Ascophyllum nodosum, sponges and ascidians on tide-swept mid eulittoral rock

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Frances Perry & Charlotte Marshall

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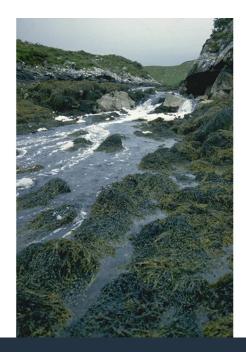
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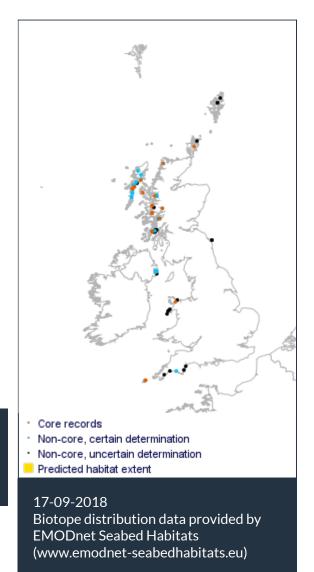






Ascophyllum nodosum, sponges and ascidians on tide-swept mid eulittoral rock
Photographer: Rohan Holt

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Researched by Frances Perry & Charlotte Marshall Refereed by This information is not refereed

Summary

■ UK and Ireland classification

EUNIS 2008		Ascophyllum nodosum, sponges and ascidians on tide-swept mid eulittoral rock
JNCC 2015	LR.HLR.FT.AscT	Ascophyllum nodosum, sponges and ascidians on tide-swept mid eulittoral rock
JNCC 2004	LR.HLR.FT.AscT	Ascophyllum nodosum, sponges and ascidians on tide-swept mid eulittoral rock
	LR.SLR.F.Asc.T	Ascophyllum nodosum, sponges and ascidians on tide-swept mid eulittoral rock

Description

Very sheltered to extremely sheltered areas of mid eulittoral rock that are subject to strong to moderate tidal streams, such as the narrows in sea lochs, and characterized by the wrack

Ascophyllum nodosum. The wracks Fucus vesiculosus and Fucus serratus are occasionally present. The increased water movement encourages a rich associated fauna including several filter-feeding groups. These include the sponges Leucosolenia spp., Grantia compressa, Halichondria panicea and Hymeniacidon perleve which frequently occur on steep and overhanging faces of boulders and bedrock. It also includes the sea squirts *Dendrodoa grossularia* and *Ascidiella scabra*, which occur on steep surfaces and beneath boulders. Hydroids such as the pink Clava multicornis can form colonies on Ascophyllum nodosum while Dynamena pumila is more often found on Fucus vesiculosus or Fucus serratus. Underneath the canopy formed by the brown seaweeds is a diverse community of the red seaweeds Gelidium pusillum, Chondrus crispus, Lomentaria articulata, Membranoptera alata and coralline crusts, but the green seaweeds Ulva (syn. Enteromorpha) intestinalis, Ulva lactuca and Cladophora rupestris can be present. The filamentous red seaweed Polysiphonia lanosa can usually be found growing on Ascophyllum nodosum. On the rock beneath are the limpet Patella vulgata and the barnacle Semibalanus balanoides, while the crab Carcinus maenas and a variety of winkles including Littorina littorea, Littorina mariae and Littorina obtusata can be found on or among the boulders. The whelk Nucella lapillus can either be found in cracks and crevices or preying on the barnacles.

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

↓ Depth range

Mid shore

Additional information

-

✓ Listed By

- none -

& Further information sources

Search on:



Habitat review

2 Ecology

Ecological and functional relationships

The moderately strong to very strong tidal streams associated with this biotope support a rich and varied marine life, of which the suspension feeders and autotrophs are the dominant trophic groups. Ascophyllum nodosum, the knotted wrack, forms a canopy in this biotope. The serrated wrack Fucus serratus and bladder wrack Fucus vesiculosus may also form part of this canopy but the long lived Ascophyllum nodosum tends to dominate in terms of abundance and standing biomass. The canopy layer limits light penetration and the understorey is dominated by shade tolerant foliose and red seaweeds including Chondrus crispus, Corallina officinalis, Mastocarpus stellatus and encrusting calcareous algae. The filamentous red seaweed Polysiphonia lanosa is possibly the most commonly occurring red algal species in this biotope. It has root like fibres which penetrate the tissue of Ascophyllum nodosum and, less frequently, Fucus sp. (Fish & Fish, 1996). Green algae, especially Ulva sp. and Cladophora rupestris may also be found.

Suspension feeders representing several phyla are commonly associated with this biotope. Representatives of the sponge and ascidian communities, that give the biotope its name, are varied and diverse. Both encrusting sponges, including the breadcrumb sponge *Halichondria panicea* and *Hymeniacidon perleve*, and solitary forms such as the purse sponge *Grantia compressa* are found. Similarly, both colonial and solitary ascidians are found although the baked bean ascidian *Dendrodoa grossularia*, for example, is far more abundant and frequently associated with this biotope than the colonial star ascidian *Botrylloides leachi*. Large stands of hydroids may be found on the fucoids including *Dynamena pumila* and the pink hydroid *Clava multicornis*. In general, *Ascophyllum nodosum* is remarkably free of epiphytes even when adjacent plants of other species of fucoid algae are heavily infested (Filion-Myclebust & Norton, 1981). This is due to the fact that *Ascophyllum nodosum* repeatedly sloughs its entire outer epidermis, and potential epiphytes, including spores and germlings of other algae that had settled on the surface are, therefore, discarded with it (Filion-Myclebust & Norton, 1981).

A variety of winkles, most commonly the common periwinkle *Littorina littorea* and flat periwinkle *Littorina obtusata* graze on microorganisms, detritus and algae in this biotope. Whilst the common periwinkle grazes on rock in the biotope, *Ascophyllum nodosum* is the preferred food for the flat periwinkle (Fish & Fish, 1996). The flat periwinkle lays its eggs on *Ascophyllum nodosum*, *Fucus vesiculosus* and *Fucus serratus* and, occasionally, on the rock surface (Fish & Fish, 1996). The common limpet *Patella vulgata* can be abundant and grazes on tough plants including *Fucus* sp. and encrusting red algae. Grazing by *Patella vulgata* can be an important structuring feature on rocky shores and is often considered to be a keystone species on north-east Atlantic rocky shores. Reductions in limpet density have been observed to have a significant impact on rocky shore community composition, particularly of fucoid algae and barnacles (Hawkins & Hartnoll, 1985; Raffaelli & Hawkins, 1999).

Grazing on rocky shores can exert significant controlling influences on the algal vegetation, particularly by patellid limpets and littorinid snails which are usually the most prominent graders (Hartnoll & Hawkins, 1985; Raffaelli & Hawkins, 1996; Jenkins et al., 1999, 2008). There may also significant effects caused by 'mesograzers' - amphipods such as *Hyale prevostii* and isopods, which are much smaller but may occur in high densities (Brawley, 1992b). The exclusion of fucoids from exposed shores, and hence the presence of dense beds of fucoids on sheltered shores, results from

grazing pressure on exposed shores. A dynamic balance exists between fucoids, and limpets plus barnacles and is mediated by wave action. In wave sheltered conditions the balance shifts in favour of the fucoids and in wave exposure the balance shifts towards limpets, barnacles and mussels. Limpet grazing normally prevents fucoids from extending onto wave exposed headlands. The Ascophylllum canopy indirectly affects limpet grazing but allows the development on a diverse understorey of red algae that reduce the grazing range of limpets (Raffaelli & Hawkins, 1996; Jenkins et al., 1999, 2004; Cervin et al., 2005; Jenkins et al., 2008). Grazing pressure varies with latitude. Southern European shores support a diverse grazing community of limpets and trochids (top-shells) but this diversity decreases with increasing latitude so that algal domination of shores increase to the north ad Icelandic shores lack limpets and trochid grazers (Jenkins et al., 2008). Patellid limpets are also absent in the western Atlantic where it is thought that littorinid grazing may be a dominant grazer (Jenkins et al., 2008).

The common shore crab *Carcinus maenas* is the largest mobile predator frequently associated with this biotope and is likely to move between the boulders and pebbles feeding primarily on small molluscs, especially *Littorina* sp. and the common mussel *Mytilus edulis*, annelids and other crustacea. It is an omnivore and will also consume algal material. The predatory mollusc *Nucella lapillus* also feeds primarily on the common mussel, in addition to acorn barnacles (Fish & Fish, 1996) such as *Semibalanus balanoides* which can also be abundant in the biotope.

Seasonal and longer term change

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

Habitat structure and complexity

Ascophyllum nodosum communities support high levels of biodiversity (Jenkins et al., 1999; Pocklington et al., 2018) and are characterized by a diverse understorey of red algae, together with sessile and mobile invertebrates. The understorey may include, depending on location, red algae such as Osmundia pinnatifida, Lomenataria articulata, Mastocarpus stellatus, Chondrus crispus, Gelidium spp. and encrusting corallines; green algae such as Cladophora rupestris and Ulva spp.; sessile invertebrates such as Semibalanaus balanoides, Perforatus perforatus, Spirorbis spirorbis; and

mobile species such as *Carcinus maenas*, *Patella vulgata*, *Littorina littorea*, *Littoria obtusata* and *Phocus lineatus* (Jenkins *et al.*, 1999; Pocklington *et al.*, 2018). Disturbed areas may also be colonized by *Fucus vesiculosus* or *Fucus serratus* depending on wave exposure and shore height (Jenkins *et al.*, 1999, 2004; Pocklington *et al.*, 2018). The fronds themselves provide space for attachment of encrusting or sessile epifauna and epiphytic algae and provide shelter from wave action, desiccation and heat for invertebrates and understorey algae (Jenkins *et al.*, 1999; Pocklington *et al.*, 2018). Crevices in the bedrock and overhangs on fucoid rocky shores also increase habitat complexity by providing refugia for a variety of species.

Owing to the tidally swept habitat with which this biotope is associated, diversity is increased due to the presence of several filter-feeding species. The fast currents provide a continual supply of food for both active and passive suspension feeders that dominate the attached fauna. Fine sediment is removed by the current and the settlement of material, that could otherwise be detrimental to the suspension feeders, is prevented. Almost every possible substratum, including the bedrock, boulders, cobbles and overhanging faces, is covered with various flora and fauna. In addition to the luxuriant conditions for suspension feeders, Hiscock (1983) lists some the benefits of strong water movement to include the potential for a greater photosynthetic efficiency, thereby possibly increasing the depth penetration of the algae. Increased water movement has been associated with an increase in photosynthesis in several algal species including *Fucus serratus* and *Ascophyllum nodosum* (Robins, 1968, cited in Hiscock, 1983).

The algae themselves provide a substratum for epiphytic species including hydroid, sponge and ascidian communities. *Leucosolenia* sp., for example, are often found on red seaweeds. The hydroid *Dynamena pumila* may grow on several *Fucus* species whereas the spirorbid worm *Spirorbis spirorbis* grows preferentially on *Fucus serratus*. The fronds of *Ascophyllum nodosum*, however, are narrow, flexible and slimy, offering a poor support for most encrusting animals. The species is unattractive to most intertidal species with the exception of the pink hydroid *Clava multicornis*, the bryozoan *Bowerbankia imbricata* and, on sheltered shores, the tube worm *Spirorbis spirorbis*. *Ascophyllum nodosum* also supports the red algae *Polysiphonia lanosa*, which penetrates its fronds with root-like fibres. Rock surfaces may, depending on their geology, be broken and include shaded overhangs and damp crevices which, together with the shelter of the algal canopy, allow many animal species to thrive in the damp conditions.

Productivity

Rocky shore communities are highly productive and are an important source of food and nutrients for members of neighbouring terrestrial and marine ecosystems (Hill et al., 1998). Rocky shores make a contribution to the food of many marine species through the production of planktonic larvae and propagules which contribute to pelagic food chains. Production rates of Ascophyllum nodosum in Nova Scotia were estimated to be between 0.61 and 2.82 kg/m (Cousens, 1984). Raffaelli & Hawkins (1999) reported an estimate of the productivity of intertidal fucoids as 160 gC/m/year, although this figure was an estimate for moderately wave exposed habitats. The fucoids and other macroalgae associated with this biotope can exude dissolved organic carbon, which is taken-up readily by bacteria and may even be taken-up directly by some larger invertebrates. Dissolved organic carbon, algal fragments and microbial film organisms are continually removed by the sea. This may enter the food chain of local subtidal ecosystems, or be exported further offshore. Many of the species associated with this biotope make a contribution to the food of many marine species through the production of planktonic larvae and propagules, which contribute to pelagic food chains.

Recruitment processes

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

- Ascophyllum nodosum takes five years to become sexually mature (Sundene, 1973). As many as 2.5 x10° eggs m²/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 x 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). Cervin et al. (2005) reported that recruitment and subsequent growth was promoted by loss of the algal canopy and erosion of the algal turf.
- Reproduction in *Fucus serratus* commences in late spring and continues until November, with a peak in August and October. Eggs and sperm are produced separately and fertilized externally to form a planktonic zygote. Recruitment is therefore possible from sources outside the biotope. *Fucus vesiculosus* is highly fecund often bearing more than 1000 receptacles on each plant, which may produce in excess of one million eggs. In England, the species has a protracted reproduction period of about six months. Gametes may be produced from mid winter until late summer with a peak of fertility in May and June. Like *Fucus serratus*, the eggs are fertilized externally to produce a zygote. Zygotes start to develop whenever they settle, even if the substratum is entirely unsuitable. Mortality is extremely high in the early stages of germination up to a time when plants are 3 cm in length and this is due mostly to mollusc predation (Knight & Parke, 1950).
- Recruitment of *Patella vulgata* fluctuates from year to year and from place to place. *Patella vulgata* become sexually mature as males aged about nine months. Fertilization is external and the larvae is pelagic for up to two weeks before settling on rock at a shell length of about 0.2 mm. Winter breeding occurs only in southern England, in the north of Scotland it breeds in August and in north-east England in September.
- Barnacle recruitment can be very variable because it is dependent on a suite of environmental and biological factors, such as wind direction and success depends on settlement being followed by a period of favourable weather. Long-term surveys have produced clear evidence of barnacle populations responding to climatic changes. During warm periods *Chthamalus* spp. predominate, whilst *Semibalanus balanoides* does better during colder spells (Hawkins *et al.*, 1994). Release of *Semibalanus balanoides* larvae takes place between February and April with peak settlement between April and June. Release of larvae of *Chthamalus montagui* takes place later in the year, between May and August.
- Chondrus crispus has an extended reproductive period (e.g. Pybus, 1977; Fernandez & Menendez, 1991; Scrosati et al., 1994) and produces large numbers of spores (Fernandez

& Menendez, 1991). The spores of red algae are non-motile (Norton, 1992) and therefore entirely reliant on the hydrographic regime for dispersal. Hence, it is expected that *Chondrus crispus* would normally only recruit from local populations and that recovery of remote populations would be much more protracted.

- The breadcrumb sponge *Halichondria panicea* is likely to have a short, annual season of sexual reproduction (see *MarLIN* review).
- Ascidiella scabra has a high fecundity and settles readily, probably for an extended period from spring to autumn. Eggs and larvae are free-living for only a few hours and so recolonization would have to be from existing individuals no more than a few km away. It is also likely that Ascidiella scabra larvae are attracted by existing populations and settle near to adults (Svane et al., 1987).
- The flat periwinkle *Littorina obtusata* are capable of reproducing through out the year (Graham, 1988). Eggs are laid in a jelly mass, usually on the fronds of *Fucus* species and hatch three or four weeks later (Goodwin, 1978, cited in Graham, 1988). Recruitment from external sources would therefore rely on the movement of adults into the area.

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

from removal include Bertness et al. (2002), Jenkins et al. (1999, 2004), Petraitis &

Numerous studies have concluded that Ascophyllum nodosum takes long periods of time to recover

Time for community to reach maturity

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 understorey 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 understorey 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 untaken by Ingólfsson & Hawkins (2008) in Iceland found that after removing an Ascophyllum nodosum canopy, the canopy could return within 7-8 years, yet the understorey 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).

Additional information

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Preferences & Distribution

Habitat preferences

Depth Range Mid shore

Water clarity preferences

Limiting NutrientsNo informationSalinity preferencesFull (30-40 psu)Physiographic preferencesStrait / soundBiological zone preferencesEulittoral

Substratum/habitat preferences Bedrock, Cobbles, Large to very large boulders, Small boulders

Tidal strength preferences

Moderately Strong 1 to 3 knots (0.5-1.5 m/sec.), Strong 3 to 6

knots (1.5-3 m/sec.), Very Strong > 6 knots (>3 m/sec.)

Wave exposure preferences Extremely sheltered, Very sheltered

Other preferences Moderately strong to very strong tidal streams.

Additional Information

This biotope is found exclusively in tide-swept areas with a moderately strong to strong water flow. In the Menai Strait, for instance, water flow rates can reach 8 knots (Brazier et al., 1999).

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 characterized by a dense canopy of *Ascophyllum nodosum*. The fucoid *Fucus vesiculosus* is also common within this biotope. The red seaweed *Polysiphonia lanosa* is a common epiphyte on *Ascophyllum nodosum*. The 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). Several littorinids are found within this biotope and are important grazers. The crab *Carcinus maenas* and the dog whelk *Nucella lapillus* are dominant predators. The high levels of water movement within this biotope caused by tidal streams create conditions for a rich associated community. The sponges *Leucosolenia* spp., *Grantia compressa*, *Halichondria panacea* and *Hymeniacidon perleve*, as well as the ascidians *Dendrodoa grossularia* and *Ascidiella scabra* frequently occur on steep and overhanging faces of boulders and bedrock. Colonies of the hydroid *Clava multicornis* can be found on *Ascophyllum nodosum* whereas *Dynamena pumila* is more often found on *Fucus vesiculosus* or *Fucus serratus*.

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* is important to this biotope, its loss from the biotope would not result in loss of the biotope. The fucoid canopy provides protection from desiccation for the various underlying seaweeds in addition to providing a substratum for epifauna and being the primary food resource for grazers. This can facilitate the existence and survival of other intertidal species and, therefore, strongly influences the structure and function of intertidal ecosystems (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 (Aberg, 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 2.5×10^9 eggs m²/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 x 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 Iaboratory found that growth rates of both species decreased as the density of germlings increased. Of the two species, Ascophyllum nodosum germlings grew slower and were least competitive in mixed cultures. This finding was mirrored in earlier experiments undertaken by Sundene (1973). Sundene (1973) noted that the production of sexual cells in Ascophyllum nodosum was as rapid as it was in Fucus vesiculosus. It was the growth rate of Ascophyllum nodosum that led to Fucus vesiculosus being more competitive on the shore. However, Choi & Norton (2005) found that the presence of Fucus vesiculosus increased the survival of Ascophyllum nodosum when exposed to desiccation stress. This showed that the presence of a mixed culture could either facilitate germling survival or lead to competitive exclusion under different environmental conditions (Choi & Norton, 2005). Competition is reversed in mature ecosystems where Ascophyllum nodosum plants can out-compete fucoids (Keser et al., 1981).

Fucoids (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 15minute 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 fucoid algae (including Ascophyllum nodosum). They found that recruitment to artificial substrata located in different micro-habitats along a semiexposed shore was noticeably different. Under the fucoid canopy in the study area, recruitment was 10-50 times greater than it was on exposed surfaces and in tide pools. To determine if this difference was due to lower levels of mortality under the canopy or to restricted distribution capacity, newly settled recruits from under the canopy were relocated to alternative microhabitats. Mortality rates of the relocated germlings were higher in the more exposed locations. However, the difference was not great enough to explain the observed difference in the number of germlings within the two different microhabitats. Lamote & Johnson (2008) concluded that the number of recruits was greater from under the fucoid canopy because of restricted distribution abilities.

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 regrowth, 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 where re-visited three years after the harvesting event they were still almost unaltered. The reasons for the lack of re-growth were attributed to the lack of regenerative tissue found in the older flesh further down the thallus (Printz, 1959).

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 of time 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 understorey 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 understorey 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 untaken by Ingólfsson & Hawkins (2008) in Iceland found that after removing an Ascophyllum nodosum canopy, the canopy could return within 7-8 years, yet the understorey 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).

The high levels of water movement within this biotope make it a suitable habitat for many filterfeeders. The average life expectancy of Halichondria panicea is three years (Fish & Fish, 1996) with individuals reaching sexual maturity within their first year. Wapstra & van Soest (1987) found that oocytes were present in the hermaphroditic Halichondria panicea year-round. Maturation of these oocytes and the present of embryos were present from May to August when water temperatures increased. New Halichondria panicea recruits can become apparent on the shore a year after they were spawned (Vethaak, 1982). Ascidiella scabra the sea squirt is a highly fecund species (Lindsay & Thompson, 1930). Age at maturity is thought to be 6 months with a lifespan of 2-5 years. Hydroids are often the first organisms to colonize available space in settlement experiments and fouling communities (Standing, 1976; Brault & Bourget, 1985; Sebens, 1986; Jensen et al., 1994; Gili & Hughes, 1995; Hatcher, 1998). Few species of hydroids have specific substrata requirements and many are generalists, for example, Hartlaubella gelatinosa, Obelia longissima and Obelia dichotoma were reported from a variety of hard substrata, together with mud and sand in the case of Hartlaubella gelatinosa (Cornelius, 1992; Cornelius, 1995b). Hydroids are also capable of asexual reproduction and many species produce dormant, resting stages, that are very resistant of environmental perturbation (Gili & Hughes, 1995). Rapid growth, budding and the formation of stolons allows hydroids to colonize space rapidly. Fragmentation may also provide another route for short-distance dispersal. However, it has been suggested that rafting on floating debris (or hitch-hiking on ships hulls or in ship ballast water) as dormant stages or reproductive adults, together with their potentially long lifespan, may have allowed hydroids to disperse over a wide area in the long-term and explain the near cosmopolitan distributions of many hydroid species (Cornelius, 1992; Gili & Hughes, 1995).

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). Recolonization 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 the community significantly. 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 and its associated community (Jenkins et al., 1999; 2004; Cervin et al., 2005). Mass mortality due to ice scour (Aberg (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). 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.

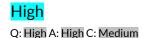
Note. The resilience and the ability to recover from human induced pressures is a combination of the environmental conditions of the site, the frequency (repeated disturbances versus a one-off event) and the intensity of the disturbance. Recovery of impacted populations will always be mediated by stochastic 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.



Resistance Resilience

Sensitivity

Temperature increase (local)







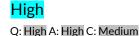
Schonbeck & Norton (1979) demonstrated that fucoids can increase tolerance in response to a gradual change in temperature through a process known as 'drought hardening'. However, acute changes in temperatures may cause damage to macroalgae and other species. Temperature ranges of species may not accurately 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.

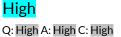
Ascophyllum nodosum is found in the middle of its range in the British Isles, with populations in the North East Atlantic as far south as Portugal and extending north to the White Sea and Iceland and west into the Kattegat on the shores of Sweden. Ascophyllum nodosum is unlikely to be affected by a short-term 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 shortterm variations in temperature. Both exposure at low tide or rising tide on a sun-heated shore involves considerable temperature changes, and during winter the air temperature may be far below freezing point. The growth of Ascophyllum nodosum has been measured between 2.5 and 35°C with an optimum between 10 and 17°C (Strömgren, 1977). Ascophyllum nodosum can be damaged by thermal pollution if the water temperature remains above 24°C for several weeks (Lobban & Harrison, 1997), and temperatures exceeding 27-28°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.

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)







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 (Strömgren, 1977). Water temperature is an excellent predictor of gamete release in Ascophyllum (Bacon & Vadas, 1991). Consequently, changes in temperatures could impact on gamete release. Investigations into the tolerance of Ascophyllum nodosum germlings from Norway, to temperatures between 7°C -17°C found that there was no difference in survival rates within the given range (Steen & Rueness, 2004). Germination of Ascophyllum nodosum has been recorded between the temperatures of 4°C and 23°C. Ascophyllum nodosum was reported to survive freezing to -20°C (MacDonald et al., 1974, cited in Åberg, 1992a).

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.

Salinity increase (local)

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

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.

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). Consequently, an increase in salinity within the benchmark may not cause negative impacts. *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. This biotope is found in both full salinity conditions (Connor *et al.*, 2004). Therefore, at the benchmark, the pressure would create hypersaline conditions. Although many species within this biotope would be able to cope with a short-term increase in salinity, long-term hypersaline conditions could cause mass mortalities of the biological community within this biotope. However, **no evidence** on the effects of hypersaline conditions on *Ascophyllum nodosum* or its associated community was found.

Salinity decrease (local)







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).

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). Similarly, both *Ascidiella scabra* and *Halichondria panicea* can be found in habitats with variable salinity and would, therefore, tolerate a decrease in the salinity within this biotope. *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) and fully saline conditions (30 -40 ppt) (Connor *et al.*, 2004). A decrease in salinity at the benchmark would create a reduced salinity regime (18-30) for a period of 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. 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 High High C: Medium C: Mediu

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 (Devinny & Volse, 1978) (see 'siltation' pressures). Changes in water motion can thus strongly influence local distribution patterns of *Fucus* spp. (Ladah *et al.*, 2008).

The high levels of water movement within this biotope make it suitable for the greater abundance of filter-feeding species such as *Halichondria panicea* and *Ascidiella scabra*. These species are absent from *Ascophyllum nodosum* biotopes that are found in areas with lower levels of water flow such as; LR.LLR.F.Asc and LR.LLR.F.Asc.FS.

Sensitivity assessment. This biotope (LR.HLR.FT.AscT) is recorded tidal currents ranging from very strong (> 6 knots; >3 m/sec) to moderately strong (1 - 3 knots; 0.5 - 1.5 m/s) (Connor *et al.*, 2004). The abundance and diversity of filter-feeders and epifauna are dependent on the high water flow. Therefore, a decrease in water flow could reduce the biodiversity and species abundance within this biotope, which would come to resemble the LR.LLR.F.Asc biotope. An increase in the level of water flow is unlikely (as is already occurs in very strong tidal conditions). However, a decrease of 0.1-0.2 m/s (the benchmark) is unlikely to have a significant effect in the already tidally-swept conditions. Therefore, resistance and resilience have been assessed as 'High' and the biotope is assessed as 'Not Sensitive' at the benchmark level.

Emergence regime changes







Q: High A: High C: High

Q: High A: High C: Medium

Q: High A: High C: Medium

Within the British Isles populations of *Ascophyllum nodosum* can suffer from bleaching and consequent mortality during exceptionally hot weather (Schonbeck & Norton, 1978, Hawkins & Hartnoll, 1985, Norton, 1985). However, these mortality events do not occur every year and tend to occur when the effects of unusually hot conditions combine with 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 fucoid canopy. Increases in temperature will be one of the effects changes in exposure will have on germlings. For further information refer to temperature pressure. Dense aggregations of algae can reduce the effect of more severe physical conditions such as those experienced with greater levels of exposure. Clumping enables organisms to retain moisture and reduce heat stress (Scrosati & DeWreede, 1998, Stafford & Davies, 2005).

Sensitivity assessment. Desiccation and the associated osmotic stress, especially when combined with high temperatures can cause mortalities (Pearson et al., 2009). The sensitivity of the characterizing species to emersion pressure will depend on the health and demography of individual populations, with germlings being most vulnerable life stage to this pressure. Ascophyllum nodosum has a level of resistance to an increase in emersion. However, an increase in the emergence time for a year is likely to change in the height of the biotope on the shore, with the top of the biotope being most sensitive to change as it is already at the upper tolerance limits. Conversely, a decrease in emergence may allow the biotope to increase its extent up the shore. Overall, an increase in emergence is likely to see all of the biotopes on the shore shifting downwards. Ascophyllum nodosum can take as many as twelve years to recover, with the return of ecosystem function taking considerably longer. Therefore, the resistance of this biotope has been assessed as 'Low' and resilience as 'Low' so that sensitivity is assessed as 'High' to changes in emergence regime at the pressure benchmark.

Wave exposure changes Medium (local)







Q: Medium A: Medium C: Medium

Q: High A: Medium C: Medium

Q: Medium A: Medium C: Medium

An increase in wave exposure generally leads to a decrease in macroalgae abundance and size (Lewis, 1961, Stephenson & Stephenson, 1972, Hawkins et al., 1992, Jonsson et al., 2006). Fucoids are highly flexible but not physically robust and an increase in wave exposure can cause mechanical damage, breaking fronds or even dislodging whole algae from the substratum. Ascophyllum nodosum is permanently attached to the substratum and would not be able to reattach 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 waves. As exposure to waves increases the fucoid population will become dominated by small juvenile algae and dwarf forms of macroalgae which are more resistant to strong wave action. An increase in wave action beyond the tolerance of these fucoid species leads to a further increase in the abundance of robust fucoids, such as Fucus spiralis f. nana and red seaweeds, such as Corallina officinalis (Connor et al., 2004).

Ascophyllum nodosum cannot resist very heavy wave action so exposure to wave action is an important factor controlling the distribution of the species, and therefore this biotope. This biotope is found in sheltered to extremely sheltered conditions. Propagule dispersal, fertilization, settlement, and recruitment are also influenced by water movement (Pearson & Brawley, 1996). An increase in water flow due to wave exposure could have negative impacts on the reproductive success of Ascophyllum nodosum. Experiments on the effect of wave action on Ascophyllum nodosum showed that a low-velocity wave can remove 99% of 15-minute old zygotes from experimental tiles Vadas et al. (1990). Further investigation with the use of refuges found that 75-90% of zygotes as old as four hours could be removed by a single wave. Current speeds over 20cm s⁻¹ make attachment success of Ascophyllum nodosum very poor (Vadas et al., 1992). These studies show the

need for periods of calm conditions for successful recruitment for *Ascophyllum nodosum*. An increase in the mean wave exposure will reduce the time during which attachment is possible. In addition, greater wave action can increase scour through increased sediment movement. Small life stages of macroalgae are likely to be affected by removing new recruits from the substratum and hence reducing successful recruitment (Devinny & Volse, 1978) (see 'siltation' pressures). The other characterizing species are found in a range of wave exposures and unlikely to be directly affected. However, loss of the fucoid cover would result in major changes to the associated community, especially attached epifauna and understorey algae.

Sensitivity assessment. As this is a very to extremely sheltered biotope a further decrease in wave exposure is unlikely, and not significant given the very strong to strong tidal flow in which the biotope occurs. An increase in wave action is likely to adversely affect fucoid cover, especially of *Ascophyllum nodosum*. The biotope 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	Not Assessed (NA)	Not assessed (NA)	Not assessed (NA)
contamination	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

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

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

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

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

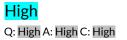
This pressure is **Not assessed** but evidence is presented where available.

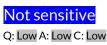
Radionuclide contamination	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR
No evidence.			
Introduction of other substances	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR

This pressure is **Not assessed**.

De-oxygenation







Reduced oxygen concentrations have been shown to inhibit both photosynthesis and respiration in macroalgae (Kinne, 1977). Despite this, macroalgae are thought to buffer the environmental conditions of low oxygen, thereby acting as a refuge for organisms in oxygen-depleted regions especially if the oxygen depletion is short-term (Frieder *et al.*, 2012). Reduced oxygen levels are likely to inhibit respiration whilst immersed, but it is unlikely to cause a loss of the macroalgae population directly. This biotope is found in a mid-eulittoral position and consequently, a proportion of time will be spent in the air where oxygen is not limited. As long as certain physical conditions are not exceeded, respiration and photosynthesis will be able to continue.

Although the macroalgae species within this biotope may not be negatively affected some of the associated fauna may be lost, causing a reduction in species richness. Josefson & Widbom (1988) investigated the response of benthic macro and meiofauna to reduced dissolved oxygen levels in the bottom waters of a fjord. At dissolved oxygen concentrations of 0.21 mg/l, the macrofaunal community was eradicated and was not fully re-established 18 months after the hypoxic event. Meiofauna seemed, however, unaffected by deoxygenation. Mobile species will be able to relocate to more optimal conditions, whereas immobile species such as barnacles are likely to be put under more stress by de-oxygenation. Complete smothering caused by the *Torrey Canyon* oil spill appeared to have little impact on barnacle species; a few *Semibalanus balanoides* died, yet *Chthamalus montagui* seemed unaffected (Smith, 1968). *Semibalanus balanoides* can respire anaerobically, so they can tolerate some reduction in oxygen concentration (Newell, 1979). When placed in wet nitrogen, where oxygen stress is maximal and desiccation stress is low, *Semibalanus balanoides* have a mean survival time of 5 days (Barnes *et al.*, 1963).

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

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

Nutrient enrichment

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

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

Not sensitive
Q: NR A: NR C: NR

The nutrient enrichment of a marine environment leads to organisms no longer being limited by the availability of certain nutrients. The consequent changes in ecosystem functions can lead to the progression of eutrophic symptoms (Bricker *et al.*, 2008), changes in species diversity and evenness (Johnston & Roberts, 2009) decreases in dissolved oxygen and uncharacteristic 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 lead to shores lacking species diversity and the domination by algae with fast growth rates (Abou-Aisha *et al.*, 1995, Archambault *et al.*, 2001, Arévalo *et al.*, 2007, Diez *et al.*, 2003, Littler & Murray, 1975).

Nutrient enrichment alters the selective environment by favouring fast growing, ephemeral species such as *Ulva lactuca* and *Ulva intestinalis* (Berger *et al.*, 2004, Kraufvelin, 2007). Rohde *et al.* (2008) found that both free growing filamentous algae and epiphytic microalgae can increase in abundance with nutrient enrichment. This stimulation of annual ephemerals may accentuate the competition for light and space and hinder perennial species development or harm their recruitment (Berger et al., 2003; Kraufvelin *et al.*, 2007). Nutrient enrichment can also enhance fouling of *Fucus* fronds by biofilms (Olsenz, 2011). Nutrient enriched environments can not only increase algae abundance but the abundance of grazing species (Kraufvelin, 2007).

White *et al.* (2011) investigated the effects of nutrient effluent from land-based finfish farms on the morphologies of *Ascophyllum nodosum* in the vicinity of the outfall pipes. It was estimated that the nitrogen effluent from the farm was 1500 kg/yr. The background levels of nitrite at the test site were 300 \square M. In comparison, the ambient nitrite levels in south-west Nova Scotia are $3 \square$ 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.

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

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

Organic enrichment

Medium

Q: High A: Medium C: Medium

Medium

Q: High A: Medium C: Medium

Medium
Q: High A: Medium C: Medium

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

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

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

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

A Physical Pressures

Resistance Resilience Sensitivity

Physical loss (to land or freshwater habitat)

None Q: High A: High C: High

Very Low Q: High A: High C: High High

Q: High A: High C: High

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

Physical change (to another seabed type)

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

Q: High A: High C: High

High

Q: High A: High C: High

This biotope occurs on rock substratum so that a change to sedimentary or soft rock substratum would lead to the direct loss of suitable attachment areas. This change in substratum would result in the loss of the characterizing species Ascophyllum nodosum along with other species found within the associated community of this biotope, 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

Not relevant (NR)

Not relevant (NR)

Not relevant (NR)

Q: NR A: NR C: NR substratum (extraction)

Q: NR A: NR C: 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 Low the surface of the substratum or seabed

Q: High A: High C: High

Low

High

Q: High A: Medium C: Medium

Q: High A: Medium C: Medium

Trampling on the rocky shore has been observed to reduce fucoid cover which decreased the microhabitat available for epiphytic species, increased bare space and increased 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. Fucoids are intolerant of abrasion from human trampling, which has been reported to reduce the cover of seaweeds on a shore (Holt et al., 1997; Tyler-Walters & Arnold, 2008).

Brosnan (1993) investigated the effect of trampling on a number of algal species, including Fucus

vesiculosus, on an intertidal rocky shore in Oregon. The effects of 250 tramples per plot, once a month for a year were recorded. Abundances of algae in each plot were reduced from 80% to 35% within a month of the introduction of the pressure and remained low for the remainder of the experiment. As few as $20 \text{ steps} / \text{m}^2$ on stations on an intertidal rocky shore in northeast England were sufficient to reduce the abundance of fucoids (Fletcher & Frid, 1996). This reduction in the complexity of the algae community, in turn, reduced the microhabitat available for epiphytic species. Trampling pressure can thus result in an increase in the area of bare rock on the shore (Hill *et al.*, 1998). Chronic trampling can affect community structure with shores becoming dominated by algal turf or crusts (Tyler-Walters & Arnold, 2008).

Pinn & Rodgers (2005) compared the biological communities found on two intertidal rocky shore ledges in Dorset. They found that the ledge 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.

Ascophyllum nodosum seems to be particularly intolerant of damage from trampling (Flavell, unpublished; cited in Holt et al., 1997), as its length means it is more likely that the thallus is 'cut' between a footstep and sharp rock (Boalch et al., 1974, Tyler-Walters & Arnold, 2008). Araujo et al. (2009) found that trampling negatively affected both Ascophyllum nodosum abundances and reduced understorey species 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 understorey 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)

Not relevant (NR)

Not relevant (NR)

Q: NR A: NR C: NR

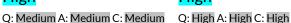
Q: NR A: NR C: NR

Q: NR A: NR C: NR

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

Changes in suspended solids (water clarity)







Not sensitive

Q: Medium A: Medium C: Medium

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

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

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

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

Smothering and siltation Medium

Medium

Medium

rate changes (light) Q: Medium A: Medium C: Medium Q: High A: High C: Medium

Q: Medium A: Medium C: Medium

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

However, germlings are likely to be smothered and killed in both scenarios and are inherently most susceptible to this pressure. Indeed early life stages are smaller in size than adults and are thus most vulnerable to this pressure as even a small load of added sediment will lead to the complete burial. Sediment deposition can reduce macroalgal recruitment by (1) reducing the amount of substratum available for attachment of propagules; (2) scour, removing attached juveniles and (3) burial, altering the light and/or the chemical micro-environment (Devinny & Volse, 1978, Eriksson & Johansson, 2003).

Ascophyllum nodosum is intolerant of sediment movement. 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/cm²). At 200 mg/cm² 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 not excessive and consequently deposited sediment will persist over a number of tides before it is all entrained and removed. This is likely to cause some damage to the characterizing species and the other associated species. Therefore, resistance is assessed as 'Medium'. Resilience is probably 'Low' so that sensitivity is assessed as 'Medium' at the level of the benchmark.

Smothering and siltation Low rate changes (heavy)

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 fucoids survival and associated communities. At the level of the benchmark (30 cm of fine material added to the seabed in a single event), smothering is likely to result in mortalities of understorey algae, invertebrate grazers and young (germling) fucoids. Water movement will remove sediment but within this biotope is it likely to take a number of tidal cycles. Resistance and resilience are assessed as 'Low' and sensitivity as 'High' to siltation at the pressure benchmark.

Litter

Not Assessed (NA)

Q: NR A: NR C: NR

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

Not assessed (NA)

Q: NR A: NR C: NR

Not assessed.

Electromagnetic changes No evidence (NEv) O: NR A: NR C: NR

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

No evidence (NEv)

Q: NR A: NR C: NR

No evidence.

Underwater noise changes

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Not relevant (NR)

Q: NR A: NR C: NR

Q: NR A: NR C: NR

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

Introduction of light or shading

No evidence (NEv)

Q: NR A: NR C: NR

Not relevant (NR)

No evidence (NEv)

Q: NR A: NR C: NR Q: NR A: NR C: NR

Increased levels of diffuse irradiation correlate with increased growth in macroalgae (Aguilaria *et al.*, 1999). Levels of diffuse irradiation increase in summer, and with a decrease in latitude. As Ascophyllum nodosum is found in the middle its natural range in the British Isles an increase in the level of diffuse irradiation will not 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 outcompete other fucoids. However, no evidence was found to support an assessment.

Barrier to species movement

Not relevant (NR)

Not relevant (NR)

Not relevant (NR)

Q: NR A: NR C: NR Q: NR A: NR C: NR Q: NR A: NR C: NR

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

Death or injury by collision

Not relevant (NR)

Not relevant (NR)

Not relevant (NR)

Q: NR A: NR C: NR

Q: NR A: NR C: 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)

Not relevant (NR)

Not relevant (NR)

Q: NR A: NR C: NR

Q: NR A: NR C: NR

Q: NR A: NR C: NR

Not relevant.

Biological Pressures

Resistance Resilience Sensitivity

Genetic modification & translocation of indigenous species

Not relevant (NR)

Not relevant (NR)

Not relevant (NR)

Q: NR A: NR C: NR

Q: NR A: NR C: 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 No evidence (NEv) invasive non-indigenous species

Not relevant (NR)

No evidence (NEv)

Q: NR A: NR C: NR

Q: NR A: NR C: NR

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 No evidence (NEv) pathogens

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

No evidence (NEv)

O: 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 canopyforming 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.

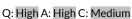
Keser et al. (1981) recorded the levels of re-growth exhibited by Ascophyllum nodosum and Fucus vesiculosus after experimental harvesting in Maine. Harvesting was simulated by cutting fronds to three different lengths, that is, frond removed to the holdfast, to 15 cm from the holdfast and to 25 cm from 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 regrowth, 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 where re-visited three years after the harvesting event they were still almost unaltered. The reasons for the lack of re-growth were attributed to the lack of regenerative tissue found in the older flesh further down the thallus (Printz, 1959). 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.

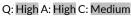
Sensitivity assessment. The removal of *Ascophyllum nodosum* canopy will significantly change the community composition of the biotope. The quantity of biomass removed from the shore and the regularity of removal will all affect how quickly the biotope will be able to recover. *Ascophyllum nodosum* probably 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











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 understorey community of sessile and mobile inveretebrates 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 fucoids, 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., Voegele, B., Philipp, E., Hanelt, D. & Wiencke, C., 1999. Effects of solar radiation on growth, photosynthesis and respiration of marine macroalgae from the Arctic. *Marine Ecology Progress Series*, **191**, 109-119.

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

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

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

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

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

Barthel, D. & Wolfrath, B., 1989. Tissue sloughing in the sponge *Halichondria panicea*: a fouling organism prevents being fouled. *Oecologia*, **78**, 357-360.

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

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

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

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

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

Bertness, M.D., 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. & Murray, S.N., 1993. Long-term effects of the water-accommodated fraction (WAF) of diesel oil on rocky shore populations maintained in experimental mesocosms. *Botanica Marina*, **36**, 313-319.

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.

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

Bradshaw, C., Veale, L.O., Hill, A.S. & Brand, A.R., 2002. The role of scallop-dredge disturbance in long-term changes in Irish Sea benthic communities: a re-analysis of an historical dataset. *Journal of Sea Research*, **47**, 161-184.

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

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.]

Brazier, D.P., Holt, R.H.F., Murray, E. & Nichols, D.M., 1999. *Marine Nature Conservation Review Sector* 10. *Cardigan Bay and North Wales: area summaries*. Peterborough: Joint Nature Conservation Committee. [Coasts and seas of the United Kingdom. MNCR Series.]

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

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

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

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

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

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

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

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

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.

Cole, S., Codling, I.D., Parr, W. & Zabel, T., 1999. Guidelines for managing water quality impacts within UK European Marine sites. *Natura 2000 report prepared for the UK Marine SACs Project.* 441 pp., Swindon: Water Research Council on behalf of EN, SNH, CCW, JNCC, SAMS and EHS. [UK Marine SACs Project.], http://www.ukmarinesac.org.uk/

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 1861075618. In JNCC (2015), *The Marine Habitat Classification for Britain and Ireland Version* 15.03. [2019-07-24]. Joint Nature Conservation Committee, Peterborough. Available from https://mhc.jncc.gov.uk/

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

Crisp, D.J. (ed.), 1964. The effects of the severe winter of 1962-63 on marine life in Britain. Journal of Animal Ecology, 33, 165-210.

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.

Davies, C.E. & Moss, D., 1998. European Union Nature Information System (EUNIS) Habitat Classification. *Report to European Topic Centre on Nature Conservation from the Institute of Terrestrial Ecology, Monks Wood, Cambridgeshire.* [Final draft with further revisions to marine habitats.], Brussels: European Environment Agency.

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

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

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. & 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.

Fernandez, C. & Menendez, M.P., 1991. Ecology of *Chondrus crispus* on the northern coast of Spain. 2. Reproduction. *Botanica Marina*, **34**, 303-310.

Filion-Myclebust, C. & Norton, T.A., 1981. Epidermis shedding in the brown seaweed *Ascophyllum nodosum* (L.) Le Jolis, and its ecological significance. *Marine Biology Letters*, **2**, 45-51.

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].

Floc'h, J. H. & Diouris, M., 1980. Initial effects of Amoco Cadiz oil on intertidal algae. Ambio, 9, 284-286.

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

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

Glegg, G. A., Hickman, L. & Rowland, S. J., 1999. Contamination of limpets (*Patella vulgata*) following the Sea Empress oil spill. *Marine Pollution Bulletin*, **38**, 119-125.

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.

Graham, A., 1988. *Molluscs: prosobranchs and pyramellid gastropods (2nd ed.).* Leiden: E.J. Brill/Dr W. Backhuys. [Synopses of the British Fauna No. 2]

Guiry, M.D. & Blunden, G., 1991. Seaweed Resources in Europe: Uses and Potential. Chicester: John Wiley & Sons.

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.

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).

Hiscock, K., 1983. Water movement. In Sublittoral ecology. The ecology of shallow sublittoral benthos (ed. R. Earll & D.G. Erwin), pp. 58-96. Oxford: Clarendon Press.

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

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.

Holt, T.J., Jones, D.R., Hawkins, S.J. & Hartnoll, R.G., 1995. The sensitivity of marine communities to man induced change - a scoping report. *Countryside Council for Wales, Bangor, Contract Science Report*, no. 65.

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

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., Wethey, D.S. & Woodin, S.A., 2008. Comparative ecology of North Atlantic shores: do differences in players matter for process? *Ecology*, **89** (11), 3-S23. 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

Jennings, S. & Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. Advances in Marine Biology, 34, 201-352.

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

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

Johnston, C.S., 1977. The sub-lethal effects of water-soluble extracts of oil on the fertilisation and development of *Fucus serratus* L. (Serrated wrack). *Rapports et Proces Verbaux des Reunions. Conseil International pour l'Exploration de la Mer*, **171**, 184-185.

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.

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.

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

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

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

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

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

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

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

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

Levin, P.S. & Mathieson, A.C., 1991. Variation in host-epiphyte relationship along a wave exposure gradient. *Marine Ecology Progress Series*, **77**, 271-278.

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.

Marchan, S., Davies, M.S., Fleming, S. & Jones, H.D., 1999. Effects of copper and zinc on the heart rate of the limpet *Patella vulgata* (L.) *Comparative Biochemistry and Physiology*, **123A**, 89-93.

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

Moore, J., 1997. Rocky shore transect monitoring in Milford Haven, October 1996. Impacts of the Sea Empress oil spill. Countryside Council for Wales Sea Empress Contract Report, **241**, 90pp.

Morrissey, J., Kraan, S. & Guiry, M.D., 2001. A guide to commercially important seaweeds on the Irish coast. Bord Iascaigh Mhara: Dun Laoghaire.

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

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

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

O'Brien, P.J. & Dixon, P.S., 1976. Effects of oils and oil components on algae: a review. British Phycological Journal, 11, 115-142.

Olsenz, 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.

Petraitis, P.S. & Dudgeon, S.R., 2005. Divergent succession and implications for alternative states on rocky intertidal shores. *Journal of Experimental Marine Biology and Ecology*, **326** (1), 14-26. 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#&39;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

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

Pybus, C., 1977. The ecology of Chondrus crispus and Gigartina stellata (Rhodophyta) in Galway Bay. Journal of the Marine Biological Association of the United Kingdom, **57**, 609-628.

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.

Rees, H.L., Waldock, R., Matthiessen, P. & Pendle, M.A., 2001. Improvements in the epifauna of the Crouch estuary (United Kingdom) following a decline in TBT concentrations. *Marine Pollution Bulletin*, **42**, 137-144.

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.

Robbins, I.J. 1985b. Ascidian growth rate and survival at high inorganic particulate concentrations. *Marine Pollution Bulletin*, **16**, 365-367.

Robins, M.W., 1968. The ecology of Alcyonium species in the Scilly Isles. Report of the Underwater Association, 3, 67-71

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.

Scanlan, C.M. & Wilkinson, M., 1987. The use of seaweeds in biocide toxicity testing. Part 1. The sensitivity of different stages in the life-history of *Fucus* and of other algae, to certain biocides. *Marine Environmental Research*, **21**, 11-29.

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 fucoid algae on the shore. *Journal of Experimental Marine Biology and Ecology*, **31**, 303-313.

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

Scrosati, R., Garbary, D.J. & McLachlan, J., 1994. Reproductive ecology of *Chondrus crispus* (Rhodophyta, Gigartinales) from Nova Scotia, Canada. *Botanica Marina*, 37, 293-300.

Seip, K.L., 1980. A computational model for growth and harvesting of the marine alga Ascophyllum nodosum. Ecological Modelling, 6, 189-199.

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.

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

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

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

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

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

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

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

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

Strömgren, T., 1977. Short-term 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

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

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

Strömgren, T., 1980a. The effect of dissolved copper on the increase in length of four species of intertidal fucoid algae. *Marine Environmental Research*, **3**, 5-13.

Strömgren, T., 1980b. The effect of lead, cadmium and mercury on the increase in length of five intertidal Fucales. *Journal of Experimental Marine Biology and Ecology*, **43**, 107-119.

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

Suryono, C.A. & Hardy, F.G., 1997. Studies on the distribution of *Fucus ceranoides* L. (Phaeophyta, Fucales) in estuaries on the north-east coast of England. *Transactions of the Natural History Society of Northumbria*, **57**, 153-168.

Svane, I, Havenhund, J.N. & Jorgensen, A.J., 1987. Effects of tissue extract of adults on metamorphosis in *Ascidia mentula* O.F. Mueller and *Ascidiella scabra* (O.F. Müller). *Journal of Experimental Marine Biology and Ecology*, **110**, 171-181.

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

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

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

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

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

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

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

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

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

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

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

Watson, D.C. & Norton, T.A., 1987. The habitat and feeding preferences of *Littorina obtusata* (L.) and *Littorina mariae* Sacchi et Rastelli. *Journal of Experimental Marine Biology and Ecology*, **112**, 61-72.

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.