areas. Wave exposure has been shown to limit size of fucoids (Blanchette, 1997) as smaller individuals create less resistance to waves. As exposure to waves increases the fucoid population will become dominated by small juvenile algae, and dwarf forms of macroalgae which are more resistant to strong wave action. An increase in wave action beyond the tolerance of these fucoid species leads to a further increase in the abundance of robust fucoids, such as *Fucus spiralis* f. *nana* and red seaweeds, such as *Corallina officinalis* (Connor *et al*,. 2004).

Ascophyllum nodosum cannot resist very heavy wave action so exposure to wave action is an important factor controlling the distribution of the species, and therefore this biotope. This biotope is found in sheltered to extremely sheltered conditions. Propagule dispersal, fertilization, settlement, and recruitment are also influenced by water movement (Pearson & Brawley, 1996). An increase in water flow due to wave exposure could have negative impacts on the reproductive success of *Ascophyllum nodosum*. Experiments on the effect of wave action on *Ascophyllum nodosum* showed that a low-velocity wave can remove 99% of 15 minute old zygotes from experimental tiles Vadas *et al.* (1990). Further investigation with the use of refuges found that 75-90% of zygotes as old as four hours could be removed by a single wave. Current speeds over 20cm s^{-1} make attachment success of *Ascophyllum nodosum* very poor (Vadas *et al.*, 1992). These studies show the need for periods of calm conditions for successful recruitment for *Ascophyllum nodosum*. An increase in the mean wave exposure will reduce the time during which attachment is possible. In addition, greater wave action can increase scour through increased sediment movement. Small life stages of macroalgae are likely to be affected by removing new recruits from the substratum and hence reducing successful recruitment (Devinny & Volse, 1978) (see 'siltation' pressures).

The other characterizing species are found in a range of wave exposures and unlikely to be directly affected. However, loss of the fucoid cover would result in major changes to the associated community, especially attached epifauna and understory algae.

Sensitivity assessment. As this is a very to extremely sheltered biotope a further decrease in wave exposure is unlikely, and not significant given the very strong to strong tidal flow in which the biotope occurs. An increase in wave action is likely to adversely affect fucoid cover, especially of *Ascophyllum nodosum*. The biotope will probably be lost if wave exposure increase from e.g. sheltered to moderately exposed. It is difficult to qualify a 3-5% change in significant wave height in terms of wave exposure, but the biotope is likely to have at least a 'Medium' resistance to an increase in wave exposure. Therefore, as resilience is probably 'Medium', sensitivity is also assessed as 'Medium'.

Chemical Pressures

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

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

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

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

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

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

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

No evidence.

Introduction of other substances	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR

This pressure is **Not assessed**.

De-oxygenation	High Q: Low A: NR C: NR	High Q: High A: High C: High	Not sensitive Q: Low A: Low C: Low

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). Reduced oxygen levels are likely to inhibit respiration whilst immersed, but it is unlikely to cause a loss of the macroalgae population directly. This biotope is found in a mid-eulittoral position and consequently, a proportion of time will be spent in the air where oxygen is not limited. As long as certain physical conditions are not exceeded, respiration and photosynthesis will be able to continue.

Although the macroalgae species within this biotope may not be negatively affected some of the associated fauna may be lost, causing a reduction in species richness. Josefson & Widbom (1988) investigated the response of benthic macro and meiofauna to reduced dissolved oxygen levels in the bottom waters of a fjord. At dissolved oxygen concentrations of 0.21 mg/l, the macrofaunal community was eradicated and was not fully re-established 18 months after the hypoxic event. Meiofauna seemed, however, unaffected by deoxygenation. Mobile species will be able to relocate to more optimal conditions, whereas immobile species such as barnacles are likely to be put under more stress by de-oxygenation. Complete smothering caused by the *Torrey Canyon* oil spill appeared to have little impact on barnacle species; a few *Semibalanus balanoides* died, yet *Chthamalus montagui* seemed unaffected (Smith, 1968). *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).

Sensitivity assessment. The characterizing species *Ascophyllum nodosum* would not be negatively affected by a decrease in oxygen within the water column at the benchmark level of this pressure. However, some of the associated faunal community within this biotope may be negatively affected. Mobile species such as littorinids and the crab *Carcinus maenas* would relocate to conditions that were less physiologically taxing and would be able to return when the pressure abated. Those immobile species such as the barnacle *Semibalanus balanoides* may experience some mortality. However, barnacles can completely recolonize within three years (Bennell, 1981).

The sheltered to extremely sheltered conditions that are characteristic of this biotope mean that water mixing is not very strong. Therefore, water movement within this area will not reverse any oxygen depletion quickly, possibly exacerbating any negative effects. However, the biotope occurs in the mid-littoral so that emergence will mitigate the effects of hypoxic surface waters. Therefore, resistance is assessed as **'High'**. Hence, resilience is assessed as **'High'**, and the biotope is assessed as **'Not sensitive'.**

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

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

Johnston & Roberts (2009) undertook a review and meta-analysis of the effect of contaminants on species richness and evenness in the marine environment. Of the 47 papers reviewed relating to nutrients as a contaminant, over 75% found that it had a negative impact on species diversity, <5% found increased diversity, and the remaining papers finding no detectable effect. Not all of the 47 papers considered the impact of nutrients on intertidal rocky shores. Yet this finding is still relevant as the meta-analysis revealed that the effects of marine pollutants on species diversity were ‘remarkably consistent’ between habitats (Johnston & Roberts, 2009). It was found that any single pollutant reduced species richness by 30-50% within any of the marine habitats considered (Johnston & Roberts, 2009). Throughout their investigation, there were only a few examples where species richness was increased due to the anthropogenic introduction of a contaminant. These examples were almost entirely from the introduction of nutrients, either from aquaculture or sewage outfalls. However research into the impacts of nutrient enrichment from these sources on intertidal rocky shores often lead to shores lacking species diversity and the domination by algae with fast growth rates (Abou-Aisha *et al.*, 1995, Archambault *et al.*, 2001, Arévalo *et al.*, 2007, Diez *et al.*, 2003, Littler & Murray, 1975).

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). Nutrient enrichment can also enhance fouling of *Fucus* fronds by biofilms (Olsenz, 2011). Nutrient enriched environments can not only increase algae abundance but the abundance of grazing species (Kraufvelin, 2007).

White *et al.* (2011) investigated the effects of nutrient effluent from land-based finfish farms on the morphologies of *Ascophyllum nodosum* in the vicinity of the outfall pipes. It was estimated that the nitrogen effluent from the farm was 1500kg y^{-1}. The background levels of nitrite at the test site were 300 µM. In comparison, the ambient nitrite levels in south-west Nova Scotia are 3 µM (White *et al.*, 2011). *Ascophyllum nodosum* at the test sites were found to be younger than those at the control sites, but significantly larger. This experiment suggested that nutrient effluent could have positive impacts on *Ascophyllum nodosum.* Yet it must be noted that the effect of the effluent on the rest of the biological community was not studied.

Changes in community composition on intertidal rocky shores can happen rapidly, and fast growing ephemeral species can become established quickly in the presence of higher concentrations of nutrients. The establishment and growth of these species are not controlled by wave exposure (Kraufvelin, 2007). However, even though these fast growing ephemeral species can become well established quickly, healthy communities on intertidal rocky shores can survive long periods of time, and maintain ecological function after these species have become established (Bokn *et al.*, 2002, 2003; Karez *et al.*,2004; Kraufvelin *et al.*, 2006; Kraufvelin, 2007).

Sensitivity assessment. A slight increase in nutrients may enhance growth rates but high nutrient concentrations could lead to the overgrowth of the algae by ephemeral green algae and an increase in the number of grazers. If the biotope is well established and in a healthy state the biotope could persist. However, the biotope is 'Not sensitive' at the pressure benchmark that assumes compliance with good status as defined by the WFD.

Organic enrichment	Medium Q: High A: Medium C: Medium	Medium Q: High A: Medium C: Medium	Medium Q: High A: Medium C: Medium

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

Johnston & Roberts (2009) undertook a review and meta-analysis of the effect of contaminants on species richness and evenness in the marine environment. Of the 49 papers reviewed relating to sewage as a contaminant, over 70% found that it had a negative impact on species diversity, <5% found increased diversity, and the remaining papers finding no detectable effect. Not all of the 49 papers considered the impact of sewage on intertidal rocky shores. Yet this finding is still relevant as the meta-analysis revealed that the effects of marine pollutants on species diversity were 'remarkably consistent' between habitats (Johnston & Roberts, 2009). It was found that any single pollutant reduced species richness by 30-50% within any of the marine habitats considered (Johnston & Roberts, 2009). Throughout their investigation, there were only a few examples where species richness was increased due to the anthropogenic introduction of a contaminant. These examples were almost entirely from the introduction of nutrients, either from aquaculture or sewage outfalls. However research into the impacts of organic enrichment from these sources on intertidal rocky shores often lead to shores lacking species diversity and the domination by algae with fast growth rates (Abou-Aisha *et al.*, 1995, Archambault *et al.*, 2001, Arévalo *et al.*, 2007, Diez *et al.*, 2003, Littler & Murray, 1975).

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). Nutrient enrichment can also enhance fouling of fucoid fronds by biofilms (Olsenz, 2011). Nutrient enriched environments cannot only increase algae abundance but the abundance of grazing species (Kraufvelin, 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.

Changes in community composition on intertidal rocky shores can happen rapidly, and fast growing ephemeral species can become established quickly in the presence of higher concentrations of nutrients. The establishment and growth of these species are not controlled by wave exposure (Kraufvelin, 2007). However, even though these fast growing ephemeral species can become well established quickly, healthy communities on intertidal rocky shores can survive long periods of time, and maintain ecological function after these species have become established (Bokn *et al.*, 2002, 2003, Karez *et al.*,2004; Kraufvelin *et al.*, 2006; Kraufvelin, 2007).

Sensitivity assessment. Little empirical evidence was found to support an assessment of this biotope at this benchmark. Due to the negative impacts that can be experienced with the introduction of excess organic carbon both resistance and resilience have been assessed as **'Medium'**. This gives an overall sensitivity assessment of **'Medium'.**

Physical Pressures

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

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

Physical change (to another seabed type)	None Q: High A: High C: High	Very Low Q: High A: High C: High	High Q: High A: High C: High

This biotope occurs on rock substratum, so that a change to sedimentary or soft rock substratum would lead to the direct loss of suitable attachment areas. This change in substratum would result in the loss of the characterizing species *Ascophyllum nodosum* along with other species found within the associated community of this biotope. Resistance is assessed as **'None'**. As this pressure represents a permanent change, recovery is impossible as a suitable substratum for the biological community of this biotope is lacking. Hence, resilience is assessed as **'Very low'.** The habitat, therefore, scores a **'High'** sensitivity. Although no specific evidence is described confidence in this assessment is 'High', due to the incontrovertible nature of this pressure.

Physical change (to another sediment type)	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

Not relevant.

Habitat structure changes - removal of substratum (extraction)	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

The species characterizing this biotope occur on rock and would be sensitive to the removal of the habitat. However, extraction of rock substratum is considered unlikely and this pressure is considered to be 'Not relevant' to hard substratum habitats.

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

Trampling on the rocky shore has been observed to reduce fucoid cover which decreased the microhabitat available for epiphytic species, increased bare space and increased cover of opportunistic species such as *Ulva* (Fletcher & Frid, 1996). This biotope is found in the mid intertidal shore; an area easily accessible by humans, especially at low tide. Fucoids are intolerant of abrasion from human trampling, which has been reported to reduce the cover of seaweeds on a shore (Holt *et al*., 1997; Tyler-Walters & Arnold, 2008).

Brosnan (1993) investigated the effect of trampling on a number of algal species, including *Fucus vesiculosus*, on an intertidal rocky shore in Oregon. The effects of 250 tramples per plot, once a month for a year were recorded. Abundances of algae in each plot were reduced from 80% to 35% within a month of the introduction of the pressure and remained low for the remainder of the experiment.

As few as 20 steps / m^2 on stations on an intertidal rocky shore in the north east of England were sufficient to reduce the abundance of fucoids (Fletcher & Frid, 1996). This reduction in the complexity of the algae community, in turn, reduced the microhabitat available for epiphytic species. Trampling pressure can thus result in an increase in the area of bare rock on the shore (Hill *et al*., 1998). Chronic trampling can affect community structure with shores becoming dominated by algal turf or crusts (Tyler-Walters & Arnold, 2008).

Pinn & Rodgers (2005) compared the biological communities found on two intertidal rocky shore ledges in Dorset. They found that the ledge which had a higher number of visitors had few branching algal species, including fucoids, but had greater abundances of crustose and ephemeral species (Pinn & Rodgers, 2005). The densities of fucoids were recorded from the intertidal rocky shore at Wembury, Devon in 1930 (Colman, 1933) and 1973 (Boalch *et al*., 1974). Boalch *et al.* (1974) found a reduction in fucoids on the shore at Wembury and that the average frond length of *Ascophyllum nodosum* was smaller.

Ascophyllum nodosum seems to be particularly intolerant of damage from trampling (Flavell, unpublished; cited in Holt *et al*., 1997), as its length means it is more likely that the thallus is ‘cut’ between a footstep and sharp rock (Boalch *et al*., 1974, Tyler-Walters & Arnold, 2008). Araujo *et al.* (2009) found that trampling negatively affected both *Ascophyllum nodosum* abundances and reduced understorey species while promoting the colonization by ephemeral green algae. However, within a year of the disturbance event, *Fucus vesiculosus* had become the dominant canopy forming species, replacing a pre-disturbance *Ascophyllum nodosum* community. The replacement of *Ascophyllum nodosum* with *Fucus vesiculosus* may have been due to the poor recovery rate of *Ascophyllum nodosum.* The increase in abundance suggests the competitive superiority of *Fucus vesiculosus* individuals in occupying newly available space in the disturbed patches. Similar results were found by Cervin *et al*. (2005) and Araujo *et al*. (2012) with *Fucus vesiculosus* outcompeting *Ascophyllum nodosum* after small scale disturbances. Rita *et al.* (2012) also undertook experiments on the effect of trampling on *Ascophyllum nodosum* and its associated communities. It was concluded that trampling caused significant damage to both the macroalgae and the understory communities, which had not recovered within five years of the initial experiment.

Sensitivity assessment. Abrasion of the substratum will cause a reduction in the abundances of *Ascophyllum nodosum*, as well as other species found in the associated community. Therefore, the resistance is assessed as **‘Low’**. Experiments undertaken on the trampling effects on *Ascophyllum nodosum* have shown that for the community to return to its pre-experimental state can take in excess of 10 years, consequently, the resilience is assessed as **‘Low’** and sensitivity as **‘High’**.

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

The species characterizing this biotope group are epifauna or epiflora occurring on hard rock, which is resistant to subsurface penetration. Therefore, ‘penetration’ is '**Not relevant**'. The assessment for abrasion at the surface only is, therefore, considered to equally represent sensitivity to this pressure’. Please refer to ‘abrasion’ above.

Changes in suspended solids (water clarity)	High Q: Medium A: Medium C: Medium	High Q: High A: Medium C: Medium	Not sensitive Q: Medium A: Medium C: Medium

Light is an essential resource for all photoautotrophic organisms and a change in turbidity would affect light availability to photosynthesising organisms during immersion which could result in reduced biomass of plants. Changes in the suspended sediment load can change the levels of scour and alter the abundances of certain species. Greater levels of suspended particulate matter may also increase the amount of material which is falling out of suspension, which could consequently smother organisms (see siltation pressures).

An increase in turbidity would alter the light available for photosynthesis during immersion. The shallow water depth within this biotope means that although light attenuation will be greater, the change in turbidity at this pressure benchmark will still allow light to penetrate to the depth at which the algae are found. *Ascophyllum nodosum* will also be able to continue to photosynthesize at low tide when the plants are emersed, as long as the plant has a sufficiently high water content and so (Beer & Kautsky, 1992).

Daly & Mathieson (1977) found that *Ascophyllum nodosum* was completely absent from an intertidal rocky shore which was subject to a high level of scour from sand movement. The lack of *Ascophyllum nodosum* from this shore was particularly conspicuous due to the high abundance of the species on a nearby rocky shore with very similar conditions, except for the level of suspended sediment. *Ascophyllum nodosum* is not likely to be directly intolerant of a decrease in suspended sediment because the species is a primary producer.

Scour caused by increased sediment in suspension can cause mortality to many of the other species found within this biotope. For example, Daly & Mathieson, (1977) found that *Semibalanus balanoides* could be totally removed from a shore if scour is severe enough. A reduction in light levels due to an increase in the level of suspended sediment will not have a negative impact on the fauna within this biotope, and it is unlikely to have a significant negative impact on the other flora species, due to the intertidal nature of the biotope. An increase in levels of suspended sediment could be beneficial to filter feeding organisms.

Sensitivity assessment. This biotope is found on the mid intertidal shore and consequently is subject to long periods of emersion during which time macroalgae can continue to photosynthesize as long as plants have a sufficiently high water content. Therefore, photosynthesis and consequently growth will not be greatly affected. The level of water movement through wave exposure and tidal streams is unlikely to be high enough to cause any significant damage through scouring. Consequently, the resistance and resilience of this biotope have been assessed as ‘High’. The sensitivity of this biotope to this pressure at the benchmark is assessed as ‘Not Sensitive’.

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

A discrete event where sediment inundates this biotope to 5 cm will have very different effects on the characterizing species and the associated community depending on the state of the tide. High tide will mean that both of the characterizing species will be vertical in the water column, meaning only a small proportion of the stipe and holdfast will be smothered, leaving the fronds sediment free, and able to continue photosynthesising. In contrast, if the tide is out then fronds of the characterizing fucoid canopy will be flat on the substratum and will be smothered by the sediment deposit. The level of water flow caused by tidal movements and wave exposure within this biotope will mean that the sediment won't be removed from the shore quickly. Smothering will prevent photosynthesis resulting in reduced growth and eventually death.

However, germlings 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. Sediment deposition can reduce macroalgal recruitment by (1) reducing the amount of substratum available for attachment of propagules; (2) scour, removing attached juveniles and (3) burial, altering the light and/or the chemical micro-environment (Devinny & Volse, 1978, Eriksson & Johansson, 2003).

Ascophyllum nodosum is intolerant of sediment movement as shown by the shore comparisons undertaken by Daly & Mathieson (1977). Daly & Mathieson (1977) compared two rocky shores which were similar except for the level of sediment movement experienced on the shore. The shore with more sediment movement was devoid of *Ascophyllum nodosum*.

Smothering will cause direct mortalities in the associated community, notably of the filter feeding sessile organisms unable to clear their feeding appendages or relocate. Airoldi & Hawkins (2007) found that *Patella vulgata* reduces its feeding activity by 35% with just 1 mm of sediment over the substratum (equivalent to 50 mg/cm^2). At 200 mg/cm^2 mortality occurred. It is possible that 5 cm of sand may create similar mortality events to other grazing organisms, as not only will they be weighted down by sand but food availability will also be restricted.

Sensitivity assessment. *Ascophyllum nodosum* adults are sediment intolerant, and germlings of *Ascophyllum nodosum* are intolerant of even small levels of sediment. Many of the smaller species found within the associated community will be totally smothered by 5 cm. The level of water movement within this biotope is not excessive and consequently deposited sediment will persist over a number of tides before it is all entrained and removed. This is likely to cause some damage to the characterizing species and the other associated species. Therefore, resistance and resilience have both been assessed as '**Medium**'. Overall the sensitivity of the biotope is assessed as '**Medium**' at the level of the benchmark.

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

Several studies found that increasing the vertical sediment burden negatively impact fucoids survival and associated communities. 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 understorey algae, invertebrate grazers and young (germling) fucoids. Water movement will remove sediment but within this biotope is it likely to take a number of tidal cycles. Resistance and resilience are assessed as **'Low'** and sensitivity as **'High'** 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) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

No evidence.

Underwater noise changes	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

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

Introduction of light or shading	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

Increased levels of diffuse irradiation correlate with increased growth in macroalgae (Aguilaria *et al*., 1999). Levels of diffuse irradiation increase in summer, and with a decrease in latitude. As *Ascophyllum nodosum* is found in the middle its natural range in the British Isles an increase in the level of diffuse irradiation will not cause a negative impact on the species or the biotope. However, it is not clear how these findings may reflect changes in light levels from artificial sources, and whether observable changes would occur at the population level as a result. There is, therefore, 'No evidence' on which to base an assessment.

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

This pressure is considered applicable to mobile species, e.g. fish and marine mammals rather than seabed habitats. Physical and hydrographic barriers may limit propagule dispersal. But propagule dispersal is not considered under the pressure definition and benchmark. Therefore this pressure is considered 'Not Relevant' for this biotope.

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 seabed habitats. NB. Collision by grounding vessels is addressed under 'surface abrasion'.

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

No relevant.

Biological Pressures

	Resistance	Resilience	Sensitivity
Genetic modification & translocation of indigenous species	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

Key characterizing species within this biotope are not cultivated or translocated. This pressure is, therefore, considered ‘Not relevant’ to this biotope.

Introduction or spread of invasive non-indigenous species	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

Thompson & Schiel (2012) found that native fucoids show high resistance to invasions by the Japanese kelp *Undaria pinnatifida*. However, the cover of *Fucus vesiculosus* was inversely correlated with the cover of the invasive *Sargassum muticum* indicating competitive interaction between the two species (Stæhr *et al*., 2000). Stæhr *et al*. (2000) determined that the invasion of *Sargassum muticum* could affect local algal communities through competition mainly for light and space.

Gracilaria vermiculophylla is suggested to be one of the most successful marine non-native species (Kim *et al*., 2010; Sfriso *et al*., 2010 cited in Thomsen *et al*., 2013). This species invades wave sheltered, shallow water areas, and have been found in biotopes naturally dominated by fucoid canopies (Weinberger *et al*., 2008). To date, *Gracilaria vermiculophylla* has only been recorded in Northern Ireland, and not on mainland Britain. The introduction of this species to intertidal rocky shores around the British Isles could have negative impacts on native fucoid biotopes and could become relevant to this specific biotope.

Sensitivity assessment. Fucoid species have been negatively affected by both the direct and indirect consequences of INNS being present. However, no evidence can be found on the impacts of INNS on *Ascophyllum nodosum* within this biotope. Literature for this pressure should be revisited.

Introduction of microbial pathogens	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

No evidence.

Removal of target species	Low Q: High A: High C: Medium	Low Q: High A: Medium C: Medium	High Q: High A: Medium C: Medium

Seaweeds have been collected from the middle of the 16th century for the iodine industry. Modern day industrial uses for seaweed are extensive and include fertilizer, animal feed, alginate extracts (Phillipi *et al*., 2014), water treatment, and human food and health supplements (Bixler & Porse, 2010). The characteristic fucoid algae within this biotope are commercially collected. These commercial harvests remove seaweed canopies which have important effects on the wider ecosystem.

Stagnol *et al.* (2013) investigated the effects of commercial harvesting of intertidal fucoids on ecosystem biodiversity and functioning. The study found that the removal of the macroalgae canopy affected the metabolic flux of the area. Flows from primary production and community respiration were lower on the impacted area as the removal of the canopy caused changes in temperature and humidity conditions (Stagnol *et al.*, 2013). Bertness *et al.* (1999) found that the presence of an *Ascophyllum nodosum* canopy reduced maximum daily rock temperatures by 5-10 °C. It was also reported that water loss via evaporation was an order of magnitude less than that in areas where the fucoid canopy had been removed (Bertness *et al.*, 1999).

Stagnol *et al.* (2013) found that suspension feeders were the most affected by the canopy removal as canopy-forming algae are crucial habitats for these species. Other studies confirm that loss of canopy had both short and long-term consequences for benthic community diversity resulting in shifts in community composition and a loss of ecosystem functioning such as primary productivity (Lilley & Schiel, 2006; Gollety *et al.*, 2008).

Studies on the effects of commercial harvesting on the faunal communities associated with *Ascophyllum nodosum* have found that removing this key species can reduce abundances of epifauna found on the un-harvested biomass (Jarvis & Seed, 1996, Johnson & Scheibling, 1987; taken from Phillipi *et al.*, 2014). Changes *Ascophyllum nodosum* have also been found to affect the large, mobile fauna such as crabs or grazing gastropods (Bertness *et al.*, 1999; Fegley, 2001; Jenkins *et al.*, 1999, 2004, Phillipi *et al.*, 2014).

However, Phillipi *et al.* (2014) replicated commercial harvesting techniques in Maine, USA where *Ascophyllum nodosum* fronds were removed 40.6 cm from the holdfast and the lowest lateral branch must remain with the holdfast (DMR, 2009). The experiment looked specifically at the effect of canopy reduction on infaunal species living within the soft sediments within intertidal rocky shores where *Ascophyllum nodosum* was present. The experiment found that invertebrate species found living on and within sediments were not negatively affected by the harvesting activity (Phillipi *et al.*, 2014).

Due to the intolerance of macroalgae communities to human exploitation, the European Union put in place a framework to regulate the exploitation of algae establishing an organic label that implies that 'harvest shall not cause any impact on ecosystems' (no. 710/2009 and 834/2007).

Sensitivity assessment. The removal of *Ascophyllum nodosum* canopy will significantly change the community composition of the biotope. The quantity of biomass removed from the shore and the regularity of removal will all affect how quickly the biotope will be able to recover. *Ascophyllum nodosum* has a '**Low**' resistance to removal as it is easy to locate and has no escape strategy. Resilience is probably **'Low'**, however, recovery will only be able to start when the pressure is removed from the shore i.e. harvesting is no longer occurring. A sensitivity of **'High'** is recorded.

Removal of non-target species	Low Q: High A: High C: Medium	Low Q: High A: Medium C: Medium	High Q: High A: Medium C: Medium

Direct, physical impacts from harvesting are assessed through the abrasion and penetration of the seabed pressures. The characterizing species *Fucus vesiculosus* creates a dominant turf within this biotope. The dominance of this characterizing species means it could easily be incidentally removed from this biotope as by-catch when other species are being targeted. The loss of this species and other associated species would decrease species richness and negatively impact on the ecosystem function.

Sensitivity assessment. Removal of a large percentage of the characterizing species would alter the character of the biotope. The resistance to removal is '**Low'** due to the easy accessibility of the biotopes location and the inability of the species to evade collection. The resilience is also **'Low'**, with recovery only being able to begin when the harvesting pressure is removed altogether. Hence, sensitivity is assessed as **'High'.**

Bibliography

Åberg, P. & Pavia, H., 1997. Brown Alga *Ascophyllum nodosum. Marine Ecological Progress Series*, **158** (11), 1-119.

Åberg, P., 1992. Size-based demography of the seaweed *Ascophyllum nodosum* in stochastic environments. *Ecology*, **73:** 1488-1501.

Abou-Aisha, K.M., Kobbia, I., El Abyad, M., Shabana, E.F. & Schanz, F., 1995. Impact of phosphorus loadings on macro-algal communities in the Red Sea coast of Egypt. *Water, Air, and Soil Pollution*, **83** (3-4), 285-297.

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. & Hawkins, S.J., 2007. Negative effects of sediment deposition on grazing activity and survival of the limpet *Patella vulgata*. *Marine Ecology Progress Series*, **332**, 235-240.

Ang, P., Sharp, G. & Semple, R., 1996. Comparison of the structure of populations of *Ascophyllum nodosum* (Fucales, Phaeophyta) at sites with different harvesting histories. *Hydrobiologia*, **326** (1), 179-184.

Arévalo, R., Pinedo, S. & Ballesteros, E., 2007. Changes in the composition and structure of Mediterranean rocky-shore communities following a gradient of nutrient enrichment: descriptive study and test of proposed methods to assess water quality regarding macroalgae. *Marine Pollution Bulletin*, **55** (1), 104-113.

Araújo, R., Isabel, S.-P., Serrao, E.A. & Per, Å., 2012. Recovery after trampling disturbance in a canopy-forming seaweed population. *Marine Biology*, **159** (3), 697-707.

Araújo, R., Vaselli, S., Almeida, M., Serrão, E. & Sousa-Pinto, I., 2009. Effects of disturbance on marginal populations: human trampling on *Ascophyllum nodosum* assemblages at its southern distribution limit. *Marine Ecology Progress Series*, **378**, 81-92.

Archambault, P., Banwell, K. & Underwood, A., 2001. Temporal variation in the structure of intertidal assemblages following the removal of sewage. *Marine Ecology Progress Series*, **222**, 51-62.

Baardseth, E., 1970. Synopsis of the biological data on knotted wrack *Ascophyllum nodosum* (L.) Le Jolis. *FAO Fisheries Synopsis*, no. 38, Rev. 1.

Bacon, L.M. & Vadas, R.L., 1991. A model for gamete release in *Ascophyllum nodosum* (Phaeophyta). *Journal of Phycology*, **27**, 166-173.

Ballantine, W., 1961. A biologically-defined exposure scale for the comparative description of rocky shores. *Field Studies*, **1**, 73-84.

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.

Beer, S. & Kautsky, L., 1992. The recovery of net photosynthesis during rehydration of three *Fucus* species from the Swedish West Coast following exposure to air. *Botanica Marina*, **35** (6), 487-492.

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.

Bennell, S.J., 1981. Some observations on the littoral barnacle populations of North Wales. *Marine Environmental Research*, **5**, 227-240.

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.

Bertness, M.D., Ewanchuk, P.J., & Silliman, B.R., 2002. Anthropogenic modification of New England salt marsh landscapes. *Proceedings of the National Academy of Sciences, USA*, **99**, 1395-1398.

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

Bixler, H.J. & Porse, H., 2010. A decade of change in the seaweed hydrocolloids industry. *Journal of Applied Phycology*, **23** (3), 321-335.

Blanchette, C.A., 1997. Size and survival of intertidal plants in response to wave action: a case study with *Fucus gardneri*. *Ecology*, **78** (5), 1563-1578.

Boaden, P.J.S. & Dring, M.T., 1980. A quantitative evaluation of the effects of *Ascophyllum* harvesting on the littoral ecosystem. *Helgolander Meerestuntersuchungen*, **33**, 700-710.

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.

Bokn, T., 1987. Effects of diesel oil and subsequent recovery of commercial benthic algae. *Hydrobiologia*, **151/152**, 277-284.

Bokn, T.L., Duarte, C.M., Pedersen, M.F., Marba, N., Moy, F.E., Barrón, C., Bjerkeng, B., Borum, J., Christie, H. & Engelbert, S., 2003. The response of experimental rocky shore communities to nutrient additions. *Ecosystems*, **6** (6), 577-594.

Bokn, T.L., Moy, F.E., Christie, H., Engelbert, S., Karez, R., Kersting, K., Kraufvelin, P., Lindblad, C., Marba, N. & Pedersen, M.F., 2002. Are rocky shore ecosystems affected by nutrient-enriched seawater? Some preliminary results from a mesocosm experiment. *Sustainable Increase of Marine Harvesting: Fundamental Mechanisms and New Concepts:* Springer, pp. 167-175.

Brawley, S.H. & Johnson, L.E., 1991. Survival of fucoid embryos in the intertidal zone depends upon developmental stages and microhabitat. *Journal of Phycology*, **27** (2), 179-186.

Bricker, S.B., Clement, C.G., Pirhalla, D.E., Orlando, S.P. & Farrow, D.R., 1999. National estuarine eutrophication assessment: effects of nutrient enrichment in the nation's estuaries. NOAA, National Ocean Service, Special Projects Office and the National Centers for Coastal Ocean Science, Silver Spring, MD, 71 pp.

Bricker, S.B., Longstaff, B., Dennison, W., Jones, A., Boicourt, K., Wicks, C. & Woerner, J., 2008. Effects of nutrient enrichment in the nation's estuaries: a decade of change. *Harmful Algae*, **8** (1), 21-32.

Brinkhuis, B.H., Tempel, N.R. & Jones, R.F., 1976. Photosynthesis and respiration of exposed salt-marsh fucoids. *Marine Biology*, **34**, 339-348.

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., 1994. Effects of human trampling on marine rocky shore communities. *Journal of Experimental Marine Biology and Ecology*, **177**, 79-97.

Bryan, G.W. & Gibbs, P.E., 1983. *Heavy metals from the Fal estuary, Cornwall: a study of long-term contamination by mining waste and its effects on estuarine organisms.* Plymouth: Marine Biological Association of the United Kingdom. [Occasional Publication, no. 2.]

Cervin, G., Aberg, P. & Jenkins, S.R., 2005. Small-scale disturbance in a stable canopy dominated community: implications for macroalgal recruitment and growth. *Marine Ecology Progress Series*, **305**, 31-40.

Chock, J.S. & Mathieson, A.C., 1979. Physiological ecology of *Ascophyllum nodosum* (L.) Le Jolis and its detached ecad *scorpioides* (Hornemann) Hauck (Fucales, Phaeophyta). *Botanica Marina*, **22**, 21-26.

Choi, H.G. & Norton, T.A., 2005. Competition and facilitation between germlings of *Ascophyllum nodosum* and *Fucus vesiculosus*. *Marine Biology*, **147**(2), 525-532.

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.

Connan, S. & Stengel, D.B., 2011. Impacts of ambient salinity and copper on brown algae: 1. Interactive effects on photosynthesis, growth, and copper accumulation. *Aquatic Toxicology*, **104** (1–2), 94-107.

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

Cousens, R., 1984. Estimation of annual production by the intertidal brown algae *Ascophyllum nodosum* (L.) Le Jolis. *Botanica Marina*, **27**, 217-227.

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.

David, H.M., 1943. Studies in the autecology of *Ascophyllum nodosum*. *Journal of Ecology*, **31**, 178-198.

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.

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

Dıez, I., Santolaria, A. & Gorostiaga, J., 2003. The relationship of environmental factors to the structure and distribution of subtidal seaweed vegetation of the western Basque coast (N Spain). *Estuarine, Coastal and Shelf Science*, **56** (5), 1041-1054.

DMR, 2009. Laws and regulations, chapter 29 - seaweed. Department of Marine Resources, State of Maine. (Available from: http://www.maine.gov/dmr/commercialfishing/documents/seaweeds.graph.pdf).

Doty, S. & Newhouse, J., 1954. The distribution of marine algae into estuarine waters. *American Journal of Botany*, **41**, 508-515.

Dudgeon, S. & Petraitis, P.S., 2005. First year demography of the foundation species, *Ascophyllum nodosum*, and its community implications. *Oikos*, **109** (2), 405-415.

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.

Fegley, J., 2001. *Ecological implications of rockweed, Ascophyllum nodosum (L.) Le Jolis, harvesting.* University of Maine, Orono, ME.

Fish, J.D. & Fish, S., 1996. *A student's guide to the seashore.* Cambridge: Cambridge University Press.

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.L., 1996. The occurrence of 'green tides' - a review. In *Marine Benthic Vegetation. Recent changes and the Effects of Eutrophication* (ed. W. Schramm & P.H. Nienhuis). Berlin Heidelberg: Springer-Verlag. [Ecological Studies, vol. 123].

Foster, B.A., 1970. Responses and acclimation to salinity in the adults of some balanomorph barnacles. *Philosophical Transactions of the Royal Society of London, Series B*, **256**, 377-400.

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.

Gollety, C., Migne, A. & Davoult, D., 2008. Benthic metabolism on a sheltered rocky shore: Role of the canopy in the carbon budget. *Journal of Phycology*, **44** (5), 1146-1153.

Hartnoll, R.G. & Hawkins, S.J., 1985. Patchiness and fluctuations on moderately exposed rocky shores. *Ophelia*, **24**, 53-63.

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. & 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., Proud, S.V., Spence, S.K. & Southward, A.J., 1994. From the individual to the community and beyond: water quality, stress indicators and key species in coastal systems. In *Water quality and stress indicators in marine and freshwater ecosystems: linking levels of organisation (individuals, populations, communities)* (ed. D.W. Sutcliffe), 35-62. Ambleside, UK: Freshwater Biological Association.

Hill, S., Burrows, S.J. & Hawkins, S.J., 1998. *Intertidal Reef Biotopes (Volume VI). An overview of dynamics and sensitivity characteristics for conservation management of marine Special Areas of Conservation.* Oban: Scottish Association for Marine Science (UK Marine SACs Project)., Scottish Association for Marine Science (UK Marine SACs Project).

Holt, T.J., Hartnoll, R.G. & Hawkins, S.J., 1997. The sensitivity and vulnerability to man-induced change of selected communities: intertidal brown algal shrubs, *Zostera* beds and *Sabellaria spinulosa* reefs. *English Nature, Peterborough, English Nature Research Report* No. 234.

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

Ingolfsson, A. & Hawkins, S., 2008. Slow recovery from disturbance: a 20 year study of *Ascophyllum* canopy clearances. *Journal of the Marine Biological Association of the United Kingdom*, **88** (4), 689-691.

Jarvis, S. & Seed, R., 1996. The meiofauna of *Ascophyllum nodosum* (L.) Le Jolis: characterization of the assemblages associated with two common epiphytes. *Journal of Experimental Marine Biology and Ecology*, **199**, 249-267.

Jenkins, S.R., Hawkins, S.J. & Norton, T.A., 1999. Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community. *Marine Ecology Progress Series*, **188**, 81-92.

Jenkins, S.R., Moore, P., Burrows, M.T., Garbary, D.J., Hawkins, S.J., Ingólfsson, A., Sebens, K.P., Snelgrove, P.V., Wethey, D.S. & Woodin, S.A., 2008. Comparative ecology of North Atlantic shores: do differences in players matter for process? *Ecology*, **89** (11), 3-S23.

Jenkins, S.R., Norton, T.A. & Hawkins, S.J., 2004. Long term effects of *Ascophyllum nodosum* canopy removal on mid shore community structure. *Journal of the Marine Biological Association of the United Kingdom*, **84**, 327-329.

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/

Johnson, S. & Scheibling, R., 1987. Structure and dynamics of epifaunal assemblages on intertidal macroalgae *Ascophyllum nodosum* and *Fucus vesiculousus* in Nova Scotia, Canada. *Marine Ecology Progress Series*, **37**, 209-227.

Johnston, E.L. & Roberts, D.A., 2009. Contaminants reduce the richness and evenness of marine communities: a review and meta-analysis. *Environmental Pollution*, **157** (6), 1745-1752.

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.

Josefson, A. & Widbom, B., 1988. Differential response of benthic macrofauna and meiofauna to hypoxia in the Gullmar Fjord basin. *Marine Biology*, **100** (1), 31-40.

Karez, R., Engelbert, S., Kraufvelin, P., Pedersen, M.F. & Sommer, U., 2004. Biomass response and changes in composition of ephemeral macroalgal assemblages along an experimental gradient of nutrient enrichment. *Aquatic Botany*, **78** (2), 103-117.

Keser, M., Swenarton, J.T. & Foertch, J.F., 2005. Effects of thermal input and climate change on growth of *Ascophyllum nodosum* (Fucales, Phaeophyceae) in eastern Long Island Sound (USA). *Journal of Sea Research*, **54** (3), 211-220.

Keser, M., Vadas, R. & Larson, B., 1981. Regrowth of *Ascophyllum nodosum* and *Fucus vesiculosus* under various harvesting regimes in Maine, USA. *Botanica Marina*, **24** (1), 29-38.

Kinne, O. (ed.), 1972. *Marine Ecology: A Comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters,*Vol.1, *Environmental Factors*, part 3. New York: John Wiley & Sons.

Knight, M. & Parke, M., 1950. A biological study of *Fucus vesiculosus* L. and *Fucus serratus* L. *Journal of the Marine Biological Association of the United Kingdom*, **29**, 439-514.

Knight-Jones, E. & Stevenson, J., 1950. Gregariousness during settlement in the barnacle *Elminius modestus* Darwin. *Journal of the Marine Biological Association of the United Kingdom*, 29 (02), 281-297.

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.

Ladah, L., Feddersen, F., Pearson, G. & Serrão, E., 2008. Egg release and settlement patterns of dioecious and hermaphroditic fucoid algae during the tidal cycle. *Marine Biology*, **155** (6), 583-591.

Laffoley, D. & Hiscock, K., 1993. The classification of benthic estuarine communities for nature conservation assessments in Great Britain. *Netherlands Journal of Aquatic Ecology*, **27**, 181-187.

Lamote, M. & Johnson, L.E., 2008. Temporal and spatial variation in the early recruitment of fucoid algae: the role of microhabitats and temporal scales. *Marine Ecological Progress Series*. **368**, 93-102.

Lazo, L., Markham, J.H. & Chapman, A., 1994. Herbivory and harvesting: effects on sexual recruitment and vegetative modules of *Ascophyllum nodosum*. *Ophelia*, **40** (2), 95-113.

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.

Lewis, J.R., 1964. *The Ecology of Rocky Shores.* London: English Universities Press.

Lilley, S.A. & Schiel, D.R., 2006. Community effects following the deletion of a habitat-forming alga from rocky marine shores. *Oecologia*, **148** (4), 672-681.

Lima, F.P., Ribeiro, P.A., Queiroz, N., Hawkins, S.J. & Santos, A.M., 2007. Do distributional shifts of northern and southern species of algae match the warming pattern? *Global Change Biology*, **13** (12), 2592-2604.

Lindsay, S.J. & Thompson, H. 1930. The determination of specific characters for the identification of certain ascidians. *Journal of the Marine Biological Association of the United Kingdom*, **17**, 1-35.

Little, C. & Kitching, J.A., 1996. *The Biology of Rocky Shores.* Oxford: Oxford University Press.

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.

Lobban, C.S. & Harrison, P.J., 1997. *Seaweed ecology and physiology*. Cambridge: Cambridge University Press.

Munda, I., 1964. *The influence of salinity on the chemical composition, growth and fructification of some Fucaceae.* New York: Pergamon Press.

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

Norton, T.A. (ed.), 1985. *Provisional Atlas of the Marine Algae of Britain and Ireland*. Huntingdon: Biological Records Centre, Institute of Terrestrial Ecology.

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

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.

Pearson, G.A., Lago-Leston, A. & Mota, C., 2009. Frayed at the edges: selective pressure and adaptive response to abiotic stressors are mismatched in low diversity edge populations. *Journal of Ecology*, **97** (3), 450-462.

Petraitis, P.S. & Dudgeon, S.R., 2005. Divergent succession and implications for alternative states on rocky intertidal shores. *Journal of Experimental Marine Biology and Ecology*, **326** (1), 14-26.

Phillippi, A., Tran, K. & Perna, A., 2014. Does intertidal canopy removal of *Ascophyllum nodosum* alter the community structure beneath? *Journal of Experimental Marine Biology and Ecology*, **461**, 53-60.

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.

Printz, H.S., 1959. Investigations of the failure of recuperation and re-populating in cropped *Ascophyllum* areas. *Avhandlinger utgitt av Det Norske Videnskap-Akademi i Oslo* No. 3.

Raffaelli, D. & Hawkins, S., 1999. *Intertidal Ecology* 2nd edn.. London: Kluwer Academic Publishers.

Raffaelli, D.G. & Hawkins, S.J., 1996. *Intertidal Ecology* London: Chapman and Hall.

Rita, A., Isabel, S.-P., Serrao, E.A. & Per, Å., 2012. Recovery after trampling disturbance in a canopy-forming seaweed population. *Marine Biology*, **159** (3), 697-707.

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.

Schiel, D.R. & Foster, M.S., 2006. The population biology of large brown seaweeds: ecological consequences of multiphase life histories in dynamic coastal environments. *Annual Review of Ecology, Evolution, and Systematics*, 343-372.

Schonbeck, M.W. & Norton, T.A., 1978. Factors controlling the upper limits of fucoid algae on the shore. *Journal of Experimental Marine Biology and Ecology*, **31**, 303-313.

Scrosati, R. & DeWreede, R.E., 1998. The impact of frond crowding on frond bleaching in the clonal intertidal alga *Mazzaella cornucopiae* (Rhodophyta, Gigartinaceae) from British Columbia, Canada. *Journal of Phycology*, **34** (2), 228-232.

Sharp, G., 1987. *Ascophyllum nodosum* and its harvesting in Eastern Canada. *FAO Fisheries Technical Paper*, **281**, 3-46.

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

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.

Stafford, R. & Davies, M.S., 2005. Spatial patchiness of epilithic biofilm caused by refuge-inhabiting high shore gastropods. *Hydrobiologia*, **545** (1), 279-287.

Stagnol, D., Renaud, M. & Davoult, D., 2013. Effects of commercial harvesting of intertidal macroalgae on ecosystem biodiversity and functioning. *Estuarine, Coastal and Shelf Science*, **130**, 99-110.

Steen, H. & Rueness, J., 2004. Comparison of survival and growth in germlings of six fucoid species (Fucales, Phaeophyceae) at two different temperature and nutrient levels. *Sarsia*, **89**, 175-183.

Stengel, D.B. & Dring, M.J., 1997. Morphology and *in situ* growth rates of plants of *Ascophyllum nodosum* (Phaeophyta) from different shore levels and responses of plants to vertical transplantation. *European Journal of Phycology*, **32**, 193-202.

Stengel, D.B. & Dring, M.J., 2000. Copper and iron concentrations in *Ascophyllum nodosum* (Fucales, Phaeophyta) from different sites in Ireland and after culture experiments in relation to thallus age and epiphytism. *Journal of Experimental Marine Biology and Ecology*, **246**, 145-161.

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

Strömgren, T., 1977. Short-term effect of temperature upon the growth of intertidal Fucales. *Journal of Experimental Marine Biology and Ecology*, **29**, 181-195.

Strömgren, T., 1979a. The effect of copper on the increase in length of *Ascophyllum nodosum*. *Journal of Experimental Marine Biology and Ecology*, **37**, 153-159.

Sundene, O., 1973. Growth and reproduction in *Ascophyllum nodosum* (Phaeophyceae). *Norwegian Journal of Botany*, **20**, 249-255.

Svensson, C.J., Pavia, H. & Åberg, P., 2009. Robustness in life history of the brown seaweed *Ascophyllum nodosum* (Fucales, Phaeophyceae) across large scales: effects of spatially and temporally induced variability on population growth. Marine Biology, **156** (6), 1139-1148.

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.

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

Thomsen, M., Staehr, P., Nejrup, L. & Schiel, D., 2013. Effects of the invasive macroalgae *Gracilaria vermiculophylla* on two co-occuring foundation species and associated invertebrates. *Aquatic Invasions*, **8** (2), 133-145.

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

Ugarte, R., Sharp, G. & Moore, B., 2006. Changes in the brown seaweed *Ascophyllum nodosum* (L.) Le Jolis. plant morphology and biomass produced by cutter rake harvests in souther New Brunswick, Canada. *Journal of applied Phycology*, **18**, 351-359.

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. & Larson, B., 1978. Effects of reduced temperatures on previously stressed populations of an intertidal alga. In *Energy and environmental stress in aquatic systems* (eds. J.H. Thorp & J.W. Gibbons), DOE Symposium Series 48 (CONF-721114), pp. 434-451., Washington DC: U.S. Government Printing Office.

Vadas, R.L., Wright, W.A. & Miller, St. L., 1990. Recruitment in *Ascophyllum nodosum*: wave action as a source of mortality. *Marine Ecology Progress Series*, **61**, 263-272.

Vethaak, A.D., Cronie, R.J.A. & van Soest, R.W.M., 1982. Ecology and distribution of two sympatric, closely related sponge species, *Halichondria panicea* (Pallas, 1766) and *H. bowerbanki* Burton, 1930 (Porifera, Demospongiae), with remarks on their speciation. *Bijdragen tot de Dierkunde*, **52**, 82-102.

Wapstra, M. & van Soest, R.W.M., 1987. Sexual reproduction, larval morphology and behaviour in demosponges from the southwest of the Netherlands. Berlin: Springer-Verlag.

Weinberger, F., Buchholz, B., Karez, R. & Wahl, M., 2008. The invasive red alga *Gracilaria vermiculophylla* in the Baltic Sea: adaptation to brackish water may compensate for light limitation. *Aquatic Biology*, **3** (3), 251-264.

White, K.L., Kim, J.K. & Garbary, D.J., 2011. Effects of land-based fish farm effluent on the morphology and growth of *Ascophyllum nodosum* (Fucales, Phaeophyceae) in southwestern Nova Scotia. *Algae*, **26** (3), 253-263.