



# MarLIN

## Marine Information Network

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

# *Ascophyllum nodosum* with epiphytic sponges and ascidians on variable salinity infralittoral rock

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

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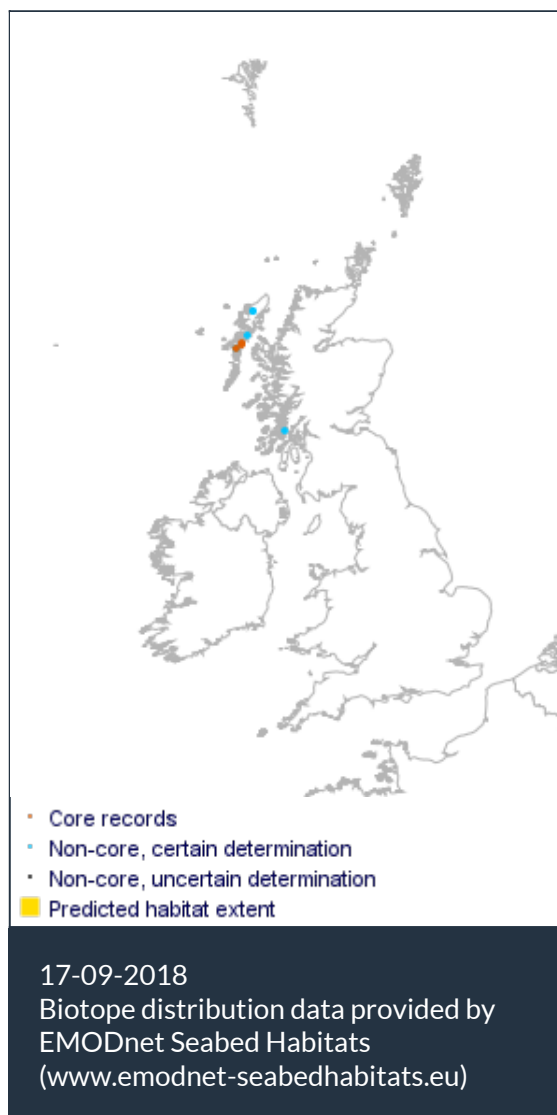


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*Ascophyllum nodosum* with epiphytes.  
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Researched by Frances Perry & Jacqueline Hill

Refereed by This information is not refereed

## Summary

### ☰ UK and Ireland classification

EUNIS 2008	A3.342	<i>Ascophyllum nodosum</i> and epiphytic sponges and ascidians on variable salinity infralittoral rock
JNCC 2015	IR.LIR.Lag.AscSpAs	<i>Ascophyllum nodosum</i> with epiphytic sponges and ascidians on variable salinity infralittoral rock
JNCC 2004	IR.LIR.Lag.AscSpAs	<i>Ascophyllum nodosum</i> with epiphytic sponges and ascidians on variable salinity infralittoral rock
1997 Biotope	IR.SIR.Lag.AscSAs	<i>Ascophyllum nodosum</i> with epiphytic sponges and ascidians on variable salinity infralittoral rock

### 🔍 Description

Dense subtidal stands of *Ascophyllum nodosum*, heavily epiphytised by sponges and ascidians in lagoon-like habitats. The wracks *Fucus vesiculosus* and *Fucus serratus* can be present along with the

brown seaweed *Chorda filum* and the red seaweed *Polyides rotunda*. The crab *Carcinus maenas* can be present between the *Ascophyllum nodosum* holdfasts along with the shrimps Mysidae. Nearby rock often supports similar biotopes of submerged fucoids and green seaweeds (FChoG). Slightly deeper rock often supports *Saccharina latissima* (Slat.Ft), usually surrounded by more extensive areas of sediment. Seagrass beds thrive well in the muddy sand of these lagoons and often cover large areas. They include both *Ruppia maritima* and *Zostera marina* (Rup and Zmar). (Information from Connor *et al.*, 2004; JNCC, 2015).

### ↓ Depth range

Lower shore, 0-5 m

### Additional information

-

### ✓ Listed By

- none -

### Further information sources

Search on:



## Habitat review

### 🔄 Ecology

#### Ecological and functional relationships

- The biotope is found in very shallow submerged rocky habitats in lagoons, subject to variable or permanently reduced salinity conditions. These particular habitat conditions lead to a variety of seaweed-dominated communities which include fucoids and green filamentous species. The fucoids, more typical of intertidal habitats, penetrate into the subtidal under the reduced salinity conditions which are not tolerated by kelps.
- The biotope is dominated by dense stands of *Ascophyllum nodosum*. The species, and the other macroalgae in the biotope, increase the amount of space available for attachment, they provide shelter from wave action, desiccation and heat, and they are an important food source. High abundances of the characterizing algae may contribute to the oxygen budget of lagoons. In the North Atlantic for example, *Ascophyllum nodosum* is of great ecological importance 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).
- *Ascophyllum nodosum* plants provide a substratum for a variety of attached animal species including the sponge *Halichondria panicea*, the sea squirts *Ciona intestinalis* and *Botryllus schlosseri* and some erect bryozoans.
- Growth of epiphytic sponges and ascidians may be slower than in tide-swept habitats because the biotope has weak tidal streams and wave exposure and so will have a limited supply of suspended particles necessary for suspension feeding. However, low water flow environments will favour active rather than passive suspension feeders.

#### Seasonal and longer term change

*Ascophyllum nodosum* has a very long lifespan where individual fronds can survive for 10-15 years and the holdfast for several decades. The longevity of *A. nodosum* contributes to the stability of the biotope. Other fucoid plants found in the biotope, such as *Fucus serratus*, have lifespans in the order of 3-5 years. However, growth rates of macroalgae 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. Faunal groups in the biotope are also likely to show seasonal variation in growth rates and recruitment.

#### Habitat structure and complexity

Fucoid biotopes 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 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

On rocky shores, only about 10% of the primary production is directly cropped by herbivores (Raffaelli & Hawkins, 1996) and this is likely to be similar for lagoon-like habitats. 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 and can make a contribution to the food of many marine species through the production of planktonic larvae and propagules which contribute to pelagic food chains. However, in lagoon-like habitats such as the SIR.AscSAs biotope, where tidal flows and wave exposure are weak larvae and propagules probably enter the food chain of local ecosystems rather than inshore subtidal or offshore ecosystems.

## Recruitment processes

Many rocky shore plants and animals, 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.

- Furoid plants are recruited from pelagic sporelings that settle on the substratum. Recruitment of *Ascophyllum nodosum* is generally poor and in the intertidal few germlings are found on the shore. However, in the sheltered conditions of the lagoon-like SIR.AscSAs biotope, recruitment from local plant stands may be more effective.
- The sponges and ascidians characterizing the biotope all have planktonic larvae and are fairly short-lived. There is therefore, high recruitment and high turnover.

## Time for community to reach maturity

The time for an *Ascophyllum nodosum* community to reach maturity is likely to be many years because the main characterizing species has very poor recruitment and is very slow growing. *Ascophyllum nodosum* does not reach sexual maturity until about 5 years of age and, in the intertidal, individual fronds can live to be up to 15 years old and whole plants for several decades. In their work on furoid 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 (1956) 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, 1956). The epiphytic species are likely to colonize algae very rapidly. Most epiphytic species are likely to have planktonic larvae and rapid growth so that colonization of the algae will be rapid. For example, settlement of new colonies of *Halichondria panicea* within one year is likely and the species increases in size by about 5% per week (Barthel, 1988). Recovery of the sea squirt *Ciona intestinalis*, may take a little longer if adult populations have been lost because the species probably has limited dispersal because the larval stage is very short (hours or days) and larvae are often retained near the adults by mucus threads. However, in Plymouth reproduction is recorded as occurring all year round so recovery from loss

within a few years should be possible. Even if some other epiphytic species take longer to return the recovery of the biotope is likely to be limited by the recovery of the key species *Ascophyllum nodosum*.

### Additional information

Information on the biotope has been based greatly on the general biology and ecology of *Ascophyllum nodosum* in the more common intertidal full salinity habitat. It is possible that in reduced and variable salinity lagoonal habitats life history characteristics of the species, such as growth rates, longevity and reproduction may be different.

## Preferences & Distribution

### Habitat preferences

<b>Depth Range</b>	Lower shore, 0-5 m
<a href="#">Water clarity preferences</a>	
<b>Limiting Nutrients</b>	Nitrogen (nitrates), Phosphorus (phosphates)
<b>Salinity preferences</b>	Full (30-40 psu), Low (<18 psu), Reduced (18-30 psu)
<b>Physiographic preferences</b>	Enclosed coast / Embayment, Isolated saline water (Lagoon)
<b>Biological zone preferences</b>	Infralittoral, Sublittoral fringe
<b>Substratum/habitat preferences</b>	Bedrock, Cobbles, Gravelly mud, Large to very large boulders, Sand, Small boulders
<b>Tidal strength preferences</b>	Moderately Strong 1 to 3 knots (0.5-1.5 m/sec.), Very Weak (negligible), Weak < 1 knot (<0.5 m/sec.)
<b>Wave exposure preferences</b>	Extremely sheltered, Ultra sheltered
<b>Other preferences</b>	

### Additional Information

## Species composition

### Species found especially in this biotope

### Rare or scarce species associated with this biotope

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### Additional information

## Sensitivity review

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

This biotope is found exclusively within lagoon or lagoon-like habitats. There are only 358 examples of these rare and unusual habitats in the UK (Bamber et al., 2001), which make up a total of 5,184 hectares of coastline habitat (UKNEA, 2011). A number of factors are thought to contribute to the rarity of these habitats in the UK. Many sedimentary lagoons do not appear in many of the areas suitable for them because of the macrotidal regimes found within the North East Atlantic (Barnes, 1991). The high energy coastlines common around the UK mean that shingle lagoons can be both created from offshore glacial deposits and removed, therefore they are often short-lived on geological time scales, and are now less common than they were at the end of the last ice age (Bamber et al., 2001). The low energy nature of lagoons also means that they can be susceptible to silting up which can elevate their basins above the level for percolation input. Combined with perimeter shingle ridges being elevated by storms, reducing water input via overtopping, can cause lagoons to become freshwater lakes (Bamber et al., 2001). The somewhat ephemeral nature of lagoons, and their susceptibility to change, means that the succession of habitats and consequently the biotopes found within them can be quicker and more noticeable than those found within other more stable physical environments.

This biotope is characterized by a dense canopy of *Ascophyllum nodosum*. The fucoids *Fucus vesiculosus* and *Fucus serratus* are also frequent within this biotope. The red seaweed *Polysiphonia lanosa* is a common epiphyte on *Ascophyllum nodosum*. 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). The crab *Carcinus maenas* and the dog whelk *Nucella lapillus* are dominant predators. Littorinids are dominant grazers in intertidal fucoids dominated communities. However, in the field, *Littorina littorea* is replaced by amphipods as the dominant mesograzer when salinities regularly fall below 12‰ (Johannesson et al., 1988). The main grazers recorded within this biotope are mysids. Mysids are similar to amphipods in their feeding habits, and it is likely that fill the functional niche as amphipods. Macroalgae have been found to contribute as much as 68% of the total diet of a species of mysid (Kibirige et al., 2003). Mysids could be an important grazing species in this subtidal biotope but no evidence was found on the impact of mysid grazing on the characterizing species.

*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 (Jenkins et al., 2008; Pocklington et al., 2018). Although *Fucus vesiculosus* and *Fucus serratus* are important to this biotope, their loss from the biotope would not result in loss of the biotope. The fucoid canopy provides protection for the various underlying seaweeds in addition to providing a substratum for epifauna and being the primary food resource for grazers (Cervin et al., 2005; Jenkins et al., 2008; Pocklington et al., 2018). 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 120 years in areas free from ice scour (Åberg, 1992a,b). However, individual fronds are more likely to last for 15 -20 years, after which they break off and new fronds grow from the holdfast. The average age within populations of



*Ascophyllum nodosum* is high, and there is little population turn over (Schiel & Foster, 2006). Åberg (1992a,b) concluded that the maximum lifespan of *Ascophyllum nodosum* in two sites in Sweden was 40-60 years, based on demographics and modelling. Furthermore, Åberg (1992a,b) suggested that 10% of sub-populations could survive as long as 120 yrs and that the mean extinction time for subpopulations was ca 163 yrs, based on his models. *Ascophyllum nodosum* takes five years to become sexually mature (Sundene, 1973). As many as  $2.5 \times 10^9$  eggs  $m^2/year$  may be produced in a mature stand of *Ascophyllum nodosum* (Åberg & Pavia, 1997). However, Åberg & Pavia (1997) estimated that ca one hundred millionths of eggs survive ( $2 \times 10^{-8}$ ) to become 1.5-year-old recruits (Åberg & Pavia, 1997). Dudgeon & Petraitis (2005) reported that germling survivorship depended on the size of the cleared area and that mortality exceeded 99.9% in the first year. Also, they estimated that it could take a minimum of 13 years for an individual to replace itself. 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 furoids (Keser et al., 1981).

Furoids (inc. *Ascophyllum nodosum*) have a low dispersal capacity, which 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 (Vadas et al., 1992). Therefore, calm conditions typical of wave sheltered habitats are required for successful recruitment in *Ascophyllum nodosum*. Lamote & Johnson (2008) studied temporal and spatial variation in recruitment of furoid 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 furoid 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.

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 in Long Island Sound in 1984 caused by water temperatures from two power plant thermal discharge pipes exceeding 27-28°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 at the end of Keser *et al.*'s (2005) study. Keser *et al.* (2005) reported that similar mortality events were observed near other power plant thermal discharge pipes in Maine (Vadas *et al.*, 1978) and Massachusetts (Wilce *et al.*, 1978).

Keser *et al.* (1981) recorded the levels of re-growth exhibited by *Ascophyllum nodosum* and *Fucus vesiculosus* after experimental 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; 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). 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 were 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).

Baardseth (1970) also reported slow re-growth of *Ascophyllum nodosum* after harvesting from the holdfast. Harvesting was found to destroy beds for extended periods 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 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).

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 and suggested 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.

There is 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; cited in Phillippi *et al.*, 2014) but that removed at the holdfast, flush to the substratum (or the holdfast is removed) recovery takes many years (Phillippi *et al.*, 2014). Numerous studies have concluded that *Ascophyllum nodosum* takes long periods to recover from removal include Bertness *et al.* (2002), Jenkins *et al.* (1999, 2004), Petraitis & Dudgeon (2005), Cervin *et al.* (2005) and Ingólfsson & Hawkins (2008). 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'. Jenkins *et al.* (1999, 2004) removed the canopy and holdfasts from quadrats and found that the understory of red algae diminished together with the diversity of mobile and sessile invertebrates. Although *Ascophyllum* showed high recruitment it was slow to recover and cleared areas were dominated by *Fucus serratus* and *Fucus vesiculosus* and a mixed canopy of *Fucus* sp and *Ascophyllum nodosum* was present 12 years later. Neither the density of *Ascophyllum* canopy nor the understory community of red algae had recovered after 12 years of study. Cervin *et al.* (2005) noted that loss of the canopy and underlying turf promoted *Ascophyllum* recruitment but that the mixed *Fucus serratus* and *Fucus vesiculosus* canopy dominated after seven years because the *Ascophyllum* recruits were too slow-growing to form a canopy. The twenty-year study undertaken by Ingólfsson & Hawkins (2008) in Iceland found that after removing an *Ascophyllum nodosum* canopy, the canopy could return within 7-8 years, yet the understory community of *Cladophora* spp. had still not recovered after 20 years. Similarly, Petraitis & Dudgeon (2005) reported that succession was dependent on clearing size and that large clearings (8 metres in diameter) were quickly colonized by *Fucus vesiculosus* and *Semibalanus balanoides* but that the dominant *Ascophyllum* canopy had not recovered after 5.5 years (the duration of the study).

*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 six 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 vary.

However, *Ascophyllum nodosum* takes a long time to recover and provides suitable habitat for the associated understorey community (Pocklington *et al.*, 2018). Pocklington *et al.* (2018) examined community disturbance after removal of 100%, 50%, 245% and 0% of *Ascophyllum nodosum* fronds (but not holdfasts). They concluded that a pulse disturbance (frond removal) of 50% loss of fronds increased the temperature under the canopy significantly and decreased the abundance of mobile invertebrates such as *Littorina obtusata*. Sessile taxa such as *Osmundia pinnatifida* and encrusting corallines could withstand a 75% loss of fronds but declined by half if 100% were removed. Therefore, the recovery of this biotope hinges on the recovery of the sufficient cover of the *Ascophyllum nodosum* canopy.

**Resilience assessment.** *Ascophyllum nodosum* has high egg and juvenile mortality rates, slow growth, and can take over five years to reach reproductive maturity. Small scale perturbations (e.g. frond removal; Keser *et al.*, 1981; Pocklington *et al.*, 2018) and small scale clearances (e.g. Cervin *et al.*, 2005; Jenkins *et al.*, 1999, 2004; Petraitis & Dudgeon, 2005) have been shown to affect intertidal communities significantly. In this subtidal biotope, the understorey of red algae is sparse and would not suffer desiccation, bleaching or temperature extremes typical of intertidal communities. Minor disturbances that result in the cutting of the frond only may allow regrowth in within two to three years depending on the length remaining, shelter and grazing pressure, based on Keser *et al.* (1981) and Phillippi *et al.* (2014). However, even small scale disturbances similar to the clearance studies (i.e. the removal of small patches, flush with the substratum and/or including the holdfast, within the bed), may require over 12 years for partial recovery of the *Ascophyllum* canopy (Jenkins *et al.*, 1999; 2004; Cervin *et al.*, 2005). Mass mortality due to ice scour (Åberg (1992a,b) or thermal effluent (Keser *et al.*, 2005) would probably require over 18 years for partial, if any, recovery (Keser *et al.*, 2005). Therefore, where resistance to a specific pressure is assessed as Medium (<25% loss) or Low (25-75% loss) or 'None' (>75% loss) then resilience is probably 'Low' (10-25 years) based on the time required for the recovery of the *Ascophyllum* canopy alone. **An exception** is made for permanent or ongoing (long-term) pressures where recovery is not possible as the pressure is irreversible, and resilience is assessed as 'Very low' by default.

**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)	High Q: High A: High C: Medium	High Q: High A: High C: High	Not sensitive Q: High A: High 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 and Iceland and west into the Kattegat on the shores of Sweden. *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 (Strömberg, 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 27-28°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 and 23°C.

In the North East Atlantic, *Fucus vesiculosus* occurs from Northern Russia to Morocco (Powell, 1963). *Fucus vesiculosus* can tolerate temperatures as high as 30°C (Lüning, 1990) and did not show any sign of damage during the extremely hot UK summer of 1983 when average temperatures were 8°C hotter than normal (Hawkins & Hartnoll, 1985). *Fucus vesiculosus* also tolerates extended periods of freezing in the northern part of its range. *Fucus serratus* is found along the Atlantic coast of Europe from Svalbard to Portugal and on the shores of north-east America and is within its thermal range in the British Isles. Nielsen *et al.* (2014) found no negative effects on growth rates of adult *Fucus serratus* to water temperatures of 22°C (based on a laboratory experiment with specimens collected from Firth of Forth, Scotland) and Arrontes (1993) observed that *Fucus serratus* survived in laboratory experiments for 1 week at 25°C. Nielsen *et al.* (2014) did, however, report that germlings were negatively affected by increased temperature indicating that early life stages are more vulnerable than mature algae to this pressure.

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 *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 this species can extend down to Portugal, a short term acute temperature increase, leaving no time for acclimation, might be

expected to result in some damage to or mortality of *Ascophyllum*, especially if the increase occurred during the summer months. However, the observations of Hawkins & Hartnoll (1985) suggest otherwise. Therefore, resistance is assessed as 'High' at the benchmark (an increase of 5°C for one month) in UK waters. Resilience is assessed as 'High' so that sensitivity is assessed as a 'Not sensitive' at the benchmark level.

### Temperature decrease (local)

High

Q: High A: High C: Medium

High

Q: High A: High C: High

Not sensitive

Q: High A: High 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 and Iceland and west into the Kattegat on the shores of Sweden. The growth of *Ascophyllum nodosum* has been measured between 2.5 and 35°C with an optimum between 10 and 17°C (Strömberg, 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 and 23°C. *Ascophyllum nodosum* was reported to survive freezing to -20°C (MacDonald *et al.*, 1974, cited in Åberg, 1992a).

In the North East Atlantic, *Fucus vesiculosus* occurs from Northern Russia to Morocco (Powell, 1963). *Fucus vesiculosus* can tolerate temperatures as high as 30°C (Lüning, 1990) and did not show any sign of damage during the extremely hot UK summer of 1983 when average temperatures were 8°C hotter than normal (Hawkins & Hartnoll, 1985). *Fucus vesiculosus* also tolerates extended periods of freezing in the northern part of its range. *Fucus serratus* is found along the Atlantic coast of Europe from Svalbard to Portugal and on the shores of north-east America and is within its thermal range in the British Isles. Lüning (1984) reported that *Fucus serratus* survived in the laboratory for a week a range temperature between 0°C and 25°C and placed this species in his 'cold temperature North Atlantic group'.

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, mobile species such as *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. It is unlikely to be affected by a short-term change of 5°C for one month or 2°C for a year in UK waters as it survives harsher winter conditions in northern waters of Iceland and in Sweden where populations are subject to ice scour (Åberg, 1992a,b; Ingólfsson & Hawkins, 2008). Therefore, resistance is assessed as 'High' at the benchmark

(an increase of 5°C for one month) in UK waters. Resilience is assessed as '**High**' so that sensitivity is assessed as a '**Not sensitive**' at the benchmark level.

<b>Salinity increase (local)</b>	No evidence (NEv)	Not relevant (NR)	No evidence (NEv)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

Variation in salinity within saline lagoons is a characteristic of the habitat. In larger lagoons it is also possible to get different salinities within different areas of the lagoon itself. Therefore, all species found within saline lagoon communities must be able to tolerate salinity fluctuations. All lagoons are affected by short, medium and long-term changes in salinity (Bamber *et al.*, 2001). Semi-diurnal tides cause differences in salinity over short periods, response to changes in rainfall can cause medium-term changes and seasonal rainfall and drought can cause longer-term salinity trends (Bamber *et al.*, 2001). 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' salinity (18 – 35 ppt) (Connor *et al.*, 2004). Hence, 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. 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 (Newell, 1979). *Fucus vesiculosus* is well adapted to cope with varying salinities and can grow in full saline to brackish conditions. Bäck *et al.* (1991) compared *Fucus vesiculosus* individuals from Atlantic and Baltic populations. Both populations were able to withstand a wide range of salinities in laboratory cultures. The Atlantic population showed better growth in higher salinities and virtually no growth at 5 ppt. Those individuals kept at 5 ppt mortality occurred after seven weeks. In contrast, the Baltic wracks grew better in conditions with lower salinities. But growth was negligible at the highest tested salinity of 45 ppt (Bäck *et al.*, 1991). Growth rates for *Fucus serratus* are maximal at a salinity of 20 psu with the critical limit for recruitment set at 7 psu (Malm *et al.*, 2001). *Semibalanus balanoides* can tolerate salinities between 12 and 50 psu; below and above this cirral activity ceases (Foster, 1970). *Carcinus maenas* is mobile can move to suitable conditions on the shore.

**Sensitivity assessment.** 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. However, **no evidence** on the effects of hypersaline conditions on *Ascophyllum nodosum* or its associated community was found.

<b>Salinity decrease (local)</b>	High	High	Not sensitive
	Q: High A: Medium C: Medium	Q: High A: High C: High	Q: High A: Medium C: Medium

Variation in salinity within saline lagoons is a characteristic of the habitat. In larger lagoons it is also possible to get different salinities within different areas of the lagoon itself. Therefore, all species found within saline lagoon communities must be able to tolerate salinity fluctuations. All lagoons are affected by short, medium and long-term changes in salinity (Bamber *et al.*, 2001). Semi-diurnal tides cause differences in salinity over short periods, response to changes in rainfall can cause medium-term changes and seasonal rainfall and drought can cause longer-term salinity trends (Bamber *et al.*, 2001). 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 8 psu (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 seven 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).

*Fucus vesiculosus* is well adapted to cope with varying salinities and can grow in full saline to brackish conditions. *Fucus vesiculosus* is the dominant large perennial seaweed in the Baltic Sea growing in salinities down to 4 psu (Kautsky, 1992). Bäck *et al.* (1991) compared *Fucus vesiculosus* individuals from Atlantic and the Baltic populations. Both populations were able to withstand a wide range of salinities in laboratory cultures, yet some differences were recorded. The Atlantic population showed better growth in higher salinities and virtually no growth at 5 ppt. Those individuals kept at 5 ppt mortality occurred after seven weeks. In contrast, the Baltic wracks grew better in conditions with lower salinities (Bäck *et al.*, 1991). Serrao *et al.* (1996a) found that lower salinities can negatively affect both the fertilization rates and recruitment success of *Fucus vesiculosus*. Serrao *et al.* (1996a) also concluded that the osmotic tolerances of *Fucus vesiculosus* gametes limit the species distribution in the Baltic Sea.

Growth rates for *Fucus serratus* are maximal at a salinity of 20 psu with the critical limit for recruitment set at 7 psu (Malm *et al.*, 2001). Sufficient salinity is essential for successful fertilization and germination in *Fucus* (e.g., Brawley, 1992; Serrão *et al.*, 1999). Malm *et al.* (2001) found that fertilization success in *Fucus serratus* decreased substantially with strongly reduced salinity. Indeed the study found that fertilization success was 87% at 9 psu but declined to 5% at 6 psu (Malm *et al.*, 2001). Reduced salinity also affects dispersal by decreasing the swimming performance of furoid sperm (Serrão *et al.*, 1996a). These studies show that low salinities limit the recruitment and fertilization success of fucoids.



A number of the other species within the biotope can also be found within rockpools where hyposaline conditions can be found for short periods (Newell, 1979). Consequently, a decrease in salinity within the benchmark of this pressure may not cause significant mortalities. For example, *Semibalanus balanoides* can tolerate salinities between 12 and 50 psu, below and above this cirral activity ceases (Foster, 1970). *Carcinus maenas* is a mobile species and can move to suitable conditions on the shore.

**Sensitivity assessment.** This biotope is recorded from both variable (18 – 40 ppt) (Connor *et al.*, 2004). A decrease in salinity at the benchmark would create a reduced salinity regime (18-30) for a year. As *Ascophyllum nodosum* occurs in estuarine conditions, inhabits areas subject to salinities as low as 8 psu, and can tolerate seven days at a salinity of 5 (Laffoley & Hiscock, 1993; Connan & Stengel, 2011) it is unlikely to suffer a reduction in abundance due to a reduction in salinity at the benchmark level. Similarly, both of the characteristic *Fucus* spp. can tolerate low salinity. Therefore, resistance is assessed as '**High**' at the benchmark so that resilience is assessed as '**High**' and sensitivity as '**Not sensitive**' at the benchmark level.

#### Water flow (tidal current) changes (local)

**High**

Q: High A: Medium C: Medium

**High**

Q: High A: High C: High

**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 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, water flow likely exerts a very similar pressure on fucoids.

*Fucus vesiculosus* individuals of 10 cm or larger have been recorded to be completely removed at 7-8 m/s (Jonsson *et al.*, 2006). Flow rates at which adult *Ascophyllum nodosum* are removed are not known. However, Thompson & Wernberg (2005) provide strong evidence of an increase in the break force required to remove algae with an increase in thallus size. 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.

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. The attachment success of *Ascophyllum nodosum* was poor at current speeds of over 20 cm/s (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 could 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 (Deviny & 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 lagoonal biotope (IR.LIR.Lag.AscSpAs) is recorded from weak (<1 kn, <0.5 m/s) to negligible tidal flow. A further decrease in water flow is unlikely to be relevant. Also, *Ascophyllum nodosum* is recorded in tide-swept conditions (e.g. LR.HLR.FT.AscT) in strong (1.5-3 m/s) to very strong (>3 m/s) water flow. Therefore, a change in the current flow of 0.1-0.2 m/s is unlikely to have an impact on many examples of this biotope. Hence, resistance and resilience have been assessed as '**High**' and the biotope is assessed as '**Not Sensitive**' at the benchmark level.

#### Emergence regime changes

**Medium**

Q: Low A: NR C: NR

**Medium**

Q: High A: High C: Medium

**Medium**

Q: Low A: Low C: Low

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 large tides and result in rapid changes that 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 that 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 several intertidal macroalgae fall within Portugal. Lima *et al.* (2007) mapped the readjustment 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 than the warm adapted species.

Information regarding the effect of changes in the level of exposure on *Ascophyllum nodosum* germlings was not available. Germlings would be protected from desiccation stresses due to air exposure because of the protection provided to them by the furoid 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).

*Fucus vesiculosus* can tolerate desiccation until the water content is reduced to ~30%. If desiccation occurs beyond this level, irreversible damage occurs. Individuals at the top of the shore probably live at the upper limit of their physiological tolerance and therefore, are likely to be unable to tolerate increased desiccation and would be displaced by more physiologically tolerant species. Tolerance to this pressure is likely to vary on a geographical scale. Gylle *et al.* (2009) found that *Fucus vesiculosus* populations that occur naturally in fully saline conditions had a higher emersion stress tolerance compared to brackish populations. Early life history stages are more susceptible to this pressure compared to adults (Henry & Van Alstyne, 2004). Germlings are, however, protected from desiccation by the canopy of adults. Brawley & Johnson (1991) showed that germling survival under the adult canopy was close to 100% whereas survival on the adjacent bare rock was close to 0% during exposure to aerial conditions. *Fucus serratus* is more susceptible to desiccation than other *Fucus* species that are located further up the shore and subjected more frequently to aerial exposure (Schonbeck & Norton, 1978). In experiments, (Schonbeck & Norton, 1978) *Fucus serratus* did not survive transplantation further up the shore, e.g. in the *Fucus spiralis* belt. The critical water content for *Fucus serratus* is estimated at 40% with water losses past this point causing irreversible damage. Beer *et al.* (2014) found that *Fucus serratus* could not regain any positive photosynthetic rates after rehydrating from 10% water content.

**Sensitivity assessment.** This lagoonal biotope IR.LIR.Lag.AscSpAs occurs in the shallow sublittoral. However, lagoons are isolated water bodies and may experience changes in water level due to changes in inflow from the sea or rivers, periods of drought or human interference (e.g. drainage) and the pressure is considered relevant. 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. An increase in the emergence time for a year is likely to change in the height of the biotope on the shore, and exposure the biotope to intertidal conditions. It is likely to transition into an intertidal equivalent (e.g. LR.LLR.F.Asc) over time. Conversely, a decrease in emergence may allow the biotope to increase its extent up the shore, although its lower limit may be lost. Nevertheless, the change in the biotope within a year (the benchmark) may be small and the dominant canopy may not be lost. Therefore, resistance is assessed as '**Medium**'. Hence, resilience is probably also '**Medium**' and sensitivity is assessed as '**Medium**'.

#### Wave exposure changes (local)

**Medium**

Q: Medium A: Medium C: Medium

**Medium**

Q: High A: Medium C: Medium

**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). Fucooids 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 the size of furoids (Blanchette, 1997) as smaller individuals create less resistance to waves. As exposure to waves increases the furoid 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 furoid species leads to a further increase in the abundance of robust furoids, 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  $20 \text{ cm s}^{-1}$  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 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 (Devanny & 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 furoid cover would result in major changes to the associated community, especially attached epifauna and understory algae.

**Sensitivity assessment.** As this is an extremely sheltered biotope a further decrease in wave exposure is unlikely. An increase in wave action is likely to adversely affect furoid cover, especially of *Ascophyllum nodosum*. The biotope would probably be lost if wave exposure increased 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
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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. 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 extremely wave sheltered conditions and the weak to very weak water flows which are characteristic of this biotope mean that water mixing is not very strong. Water retention rates within lagoons are also known to be high, with very low flushing times. Therefore, water movement within this area will not reverse any oxygen depletion quickly, possibly exacerbating any negative effects. The characterizing fucoid species may 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 the crab *Carcinus maenas* would relocate to conditions

that were less physiologically taxing and would be able to return when the pressure abated. Mysids may also be able to relocate. Those immobile species such as the barnacle *Semibalanus balanoides* may experience some mortality. However, barnacles can completely recolonize within three years (Bennell, 1981). Therefore, as the furoid canopy may survive a reduction in oxygen level to 2 mg/l or below for a week, 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 microalgal 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 led 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 1500 kg/yr. The background levels of nitrite at the test site were 300  $\mu$ M. In comparison, the ambient nitrite levels in south-west Nova Scotia are 3  $\mu$ M (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. Major declines of *Fucus vesiculosus* were reported from all over the Baltic Sea associated with eutrophication from nutrient enrichment

(Kautsky *et al.*, 1986). In experimental rocky shore communities, Krauflin *et al.* (2006) found only minor effects on the furoid community structure as a response to high nutrient levels during the first three years of the experiment. However, during the 4<sup>th</sup> year of exposure *Fucus serratus* started to decline and population consequently crashed in the 5<sup>th</sup> year. The study observed full recovery of the algal canopy and animal community in less than two years after conditions returned to normal (Krauflin *et al.*, 2006).

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, 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).

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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.

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**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'.

## A Physical Pressures

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

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



**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, and reclassification of the biotope. Therefore, 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' and sensitivity is assessed as '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 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

No studies of the effects of trampling or netting on lagoons were found but studies of the effects on emergent algal communities are probably indicative. Trampling on the rocky shore has been observed to reduce furoid cover which decreased the microhabitat available for epiphytic species, increased bare space and increased the 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. Furoids 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<sup>2</sup> on stations on an intertidal rocky shore in northeast England were sufficient to reduce the abundance of furoids (Fletcher & Frid, 1996). A trampling intensity of 20 steps per m<sup>2</sup> per spring tide could be exceeded by only five visitors taking the same route out and back again across the rocky shore in each spring tide. 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 that 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 (accessed by the public) and that the average frond length of *Ascophyllum nodosum* was smaller.

*Fucus vesiculosus* can generate vegetative regrowth in response to wounding from physical disturbance. McCook & Chapman (1992) experimentally tested the recovery of damaged *Fucus vesiculosus*. The study found that vegetative sprouting of *Fucus vesiculosus* holdfasts made a significant addition to the regrowth of the canopy, even when holdfasts were cut to less than 2 mm tissue thickness. Four months after cutting, sprouts ranged from microscopic buds to shoots about 10 cm long with mature shoots widespread after 12 months. Vegetative regrowth in response to wounding has been suggested as an important means of recovery from population losses (McLachan & Chen, 1972).

*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 understory species and promoted 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 Jenkins *et al.* (2004), 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. They 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 over 12 years. Hence, 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)

**Medium**

Q: Medium A: Medium C: Medium

**Medium**

Q: High A: Medium C: Medium

**Medium**

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 sufficient water content (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. The distribution of both *Ascophyllum nodosum* and *Fucus vesiculosus* occur along a depth gradient that strongly correlates with light penetration. In areas with low sedimentation, *Fucus vesiculosus* can survive down to 9-10 m depth (Eriksson & Bergstrom, 2005). Changes in suspended solids affecting water clarity may have a direct impact on the photosynthesising capabilities of *Fucus vesiculosus*. Kõuts *et al.* (2006) found decreases in light intensity in the vicinity of the dredging site resulted in the net decline of *Fucus vesiculosus* biomass. A decrease in light penetration in the Kiel Fjord caused by an increase in phytoplankton density and shading from filamentous algae caused an upward shift of the lower depth limit of *Fucus vesiculosus* (Rohde *et al.*, 2008). In extreme turbidity, such as found in the Bristol Channel, *Fucus serratus* is excluded from the bottom of the intertidal (below 2 m above chart datum) due to the lack of light for sustained growth (Chapman, 1995).

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 in the shallow subtidal and is permanently immersed. An increase in suspended sediment may cause the biotope to be lost at its lowest extent due to a decrease in light levels. The levels of water movement within this biotope, through water flow and wave exposure, are very unlikely to cause any significant damage through scour. Hence, the resistance and resilience of this biotope have been assessed as '**Medium**' so that the sensitivity to this pressure is assessed as '**Medium**'.

**Smothering and siltation rate changes (light)****Medium**

Q: Medium A: Medium C: Medium

**Medium**

Q: High A: High 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 furoid 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 (Deviny & Volse, 1978, Eriksson & Johansson, 2003). Eriksson & Johansson (2003) found that sedimentation had a significant negative effect on the recruitment success of *Fucus vesiculosus*. Even fine sediment fractions can reduce the successful attachment of furoids by as much as 90% (Schiel & Foster, 2006).

*Ascophyllum nodosum* is intolerant of sediment movement. Daly & Mathieson (1977) compared two rocky shores that 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<sup>2</sup>). At 200 mg/cm<sup>2</sup> 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 smothered by 5 cm. The level of water movement within this biotope is small 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 is assessed as '**Medium**'. Resilience is probably '**Low**' so that sensitivity 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: High C: Medium

**High**

Q: Medium A: Medium C: Medium

Several studies found that increasing the vertical sediment burden negatively impact furoids 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 understory algae, invertebrate grazers and young (germling) furoids. Water movement will remove sediment but

within this biotope it is 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.

<b>Litter</b>	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR
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Not assessed.

<b>Electromagnetic changes</b>	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR
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No evidence.

<b>Underwater noise changes</b>	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR
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Species characterizing this habitat do not have hearing perception but vibrations may cause an impact, however, no studies exist to support an assessment.

<b>Introduction of light or shading</b>	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR
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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 negatively impact 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.

Cervin *et al.* (2005) noted that loss of canopy and degradation of the underlying turf promoted the recruitment of *Ascophyllum nodosum* to experimental plots. They also reported that *Ascophyllum* recruits had low growth rates in shade, under the canopy, that prevented the development of mature *Ascophyllum* plants. The modal size of *Ascophyllum* plants without canopy after six years was over twice that of individuals that grew under an intact canopy and the maximum size was six times greater (Cervin *et al.*, 2005). It is possible that artificial shading, e.g. from a jetty, could slow the growth of *Ascophyllum* and decrease its ability to compensate for grazing or its ability to out-compete other fucoids. However, **no evidence** was found to support an assessment.

<b>Barrier to species movement</b>	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR
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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

Not relevant.

** Biological Pressures**

Resistance

Resilience

Sensitivity

**Genetic modification & translocation of indigenous species**

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not 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 was 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

**Medium**

Q: High A: High C: Medium

**Medium**

Q: High A: High C: Medium

Seaweeds have been collected from the middle of the 16th century for the iodine industry. Modern industrial uses for seaweed are extensive and include fertilizer, animal feed, alginate extracts (Phillippi *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. 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).

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 Phillippi *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; Pocklington *et al.*, 2018). Phillippi *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 (Phillippi *et al.*, 2014). However, Pocklington *et al.* (2018) examined community disturbance after removal of 100%, 50%, 245% and 0% of *Ascophyllum nodosum* fronds (but not holdfasts). They concluded that a pulse disturbance (frond removal) of 50% loss of fronds increased the temperature under the canopy significantly and decreased the abundance of mobile invertebrates such as *Littorina obtusata*. Sessile taxa such as *Osmundia pinnatifida* and encrusting corallines could withstand a 75% loss of fronds but declined by half if 100% were removed.

Keser *et al.* (1981) recorded the levels of re-growth exhibited by *Ascophyllum nodosum* and *Fucus vesiculosus* after experimental 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; 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). 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 were 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). There is 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; cited in Phillippi *et al.*, 2014). However, Keser *et al.* (1981) noted that repeated annual harvest reduced biomass and suggested staggering annual harvest between sites to prevent large-scale destruction of the resource.

**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* probably has a 'Low' resistance to removal as it is easy to locate and has no escape strategy. However, resilience to harvesting (the removal of fronds above the holdfast) is probably 'Medium' (2-10 years) depending on the cut length, site, grazing pressure and age-size composition of the population (Keser *et al.*, 1981; Phillippi *et al.*, 2014). Therefore, sensitivity is assessed as 'Medium'.

#### Removal of non-target species

**Low**

Q: High A: High C: Medium

**Low**

Q: High A: High C: Medium

**High**

Q: High A: High C: Medium

Direct, physical impacts from harvesting, trampling or removal are assessed through the abrasion and penetration of the seabed pressures. This pressure focuses on the biological effects of the incidental (accidental) removal of a proportion of the dominant members of the community. Loss of the *Ascophyllum* canopy has been shown to alter the understory community of sessile and mobile invertebrates and red algal turf species significantly (Jenkins *et al.*, 1999, 2004; Cervin *et al.*, 2005; Phillippi *et al.*, 2014; Pocklington *et al.*, 2018). Subsequent recovery of the community results in intermediary communities, dominated by space and grazers or dominated by other furoids, that may not correspond to this biotope.

**Sensitivity assessment.** Removal of a large percentage of the dominant characterizing species would alter the character of the biotope. The resistance to incidental removal is assessed as 'Low' due to the easy accessibility of the biotopes location and the inability of the species to evade removal. Therefore, resilience is assessed as 'Low' and sensitivity is as 'High'.



## Bibliography

- Åberg, P. & Pavia, H., 1997. Temporal and multiple scale spatial variation in juvenile and adult abundance of the brown alga *Ascophyllum nodosum*. *Marine Ecology Progress Series*, **158**, 111-119. DOI <https://doi.org/10.3354/meps158111>
- Åberg, P., 1992a. A demographic study of two populations of the seaweed *Ascophyllum nodosum*. *Ecology*, **73** (4), 1473-1487. DOI <https://doi.org/10.2307/1940691>
- Åberg, P., 1992b. Size-based demography of the seaweed *Ascophyllum nodosum* in stochastic environments. *Ecology*, **73** (4), 1488-1501. DOI <https://doi.org/10.2307/1940692>
- 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., Voegelé, 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.
- Airoidi, L., 2003. The effects of sedimentation on rocky coast assemblages. *Oceanography and Marine Biology: An Annual Review*, **41**, 161-236
- Airoidi, 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. DOI <https://doi.org/10.3354/meps332235>
- 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., Serrão, E.A. & Per, Â., 2012. Recovery after trampling disturbance in a canopy-forming seaweed population. *Marine Biology*, **159** (3), 697-707. DOI <https://doi.org/10.1007/s00227-011-1847-8>
- 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. DOI <https://doi.org/10.3354/meps07814>
- 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.
- Bäck, S., Collins, J.C. & Russell, G., 1991. Aspects of the reproductive biology of *Fucus vesiculosus* from the coast of south west Finland. *Ophelia*, **34**, 129-141.
- 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.
- Bamber, R.N., Gilliland, P.M. & Shardlow, M.E.A., 2001. *Saline lagoons: a guide to their management and creation* (interim version). Peterborough: English Nature.
- 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.
- Barnes, R.S.K., 1991. Dilemmas in the theory and practice of biological conservation as exemplified by British coastal lagoons. *Biological Conservation*, **55**, 315 - 323.
- 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.
- Beer, S., Björk, M. & Beardall, J., 2014. *Photosynthesis in the Marine Environment*. John Wiley & Sons.
- Bellgrove, A., McKenzie, P.F., McKenzie, J.L. & Sfiligoj, B.J., 2010. Restoration of the habitat-forming furoid 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.
- Berger, R., Henriksson, E., Kautsky, L. & Malm, T., 2003. Effects of filamentous algae and deposited matter on the survival of *Fucus vesiculosus* L. germlings in the Baltic Sea. *Aquatic Ecology*, **37** (1), 1-11.
- Bergström, L., Berger, R. & Kautsky, L., 2003. Negative direct effects of nutrient enrichment on the establishment of *Fucus vesiculosus* in the Baltic Sea. *European Journal of Phycology*, **38** (1), 41-46.
- 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 furoid embryos in the intertidal zone depends upon developmental stages and microhabitat. *Journal of Phycology*, **27** (2), 179-186.
- Brawley, S.H., 1992b. Mesoherbivores. In *Plant-animal interactions in the marine benthos* (ed. D.M John, S.J. Hawkins & J.H. Price), pp. 235-263. Oxford: Clarendon Press. [Systematics Association Special Volume, no. 46.]
- 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.
- Brown, A.E., Burn, A.J., Hopkins, J.J. & Way, S.F., 1997. The habitats directive: selection of Special Areas of Conservation in the UK. *Joint Nature Conservation Committee, Peterborough, JNCC Report no. 270*.
- 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.]
- Bulleri, F. & Airoidi, L., 2005. Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea. *Journal of Applied Ecology*, **42** (6), 1063-1072.
- Cervin, G., Åberg, 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. DOI <https://doi.org/10.3354/meps305031>
- Chapman, A.R.O. (1995). Functional ecology of furoid algae: twenty-three years of progress. *Phycologia*, **34**(1), 1-32.
- 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.
- Devlinny, J. & Volse, L., 1978. Effects of sediments on the development of *Macrocystis pyrifera* gametophytes. *Marine Biology*, **48** (4), 343-348.
- Diez, 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: <https://www.maine.gov/dmr/laws-regulations/regulations/documents/29.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. DOI <https://doi.org/10.1111/j.0030-1299.2005.13782.x>
- Eriksson, B.K. & Bergström, L., 2005. Local distribution patterns of macroalgae in relation to environmental variables in the northern Baltic Proper. *Estuarine, Coastal and Shelf Science*, **62** (1), 109-117.
- 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.
- Firth, L., Thompson, R., Bohn, K., Abbiati, M., Airolidi, L., Bouma, T., Bozzeda, F., Ceccherelli, V., Colangelo, M. & Evans, A., 2014. Between a rock and a hard place: Environmental and engineering considerations when designing coastal defence structures. *Coastal Engineering*, **87**, 122-135.
- 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.
- Fredersdorf, J., Müller, R., Becker, S., Wiencke, C. & Bischof, K., 2009. Interactive effects of radiation, temperature and salinity on different life history stages of the Arctic kelp *Alaria esculenta* (Phaeophyceae). *Oecologia*, **160** (3), 483-492.
- 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.
- Green, D., Chapman, M. & Blockley, D., 2012. Ecological consequences of the type of rock used in the construction of artificial boulder-fields. *Ecological Engineering*, **46**, 1-10.
- Gylle, A.M., Nygård, C.A. & Ekelund, N.G.A., 2009. Desiccation and Salinity Effects on Marine and Brackish *Fucus vesiculosus* L. (Phaeophyceae). *Phycologia*, **48** (3), 156-164.
- Hammann, M., Buchholz, B., Karez, R. & Weinberger, F., 2013. Direct and indirect effects of *Gracilaria vermiculophylla* on native *Fucus vesiculosus*. *Aquatic Invasions*, **8** (2), 121-132.
- 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. & Hartnoll, R.G., 1985. Factors determining the upper limits of intertidal canopy-forming algae. *Marine Ecology Progress Series*, **20**, 265-271.
- Hawkins, S.J. & Southward, A.J., 1992. The *Torrey Canyon* oil spill: recovery of rocky shore communities. In *Restoring the Nations Marine Environment*, (ed. G.W. Thorpe), Chapter 13, pp. 583-631. Maryland, USA: Maryland Sea Grant College.
- Hawkins, S.J., Hartnoll, R.G., Kain, J.M. & Norton, T.A., 1992. Plant-animal interactions on hard substrata in the north-east Atlantic. In *Plant-animal interactions in the marine benthos* (ed. D.M. John, S.J. Hawkins & J.H. Price), pp. 1-32. Oxford: Clarendon Press. [Systematics Association Special Volume, no. 46.]
- 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.
- Henry, B.E. & Van Alstyne, K.L., 2004. Effects of UV radiation on growth and phlorotannins in *Fucus gardneri* (Phaeophyceae) juveniles and embryos. *Journal of Phycology*, **40** (3), 527-533.
- 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. DOI <https://doi.org/10.1017/S0025315408001161>
- Isaeus, M., 2004. Factors structuring *Fucus* communities at open and complex coastlines in the Baltic Sea. Department of Botany, Botaniska institutionen, Stockholm.
- 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., 2003. Barnacle larval supply to sheltered rocky shores: a limiting factor? *Hydrobiologia*, **503** (1), 143-151. DOI <https://doi.org/10.1023/b:Hydr.0000008496.68710.22>
- 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., Wetthey, D.S. & Woodin, S.A., 2008. Comparative ecology of North Atlantic shores: do differences in players matter for process? *Ecology*, **89** (11), 3-523. DOI <https://doi.org/10.1890/07-1155.1>
- 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. DOI <https://doi.org/10.1017/S0025315404009221h>
- 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 vesiculosus* 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.
- Kautsky, H., 1992. The impact of pulp-mill effluents on phytobenthic communities in the Baltic Sea. *Ambio*, **21**, 308-313.
- Kautsky, N., Kautsky, H., Kautsky, U. & Waern, M., 1986. Decreased depth penetration of *Fucus vesiculosus* (L.) since the 1940s indicates eutrophication of the Baltic Sea. *Marine Ecology Progress Series*, **28**, 1-8.
- 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. DOI <https://doi.org/10.1016/j.seares.2005.05.001>
- 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.
- Kim, S.Y., Weinberger, F. & Boo, S.M., 2010. Genetic data hint at a common donor region for invasive Atlantic and Pacific population of *Gracilaria vermiculophylla* (Gracilariales, Rhodophyta) 1. *Journal of Phycology*, **46** (6), 1346-1349.
- 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.
- Kinne, O., 1977. International Helgoland Symposium "Ecosystem research": summary, conclusions and closing. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **30**(1-4), 709-727.
- 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, M., 1947. A biological study of *Fucus vesiculosus* and *Fucus serratus*. *Proceedings of the Linnean Society of London*, Wiley Online Library, **159** (2) pp. 87-90.
- 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.
- Köuts, T., Sipelgas, L. & Raudsepp, U., 2006. High resolution operational monitoring of suspended matter distribution during harbour dredging. *EuroGOOS Conference Proceedings*, pp. 108-115.
- Kraufvelin, P., 2007. Responses to nutrient enrichment, wave action and disturbance in rocky shore communities. *Aquatic Botany*,

87 (4), 262-274.

- Kraufvelin, P., Moy, F.E., Christie, H. & Bokn, T.L., 2006. Nutrient addition to experimental rocky shore communities revisited: delayed responses, rapid recovery. *Ecosystems*, **9** (7), 1076-1093.
- Kraufvelin, P., Ruuskanen, A., Nappu, N. & Kiirikki, M., 2007. Winter colonisation and succession of filamentous algae and possible relationships to *Fucus vesiculosus* settlement in early summer. *Estuarine Coastal and Shelf Science*, **72**, 665-674.
- 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.
- Lehvo, A., Bäck, S. & Kiirikki, M., 2001. Growth of *Fucus vesiculosus* L. (Phaeophyta) in the northern Baltic proper: energy and nitrogen storage in seasonal environment. *Botanica Marina*, **44** (4), 345-350.
- 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.
- Lüning, K., 1990. *Seaweeds: their environment, biogeography, and ecophysiology*: John Wiley & Sons.
- Malm, T., 1999. Distribution patterns and ecology of *Fucus serratus* L. and *Fucus vesiculosus* L. in the Baltic Sea. PhD thesis, Stockholm University.
- Malm, T., Kautsky, L. & Engkvist, R., 2001. Reproduction, recruitment and geographical distribution of *Fucus serratus* L. in the Baltic Sea. *Botanica Marina*, **44** (2), 101-108.
- Mann, K.H., 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. I. Zonation and biomass of seaweeds. *Marine Biology*, **12**, 1-10.
- McCook, L. & Chapman, A., 1992. Vegetative regeneration of *Fucus* rockweed canopy as a mechanism of secondary succession on an exposed rocky shore. *Botanica Marina*, **35** (1), 35-46.
- McLachlan, J. & Chen, L.-M., 1972. Formation of adventive embryos from rhizoidal filaments in sporelings of four species of *Fucus* (Phaeophyceae). *Canadian Journal of Botany*, **50** (9), 1841-1844.
- Middelboe, A.L., Sand-Jensen, K. & Binzer, T., 2006. Highly predictable photosynthetic production in natural macroalgal communities from incoming and absorbed light. *Oecologia*, **150** (3), 464-476.
- 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.
- Nielsen, M., Krause-Jensen, D., Olesen, B., Thinggaard, R., Christensen, P. & Bruhn, A., 2014a. Growth dynamics of *Saccharina latissima* (Laminariales, Phaeophyceae) in Aarhus Bay, Denmark, and along the species' distribution range. *Marine Biology*, **161** (9), 2011-2022.
- Norton, T.A. (ed.), 1985. *Provisional Atlas of the Marine Algae of Britain and Ireland*. Huntingdon: Biological Records Centre, Institute of Terrestrial Ecology.
- Olsen, J.L., 2011. Stress ecology in *Fucus*: abiotic, biotic and genetic interactions. *Advances in Marine Biology*, **59**, 37-105. DOI <https://doi.org/10.1016/B978-0-12-385536-7.00002-9>
- 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.

- Petratits, 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. DOI <https://doi.org/10.1016/j.jembe.2005.05.013>
- 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. DOI <https://doi.org/10.1016/j.jembe.2014.07.018>
- 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.
- Pocklington, J.B., Jenkins, S.R., Bellgrove, A., Keough, M.J., O'Hara, T.D., Masterson-Algar, P.E. & Hawkins, S.J., 2018. Disturbance alters ecosystem engineering by a canopy-forming alga. *Journal of the Marine Biological Association of the United Kingdom*, **98** (4), 687-698. DOI <https://doi.org/10.1017/S0025315416002009>
- Powell, H., 1963. Speciation in the genus *Fucus* L., and related genera. In Harding, J. and Tebble, N. (eds.). *Speciation in the Sea*, London: Systematics Association, pp. 63-77.
- Printz, H.S., 1959. Investigations of the failure of recuperation and re-populating in cropped *Ascophyllum* areas. *Avhandlingar utgitt av Det Norske Videnskap-Akademi i Oslo* No. 3.
- Raffaelli, D.G. & Hawkins, S.J., 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. & Norton, T., 1979. Drought-hardening in the upper-shore seaweeds *Fucus spiralis* and *Pelvetia canaliculata*. *Journal of Ecology*, **67**, 687-696.
- Schonbeck, M.W. & Norton, T.A., 1978. Factors controlling the upper limits of furoid 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, Gigartinales) from British Columbia, Canada. *Journal of Phycology*, **34** (2), 228-232.
- Serrão, E.A., Brawley, S.H., Hedman, J., Kautsky, L. & Samuelsson, G., 1999. Reproductive success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic Sea. *Journal of Phycology*, **35** (2), 254-269.
- Serrão, E.A., Kautsky, L. & Brawley, S.H., 1996a. Distributional success of the marine seaweed *Fucus vesiculosus* L. in the brackish Baltic Sea correlates with osmotic capabilities of Baltic gametes. *Oecologia*, **107** (1), 1-12.
- Serrão, E.A., Kautsky, L., Lifvergren, T. & Brawley, S.H., 1997. Gamete dispersal and pre-recruitment mortality in Baltic *Fucus vesiculosus* (Abstract only). *Phycologia*, **36** (Suppl.), 101-102.
- Sfriso, A., Maistro, S., Andreoli, C. & Moro, I., 2010. First record of *Gracilaria vermiculophylla* (Gracilariales, Rhodophyta) in the po delta lagoons, Mediterranean sea (Italy) 1. *Journal of Phycology*, **46** (5), 1024-1027.
- 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.
- Spencer, T. & Brooks, S., 2012. Methodologies for measuring and modelling change in coastal saline lagoons under historic and accelerated sea-level rise, Suffolk coast, eastern England. *Hydrobiologia*, **693** (1), 99-115.
- 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., 2004. Effects of reduced salinity on reproduction and germling development in *Sargassum muticum* (Phaeophyceae, Fucales). *European Journal of Phycology*, **39** (3), 293-299.
- Steen, H. & Rueness, J., 2004. Comparison of survival and growth in germlings of six furoid 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.
- Strömngren, T., 1977. Short-term effects of temperature upon the growth of intertidal fucales. *Journal of Experimental Marine*

*Biology and Ecology*, **29** (2), 181-195. DOI [https://doi.org/10.1016/0022-0981\(77\)90047-8](https://doi.org/10.1016/0022-0981(77)90047-8)

Strömberg, 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.

Tatarenkov, A., Bergström, L., Jönsson, R.B., Serrão, E.A., Kautsky, L. & Johannesson, K., 2005. Intriguing asexual life in marginal populations of the brown seaweed *Fucus vesiculosus*. *Molecular Ecology*, **14** (2), 647-651.

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-occurring 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 Cynfor Cefn Gwlad Cymru / Countryside Council for Wales from the Marine Life Information Network (MarLIN) [Contract no. FC 73-03-327], Marine Biological Association of the UK, Plymouth, 48 pp. Available from: [www.marlin.ac.uk/publications](http://www.marlin.ac.uk/publications)

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.

UKNEA (UK National Ecosystem Assessment), 2011. The UK National Ecosystem Assessment: Synthesis of the Key Findings. UNEP-WCMC, Cambridge, pp. <http://uknea.unep-wcmc.org/>

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., 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.

Wilce, R., Foertch, J., Grocki, W., Kilar, J., Levine, H. & Wilce, J., 1978. Benthic studies in the vicinity of pilgrim nuclear power station, 1969-1977. *Boston Edison Co.*, 307-656 pp.