Fucus vesiculosus on full salinity moderately exposed to sheltered mid eulittoral rock

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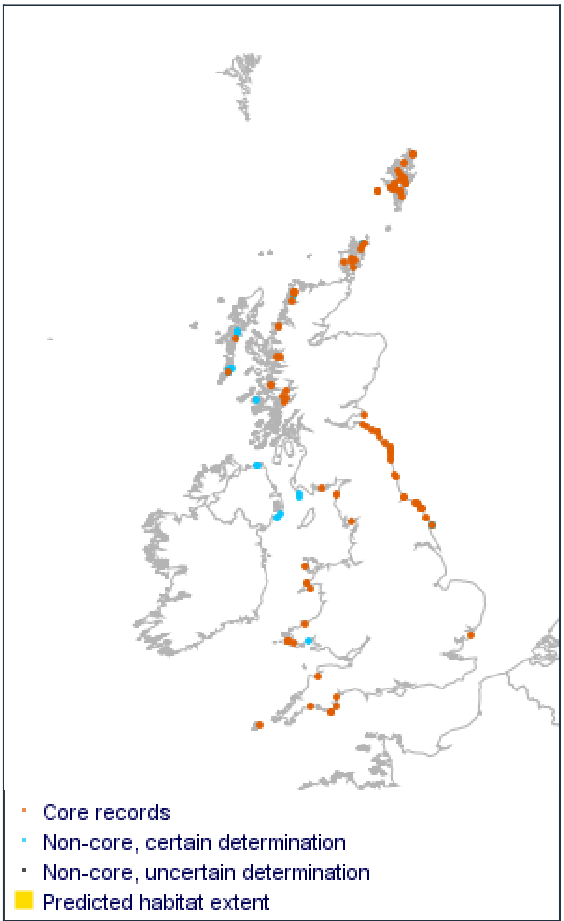
***Fucus vesiculosus* on full salinity moderately exposed to sheltered mid eulittoral rock**
Photographer: David Connor



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

Researched by Frances Perry & Emilia d'Avack **Refereed by** Admin

Summary

UK and Ireland classification

EUNIS 2008	A1.3131	*Fucus vesiculosus* on full salinity moderately exposed to sheltered mid eulittoral rock
JNCC 2015	LR.LLR.F.Fves.FS	*Fucus vesiculosus* on full salinity moderately exposed to sheltered mid eulittoral rock
JNCC 2004	LR.LLR.F.Fves.FS	*Fucus vesiculosus* on full salinity moderately exposed to sheltered mid eulittoral rock
1997 Biotope		

Description

Moderately exposed to sheltered mid eulittoral bedrock and large boulders characterized by a dense canopy of the wrack *Fucus vesiculosus* (Abundant to Superabundant). Beneath the seaweed canopy the rock surface has a sparse covering of the barnacle *Semibalanus balanoides* and the limpet *Patella vulgata*. The mussel *Mytilus edulis* is confined to pits and crevices. A variety of winkles including *Littorina littorea*, *Littorina saxatilis* and the whelk *Nucella lapillus* are found beneath the seaweeds, whilst *Littorina obtusata/mariae* graze on the fucoid fronds. The calcareous tube-forming polychaete *Spirorbis spirorbis* may also occur epiphytically on the fronds. In areas of localised shelter the wrack *Ascophyllum nodosum* may occur, though never at high abundance. Damp cracks and crevices often contain patches of the red seaweed *Mastocarpus stellatus* and even the wrack *Fucus serratus* may be present. The crab *Carcinus maenas*may be present in pools or among the boulders. This biotope usually occurs between the wrack *Fucus spiralis* (Fspi) and the *F. serratus* (Fserr) zones; both of these fucoids may be present in this biotope, though never at high abundance (typically less than Frequent). In some sheltered areas *Fucus vesiculosus* forms a narrow zone above the *A. nodosum* zone (Asc). Where freshwater runoff occurs on more gradually sloping shores *Fucus vesiculosus* may be replaced by the wrack *Fucus ceranoides* (Fcer). On some shores, particularly those which are moderately exposed to wave action, temporal fluctuations in the abundance of limpets, barnacles and fucoid seaweeds may occur. As a result, over a number of years, a single shore may cycle between the barnacle-*Patella vulgata* dominated biotope (Sem.FvesR), through this mosaic (FvesB) to a *Fucus vesiculosus*-dominated biotope (Fves). (Information from Connor *et al.*, 2004; JNCC, 2015).

Depth range

Mid shore

Additional information

-

Listed By

- none -

Further information sources

Search on:

G G G JNCC

Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

This biotope is characterized by a dense canopy of *Fucus vesiculosus.* Beneath the fucoid canopy the barnacle *Semibalanus balanoides*, the limpet *Patella vulgata*, and a variety of Littorinids are dominant faunal grazers. The mussel *Mytilus edulis* is confined to fissures and crevices where the environmental conditions are less severe. Carnivores within these biotopes include *Nucella lapillus* and *Carcinus maenus.* Other species of macroalgae can be found within these biotopes but are not as common as *Fucus vesiculosus.*

Fucus vesiculosus is the key structuring species of this biotope. The macroalgae forms a canopy that provides protection from desiccation for underlying fauna. the macroalgae forms a canopy that provides protection from desiccation for the various underlying foliose red seaweeds in addition to providing a substratum for a diverse range of epifauna. As ecosystem engineers fucoid algal canopies modify habitat conditions. This can facilitate the existence and survival of other intertidal species and therefore strongly influencing the structure and functioning of intertidal ecosystems (Jenkins *et al*., 2008).

Resilience and recovery rates of habitat

Since the 1940s major declines in the distribution of *Fucus vesiculosus* (Kautsky *et al*., 1986) and even local extinctions (Nilsson et al., 2005) have been observed in the Baltic Sea where the species dominates the shallow hard-bottom areas. The decline was likely a consequence of increased anthropogenic stress. Large-scale disappearance of *Fucus vesiculosus* from an ecosystem can result in changes in the community composition (Wikstrom & Kautsky, 2007). The canopy created by *Fucus vesiculosus* forms a microclimate for the understory fauna and flora. Removal of the canopy exposes under lying fauna and flora to environmental conditions with which they would be intolerant of resulting in mortality events.

Fucus vesiculosus recruits readily to cleared areas of the shore and full recovery takes 1-3 years in British waters (Hartnoll & Hawkins, 1985). Keser & Larson (1984) investigated the recovery of Fucus vesiculosus to plots which had been scraped clean and burned with a propane torch. *Fucus vesiculosus* was the first perennial alga to colonize the experimentally denuded transects, even at sites and tidal levels that had been dominated by *Ascophyllum* or *Chondrus* beforehand. Recovery occurred at all sites between 3 to 21 months. The study found newly settled germlings of *Fucus vesiculosus* in most months, indicating a broad period of reproduction. When grazers are excluded from areas of intertidal shores fucoids have the ability to rapidly recolonize areas, they can even be found in areas, which in a balanced ecosystem, they do not normally occur (Burrows & Lodge, 1950, Southward & Southward, 1978). Fucoid distributions return to their recognized zones when grazers are re-established on a shore (Burrows & Lodge, 1950, Southward & Southward, 1978). Although intertidal shores can rapidly regain fucoids it can take considerably longer for ecosystem function to return if grazers have also been lost (Hawkins & Southward, 1992). If the whole community is removed, recovery is likely to occur at a much lower pace. Indeed, Hawkins & Southward (1992) found that, after the M.V. Torrey Canyon oil spill, it took between 10 and 15 years for the *Fucus* spp. to return to 'normal' levels of spatial and variation in cover on moderately exposed shores. Therefore, for factors which are likely to totally destroy the biotope, recoverability is likely to be low.

Fucus vesiculosus growth rates can vary both spatially and temporally (Lehvo et al., 2001).

Temperature, exposure, and light availability are some of the factors which cause these changes in growth rates (Strömgren, 1977, Knight & Parke, 1950, Middelboe et al., 2006). Strömgren (1977) investigated the effect of short-term increases in temperature on the growth rate of Fucus vesiculosus. It was found that the growth rate of the control sample kept at 7°C was 20 times lower than the sample introduced to temperatures of 35°C (Strömgren 1977). When the effect of temperature was investigated on the shore, relative growth rates in summer were found to be as high as 0.7% / day in summer, compared to less than 0.3% / day in winter (Lehvo et al., 2001). For macroalgae the trend is for shorter individuals in situations with greater wave exposure (Lewis, 1961, Stephenson & Stephenson, 1972, Hawkins *et al.*, 1992, Jonsson *et al.*, 2006). *Fucus vesiculosus* also comply with this trend, and growth rates mirror this difference in physiology. On Sgeir Bhuidhe, an exposed shore in Scotland, *Fucus vesiculosus* grew on average 0.31 cm / week. On a sheltered Scottish shore the average increased to 0.68 cm / week (Knight & Parke, 1950).

The development of the receptacles takes three months from initiation until when gametes are released (Knight, 1947). On British shores, receptacles are initiated around December and may be present until late summer (Knight , 1947). The alga is dioecious, and gametes are generally released into the seawater under calm conditions (Mann, 1972; Serrão et al., 2000) and the eggs are fertilized externally to produce a zygote. Serrão *et al.* (1997) determined that the wrack had a short-range dispersal capacity. Under calm conditions in which eggs are released, most eggs fall in the immediate vicinity of the parent plants. The egg becomes attached to the rock within a few hours of settlement and adhere firmly enough to resist removal by the next returning tide and germling may be visible to the naked eye within a couple of weeks (Knight & Parke, 1950). Despite the poor long range dispersal, the species is highly fecund often bearing more than 1000 receptacles on each plant, which may produce in excess of one million eggs. On the coast of Maine, sampling on three separate occasions during the reproductive season revealed 100% fertilization on both exposed and sheltered shores (Serrão *et al.*, 2000). Fertilization is thus not considered as a limiting factor in reproduction in this species (Serrão *et al.*, 2000).

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). While *Fucus vesiculosus* may resist some degree of environmental stress, their long-term persistence depends on their reproductive ability as well as the survival and growth of early life history stages (germlings) that are generally more susceptible to natural and anthropogenic stressors than adults (Steen, 2004; Fredersdorf *et al.*, 2009). It is therefore necessary to include early life stage responses in the assessment of effects of environmental changes on fucoid algae as only considering fully developed adults specimens may lead to false conclusions (Nielsen et al., 2014).

Genetic diversity can influence the resilience of fucoids in particular when pressure persists over a long period of time. Genetically diverse populations are generally more resilient to changes in environmental conditions compared to genetically conserved populations. Tatarenkov *et al.* (2007) determined a high level of genetic variation in Fucus vesiculosus and extensive phenotypic variation. They suggested this might explain why the species is more successful than most fucoid species in colonizing marginal marine environments such as low-salinity estuaries, showing a range of morphological, physiological and ecological adaptations (Tatarenkov *et al.* 2005). Pressures causing a rapid change will have a greater impact as the natural ability of the species to adapt is compromised.

In addition to sexual reproduction, *Fucus vesiculosus* is also able to generate vegetative regrowth in response to wounding. McCook & Chapman (1992) experimentally damaged Fucus vesiculosus holdfasts to test the ability of the wrack to regenerate. The study found that vegetative sprouting of *Fucus vesiculosus* holdfasts made a significant addition to the regrowth of the canopy, even when holdfasts were cut to less than 2 mm tissue thickness. Four months after cutting, sprouts ranged from microscopic buds to shoots about 10 cm long with mature shoots widespread after 12 months. Vegetative regrowth in response to wounding has been suggested as an important mean of recovery from population losses (McLachan & Chen, 1972). The importance of regeneration will depend on the severity of damage, not only in terms of the individuals but also in terms of the scale of canopy removal (McLachan & Chen, 1972).

Resilience assessment. If specimens of *Fucus vesiculosus* remain in small quantities it is likely that re-growth will occur rapidly due to efficient fertilization rates and recruitment over short distances. The ability of *Fucus vesiculosus* to re-grow from damaged holdfasts will also aid in recolonization. Recovery is likely to occur within two years resulting in a 'High' resilience score. However, if the population is removed (resistance is 'None') , recovery may take longer, perhaps up to 10 years (as seen after the *M.V. Torrey Canyon* oil spill) so the resilience would be scored as 'Medium'.

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

Hydrological Pressures

	Resistance	Resilience	Sensitivity
Temperature increase (local)	High Q: High A: High C: Medium	High Q: High A: High C: Medium	Not sensitive Q: High A: High C: Medium

In the north east Atlantic *Fucus vesiculosus* occurs from Northern Russia to Morocco (Powell, 1963). Within this range *Fucus vesiculosus* can survive in a wide variety of temperatures. *Fucus vesiculosus* is able to tolerate temperatures as high as 30 °C (Lüning,1990) and did not show any sign of damage during the extremely hot UK summer of 1983, when average temperatures were 8 °C hotter than normal (Hawkins & Hartnoll, 1985). *Fucus vesiculosus* also tolerates extended periods of freezing in the northern part of its range.

Sensitivity assessment. Both *Fucus spiralis* and *Fucus vesiculosus* are found in the middle of their natural temperature range in the British Isles and will therefore not be affected by an increase in 5 °C for one month or an increase of 2 °C for one year. Both resistance and resilience are thus assessed as 'High' (no impact to recover from). The biotope is 'Not Sensitive' to this pressure at the pressure benchmark.

Temperature decrease (local)	High Q: High A: High C: Medium	High Q: High A: High C: Medium	Not sensitive Q: High A: High C: Medium

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

Fucus vesiculosus is well adapted to cope with varying salinities and can grow in full saline to brackish conditions. Indeed *Fucus vesiculosus* is the dominant large perennial seaweed in the Baltic Sea growing in salinities down to 4 psu (Kautsky, 1992). Bäck *et al.* (1992) compared *Fucus vesiculosus* individuals from Atlantic and the Baltic populations. Both populations were able to withstand wide range of salinities in laboratory cultures, yet some differences were recorded. The Atlantic population showed better growth in higher salinities and virtually no growth at 5 ppt. For individuals kept at 5 ppt mortality occurred after 7 weeks. In contrast the Baltic wracks grew better in conditions with lower salinities. Growth was negligible at the highest tested salinity (45 ppt). Back *et al.*, (1992) demonstrate that sensitivity of *Fucus vesiculosus* to changes in salinity differ between populations.

Serrao *et al.* (1996a) found that lower salinities can negatively affect both the fertilization rates and recruitment success of *Fucus vesiculosus*. Serrao *et al.* (1996a) also concluded that the osmotic tolerances of *Fucus vesiculosus* gametes limit the species distribution in the Baltic Sea. These studies show that low salinities limit the recruitment and fertilization success of fucoids. There is also evidence suggesting that reduced salinities can influence the rate of receptacle maturation in fucoids (Munda, 1964). Rate of fructification in both *Ascophylum nodosum* and *Fucus vesiculosus* has been measured to increase in diluted seawater (Munda, 1964).

Sensitivity assessment. An increase in salinity for this biotope would mean salinity levels would become hyper-saline. *Fucus vesiculosus* is not adapted for these conditions and a change in this pressure at this benchmark would cause some mortality. Other species within this biotope may be able to tolerate an increase in salinity, however the loss of *Fucus vesiculosus* would lead to a change in the biotope. Both resistance and resilience are thus assessed as 'Medium'. The biotope has a 'Medium' sensitivity to this pressure at the pressure benchmark.

Salinity decrease (local)	High Q: High A: High C: Medium	High Q: High A: High C: Medium	Not sensitive Q: High A: High C: Medium

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Sensitivity assessment. *Fucus vesiculosus* found in the middle of its natural range in the UK will not be affected by a decrease in one MNCR salinity category. Both resistance and resilience are thus assessed as 'High' (no impact to recover from). The biotope is 'Not Sensitive' to this pressure at the pressure benchmark.

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

Water motion is a key determinant of marine macroalgal ecology, influencing physiological rates and community structure (Hurd, 2000). Higher water flow rates increase mechanical stress on macroalgae by increasing drag. This can result in individuals being torn off the substratum. Once removed, the attachment cannot be reformed causing the death of the algae. Any sessile organism attached to the algae will also be lost. Fucoids are however highly flexible and are able to re-orientate their position in the water column to become more streamlined. This ability allows fucoids to reduce the relative velocity between algae and the surrounding water, thereby reducing drag and lift (Denny *et al.*, 1998).

Jonsson *et al.* (2006) found that flow speed of 7-8 m/s completely dislodged *Fucus vesiculosus* individuals larger than 10 cm. Smaller individuals are likely to better withstand increased water flow as they experience less drag. The risk of dislodgement is greater where algae are attached to pebbles instead of bedrock. Depending on the size of the pebbles, individuals may eventually reach a critical size when the drag force exceeds gravity and the plant will be moved together with its substratum (Malm, 1999). This risk is increased during the late phase of reproduction when *Fucus vesiculosus* receptacles become swollen and gas-filled increasing the uplifting force of water flow (Isaeus, 2004).

Propagule dispersal, fertilization, settlement, and recruitment are also influenced by water movement (Pearson & Brawley, 1996). In addition, increased water flow increases 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).

On the other hand, a reduction in water flow can cause a thicker boundary layer resulting in lower absorption of nutrients and CO_2 by the macroalgae. Slower water movement can also cause oxygen deficiency directly impacting the fitness of algae (Olsenz, 2011).

This *Fucus vesiculosus* biotope is recorded in moderately exposed to very sheltered wave exposures. The water flows experienced by this biotope range from negligible - 1.5 m/s (Connor *et al.*, 2004). The water flows which are created by wave movement in moderately exposed locations will exceed the water flows which are characteristic of this biotope.

Sensitivity assessment. This biotope is characteristic of moderately exposed to very sheltered conditions. In those examples of this biotope which are found in moderately exposed conditions water movement from wave action will exceed the strength of any tidal flow. This suggests that an increase in water flow of 0.2m/s would not have a negative effect on this biotope as it can tolerate greater water movement caused by waves. Based on the available evidence the characterizing species *Fucus vesiculosus* can adapt to high flow rates and the biotope is therefore considered to be 'Not sensitive' to an increase in water flow. A decrease in water flow may have some effects on recruitment and growth, but this is not considered to be lethal at the pressure benchmark and resistance is therefore assessed as 'High' and resilience as 'High' by default, so that the biotope is considered to be 'Not sensitive'.

Emergence regime changes	None Q: High A: Medium C: Medium	Medium Q: High A: High C: Medium	Medium Q: High A: Medium C: Medium

Emergence regime is a key factor structuring intertidal biotopes. Increased emergence may reduce habitat suitability for the characterizing species. Changes in emergence can lead to; greater exposure to desiccation, reduced levels of time for nutrient uptake and photosynthesising opportunities for the characterizing species.

During the initial stages of drying, when alga are exposed to air, photosynthetic rates increase due to the higher diffusion rate of CO_2 in air relative to water (Johnson *et al.*, 1974). However this peak in photosynthesis is usually followed by a gradual decline in the rate of photosynthesis as the surface of the alga dries, thereby preventing further dissolution and uptake of CO_2 (Beer & Kautsky 1992). Photosynthesis eventually ceases at a critical state of dehydration when the low water content of the thallus disrupts the functioning of the photosynthetic apparatus (Quadir *et al.* 1979). *Fucus vesiculosus* can tolerate desiccation until the water content is reduced to ~ 30%. If desiccation occurs beyond this level, irreversible damage occurs. Individuals at the top of the shore probably live at the upper limit of their physiological tolerance and are therefore likely to be unable to tolerate increased desiccation and would be displaced by more physiologically tolerant species. Tolerance to this pressure is likely to vary on a geographical scale. Gylle *et al.* (2009) found that *Fucus vesiculosus* populations naturally occurring in fully saline conditions had a higher emersion stress tolerance compared to brackish populations. Early life history stages are more susceptible to this pressure compared to adults (Henry & Van Alstyne, 2004). Germlings are however protected from desiccation by the canopy of adults. A study by Brawley & Jonhnson (1991) showed that germling survival under adult canopy was close to 100% whereas survival on adjacent bare rock was close to 0% during exposure to aerial conditions. The *Fucus* canopy is also likely to protect other underlying species to a great extent. Mortalities of other component of the community will however occur if the canopy is removed (see ‘abrasion’ pressure). *Fucus spiralis* is more tolerant of desiccation stress than *Fucus vesiculosus,* and is the characterizing species for a very similar biotope to this one which is found further up the shore. An increase in emergence may cause the biotope to change to one more typical of an upper shore location. Alternatively if levels of emergence were to increase then *Fucus vesiculosus* may be out-competed by a faster growing algae species such as *Fucus serratus*, an algae species which is found in a number of biotopes which characterize lower shore zones.

Fucoid dominated biotopes are found in the eulittoral zone and are subjected to cyclical immersion and emersion caused by the tides. During the initial stages of drying, when alga are exposed to air, photosynthetic rates increase due to the higher diffusion rate of CO_2 in air relative to water (Johnson *et al*., 1974). However this peak in photosynthesis is usually followed by a gradual decline in the rate of photosynthesis as the surface of the alga dries, thereby preventing further dissolution and uptake of CO_2 (Beer & Kautsky 1992). Photosynthesis eventually ceases at a critical state of dehydration when the low water content of the thallus disrupts the functioning of the photosynthetic apparatus (Quadir *et al*. 1979).

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Sensitivity assessment. Desiccation and the associated osmotic stress, especially when combined with high temperatures can cause mortalities (Pearson *et al*., 2009). The sensitivity of *Fucus vesiculosus* to emersion pressure will depend on individual populations as well as the life stage, with germlings being most vulnerable. A change in emergence is likely to cause a change in biotope. Resistance has been assessed as 'None' and resilience is assessed as 'Low'. Overall the biotope has a 'Medium' sensitivity to changes in emergence regime at the pressure benchmark.

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

An increase in wave exposure generally leads to a decrease in macroalgae abundance and size (Lewis, 1961, Stephenson & Stephenson, 1972, Hawkins *et al*., 1992, Jonsson *et al*., 2006). 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. 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 size of fucoids (Blanchette, 1997) as smaller individuals create less resistance to waves.

As exposure increases the fucoid population will become dominated by small juvenile algae, and dwarf forms of macroalgaes which are more resistant to this pressure. An increase in wave action beyond this would lead to a further increase in the abundance of robust fucoids and red seaweeds, such as *Corallina officinalis* (Connor *et al*,. 2004).

A recent study investigated the combined impacts of wave action and grazing on macroalgae distribution (Jonsson *et al*., 2006). It suggested that recruitment and survival of juvenile *Fucus vesiculosus* is controlled indirectly by wave exposure, through higher limpet densities at exposed locations (Jonsson *et al*,, 2006). *Fucus vesiculosus* have shown to adapt their morphology to wave exposure to help cope with the stress. For instance Bäck (1993) observed shorter individuals with narrow fronds on exposed shores lacking bladders to reduce drag. An alternative coping strategy for wave induced forces is thallus toughening. In the north and the Baltic Sea, thalli from exposed *Fucus vesiculosus* were 30% more resistant to tear and breakage compared to conspecifics from more sheltered sites (Nietsch, 2009). Furthermore, *Fucus vesiculosus* is able to regenerate from holdfasts (Malm & Kautsky, 2003).

This biotope occurs in moderately exposed to extremely sheltered conditions. Therefore an example of this biotope found in the middle of the wave exposure range would tolerate either an increase or decrease in significant wave height at the pressure benchmark. Examples of this biotope where they are on the limit of wave exposure are more likely to be sensitive to an increase in significant wave height, which could cause a shift in the character of the biotope. A decrease in wave exposure is unlikely to have an impact on this biotope as it already appears in extremely wave sheltered conditions. An example of this biotope found in moderately exposed conditions may be affected by an increase in wave exposure and could potentially change to an alternative biotope. *Fucus vesiculosus* biotopes found in situations with greater wave include a greater quantity of barnacles and limpets, LR.MLR.BF.FvesB is an example of which. Other fucoid biotopes in greater wave exposure tend to shift away from *Fucus vesiculosus* and become more dominated by *Fucus serratus* and occasionally *Fucuc spiralis.*

Sensitivity assessment. *Fucus vesiculosus* is sensitive to a change in wave action and consequently has the capacity to alter the biotope type. Increased exposure at the limits of physical tolerance of this biotope could result in a change of biomass and species richness. Resistance and resilience are both assessed as 'Medium'. Recovery will depend on the extent of loss and could potentially be faster depending on the extent of *Fucus vesiculosus* loss. Overall this biotope scores a 'Medium' sensitivity to this pressure at the pressure benchmark.

Chemical Pressures

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

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

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

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

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

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

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

No evidence.

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

This pressure is **Not assessed**.

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

Cole *et al*. (1999) suggest possible adverse effects on marine species below oxygen levels of 4 mg/l and probable adverse effects below 2 mg/l. Sustained reduction of dissolved oxygen can lead to hypoxic (reduced dissolved oxygen) and anoxic (extremely low or no dissolved oxygen) conditions. Sustained or repeated episodes of reduced dissolved oxygen have the potential to severely degrade an ecosystem (Cole *et al*., 1999).

Reduced oxygen concentrations have been shown to inhibit both photosynthesis and respiration in macroalgae (Kinne, 1977). Despite this, macroalgae are thought to buffer the environmental conditions of low oxygen, thereby acting as a refuge for organisms in oxygen depleted regions especially if the oxygen depletion is short-term (Frieder *et al*., 2012). If levels do drop below 4 mg/l negative effects on these organisms can be expected with adverse effects occurring below 2 mg/l (Cole *et al*., 1999). Reduced oxygen levels are likely to inhibit photosynthesis and respiration but not cause a loss of the macroalgae population directly. However, small invertebrate epifauna may be lost, causing a reduction in species richness.

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 de-oxygenation. Kinne (1970) reported that reduced oxygen concentrations inhibit both algal photosynthesis and respiration.

Sensitivity assessment. The characterizing species *Fucus vesiculosus*, as well as the other species within this biotope, may be negatively impacted by reduced dissolved oxygen level at the level of the benchmark (2 mg/l for 1 week). A reduction in oxygen levels at the benchmark for this pressure could result in mortalities.

The very sheltered to moderately exposed locations where this biotope is found means that there will be water mixing created by tidal streams, currents and waves in examples of this biotope which are in more exposed locations. Therefore a reduction in oxygen may have more of a negative impact on examples of this biotope in more sheltered locations, as there will be less water mixing.

However, the biotope occurs in the mid eulittoral so that a proportion of time will be spent in the air where oxygen is not limited so the metabolic processes of photosynthesis and respiration can take place. Emergence will mitigate the effects of hypoxic surface waters, as will aeration of the water column due to the exposure to wave action and water flow. Therefore, resistance is assessed as 'High'. Hence, resilience is assessed as 'High', and the biotope as 'Not sensitive'.

Nutrient enrichment	High Q: High A: Medium C: Medium	High Q: High A: High C: Medium	Not sensitive Q: High A: Medium C: Medium

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

Johnston & Roberts (2009) undertook a review and meta-analysis of the effect of contaminants on species richness and evenness in the marine environment. Of the 47 papers reviewed relating to nutrients as a 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 effect of marine pollutants on species diversity was '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).

Major declines of *Fucus vesiculosus* have been reported from all over the Baltic Sea. These declines have been associated to eutrophication from nutrient enrichment (Kautsky *et al.*, 1986). 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). High nutrient levels may directly inhibit spore settlement and hinder the initial development of *Fucus vesiculosus* (Bergström *et al.*, 2003).

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.*, 2006b; 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. However, if the biotope is well established and in a healthy state the biotope could have the potential to persist. The effect of an increase in this pressure to the benchmark level should not have a negative impact on the biotope. Therefore the resistance has been assessed as 'High'. As the resistance is high, as there will be nothing for the biotope to recover from therefore the resilience is also 'High'. These two rankings give an overall sensitivity of 'Not Sensitive'.

Organic enrichment	Medium Q: High A: Medium C: Medium	Medium Q: High A: High 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 effect of marine pollutants on species diversity was '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 (Littler & Murray, 1975; Abou-Aisha *et al.*, 1995; Archambault *et al.*, 2001; Diez *et al.*, 2003; Arévalo *et al.*, 2007).

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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*., 2006b; Kraufvelin, 2007).

Sensitivity assessment. Little empirical evidence was found to support an assessment of this biotope at this benchmark. The effect of a deposit of 100 gC/m2/yr will have different impacts depending if the deposition was chronic or acute. If the deposition is chronic growth rates may be enhanced and not create any significant negative effects on the biotope. The acute introduction of levels of organic carbon at the benchmark could lead to the overgrowth of the algae by ephemeral green algae and an increase in the number of grazers within a short period of time. 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 score of ‘Medium’.

Physical Pressures

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

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

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

This biotope occurs on rock substratum, a change towards a 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 *Fucus vesiculosus* along with other species found within the community of this biotope. Resistance is assessed as ‘None’. As this pressure represents a permanent change, recovery is impossible as the suitable substratum for fucoids is lacking. Consequently, resilience is assessed as ‘Very Low’. The habitat, therefore, scores a ‘High’ sensitivity. Although no specific evidence is described confidence in this assessment is ‘High’, due to the incontrovertible nature of this pressure.

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

Not relevant to biotopes occuring on bedrock.

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

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

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

This biotope is found on the mid intertidal shore. An area easily accessible by humans especially at low tide. Individual *Fucus* specimens are very flexible but not physically robust. Fucoids are intolerant of abrasion from human trampling, which has been shown to reduce the cover of seaweeds on a shore (Holt *et al.*, 1997).

Araujo *et al.* (2009) found that trampling negatively affected *Fucus vesiculosus* abundance and reduced understorey species while promoting the colonisation by ephemeral green algae. However, within a year of the disturbance event, *Fucus vesiculosus* recovered and greatly increased in cover becoming the dominant canopy forming species, replacing a pre-disturbance *Ascophyllum nodosum* community. The replacement of *Ascophyllum nodosum* with *Fucus vesiculosus* may have been due to the poor recovery rate of *Ascophyllum nodosum.* The increase in abundance suggests the competitive superiority of *Fucus vesiculosus* individuals in occupying newly available space in the disturbed patches. Similar results were found by Cervin *et al.* (2005) and Araujo *et al.* (2012) with *Fucus vesiculosus* outcompeting *Ascophyllum nodosum* after small-scale disturbances.

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

As few as 20 steps / m^2 on stations on an intertidal rocky shore in the north-east of England were sufficient to reduce the abundance of fucoids (Fletcher & Frid, 1996). This reduction in the complexity of the algae community, in turn, reduced the microhabitat available for epiphytic species. Trampling pressure can thus result in an increase in the area of bare rock on the shore (Hill *et al.*, 1998). Chronic trampling can affect community structure with shores becoming dominated by algal turf or crusts (Tyler-Walters, 2005).

Pinn & Rodgers (2005) compared the biological communities found on two intertidal rocky shore ledges in Dorset. They found that the ledge which had a higher number of visitors had few branching algal species, including fucoids, but had greater abundances of crustose and ephemeral species (Pinn & Rodgers, 2005).

The densities of fucoids were recorded from the intertidal rocky shore at Wembury, Devon in 1930 (Colman, 1933) and 1973 (Boalch *et al.*, 1974). Boalch *et al.* (1974) found a reduction in fucoids on the shore at Wembury and that the average frond length of *Ascophyllum nodosum, Fucus vesiculosus and Fucus serratus* was smaller.

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

Sensitivity assessment. Abrasion of the substratum will cause a reduction in *Fucus* abundance resulting in 'Low' resistance. Several studies, however, found that the seaweed is able to quickly recolonize disturbed area, out-competing other macroalgae such as *Ascophyllum nodosum*. Although *Fucus vesiculosus* may return quickly, equilibrium in the ecosystem may not have been reached, therefore resistance is 'Medium'. Overall the biotope has a 'Medium' sensitivity to the pressure.

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

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

Changes in suspended solids (water clarity)	Medium Q: Medium A: Medium C: Medium	Medium Q: High A: High C: Medium	Medium Q: Medium A: Medium C: Medium

Light is an essential resource for all photoautotrophic organisms and *Fucus vesiculosus* distribution along a depth gradient strongly correlates with light penetration. In areas with low sedimentation *Fucus vesiculosus* can survive down to 9-10 m depth (Eriksson & Bergstrom, 2005). Changes in suspended solids affecting water clarity will have a direct impact on the photosynthesising capabilities of *Fucus vesiculosus.* Irradiance below light compensation point of photosynthetic species can compromise carbon accumulation (Middelboe *et al*., 2006). Kõuts *et al.* (2006) found decreases in light intensity in the vicinity of the dredging site resulted in the net decline of *Fucus vesiculosus* biomass. A decrease in light penetration in the Kiel Fjord caused by an increase in phytoplankton density and shading from filamentous algae has caused an upwards shift of the lower depth limit of *Fucus vesiculosus* (Rohde *et al*., 2008).

Increased suspended sediment can also cover the frond surface of *Fucus vesiculosus* with a layer of sediment further reducing photosynthesis and growth rate. Sediment deposition can also interfere with attachment of microscopic stages of seaweeds reducing recruitment. Berger *et al*. (2003) demonstrated that both interference with sediment during settlement, and burial after attachment, were significant causes of mortality for *Fucus vesiculosus* germlings (see 'siltation' pressures).

Other characterizing species will also be adversely affected. In particular filter feeding organisms will have their feeding apparatus clogged with suspended particles leading to a reduction in total ingestion and a reduced scope for growth especially since cleaning the feeding apparatus is likely to be energetically expensive.

Sensitivity assessment. Changes in suspended solids reducing water clarity will have adverse effects on the biotope hindering photosynthesis and growth as well as reducing species richness. Resistance is thus assessed as 'Medium'. Once conditions return to 'normal' algae are likely to rapidly regain photosynthesising capabilities as well as growth rate. Associated communities will also recover as most of the intolerant species produce planktonic larvae and are therefore likely to be able to recolonize quickly from surrounding areas. Resilience is assessed as 'Medium'. Overall this biotope has a 'Medium' sensitivity to this pressure at the given benchmark.

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

Sedimentation can directly affect assemblages inhabiting rocky shores in different ways, particularly by the burial/smothering and scour or abrasion of organisms. *Fucus vesiculosus* attaches to the substratum by a holdfast and is consequently not able to relocate in response to increased sedimentation. Eriksson & Johansson (2003) found that sedimentation had a significant negative effect on the recruitment success of *Fucus vesiculosus*. Sediment deposition is assumed to 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 microenvironment (Devinny & Volse, 1978, Eriksson & Johansson, 2003). Berger *et al*. (2003) demonstrated that both interference with sediment during settlement, and burial after attachment, were significant causes of mortality for *Fucus vesiculosus* germlings.

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

Smothering will cause direct mortalities in the associated community, particularly in filter feeding sessile organisms unable to relocate. Low densities of herbivores on rocky shores have frequently been related with areas affected by sedimentation, the presence of herbivores is reduced since their feeding activity and movements might be limited (Airoldi & Hawkins, 2007; Schiel *et al*., 2006)

This biotope occurs in moderately exposed to very sheltered conditions. In areas with greater water flow or wave action, excess sediments will be removed from the rock surface within a few tidal cycles, reducing the time of exposure to this pressure.

Sensitivity assessment. Burial will lower survival and germination rates of spores and cause some mortality in early life stages of *Fucus vesiculosus*. Adults are more resistant but will experience a decrease in growth and photosynthetic rates. This pressure will have different impacts on different examples of this biotope depending where on certain environmental gradients they are found. Wave exposure is especially important for this pressure as it is wave energy which will be able to remove sediment from the shore. Examples of this biotope within areas which are moderately exposed to waves will not be as negatively affected by this pressure as sediment will be removed by wave action relatively quickly. Examples of this biotope which are in sheltered or very sheltered conditions sediment will be retained for longer, allowing greater negative effects to occur. Resistance and resilience have both been assessed as 'Medium'. Overall the biotope has a 'Medium' sensitivity to smothering at the level of the benchmark.

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

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. Resistance is assessed as 'Low' as all individuals exposed to siltation at the benchmark level are predicted to die. Once conditions return to normal, recovery will be enabled by vegetative growth from remaining *Fucus* tissue, resulting in a 'Medium' resilience. Overall the biotope has a 'Medium' sensitivity to siltation at the pressure benchmark.

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

Not assessed.

Electromagnetic changes	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

Not evidence.

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

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

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

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

Barrier to species movement	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

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

Death or injury by collision	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

Not relevant to seabed habitats. Collision by grounding vessels is addressed under ‘surface abrasion’.

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

Not relevant.

Biological Pressures

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

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

Introduction or spread of invasive non-indigenous species	Medium Q: High A: Medium C: Medium	Medium Q: High A: High C: Medium	Medium Q: High A: Medium C: Medium

Thompson & Schiel (2012) found that native fucoids show high resistance to invasions by the Japanese kelp *Undaria pinnatifida*. However 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.

Hammann *et al*., (2013) found that in the Baltic Sea *Gracilaria vermiculophylla* could impact *Fucus vesiculosus* through direct competition for recourses, decreasing the half-life of germlings, and increasing the level of grazing pressure. 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 fucoids, and could become relevant to this specific biotope.

Sensitivity assessment. Although evidence often indicates that invasive non-indigenous species (INIS) can have a negative impact native species, no evidence can be found on the impacts of INNS on the characterizing species of this biotope. Evidence regarding other fucoids indicate that some mortality of characterizing species can occur through direct and indirect consequences of INIS being present. Due to the current lack of INIS which could cause a negative impact on this biotope resistance has been assessed as 'High' since invasive species have the potential to alter the recognizable biotope. Resilience has also been assessed as 'High'. This assessment naturally leads to the conclusion that the biotope is 'Not Sensitive' to this pressure. However, return to 'normal' conditions is highly unlikely if an invasive species came to dominate the biotope. Indeed recovery would only be possible if the majority of the INIS were removed (through either natural or unnatural process) to allow the re-establishment of other species. Therefore actual resilience will be much lower ('Low' to 'Very Low').

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

No evidence.

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

Fucus vesiculosus is one of several harvested and exploited algal species. Seaweeds were collected from the middle of the 16th century for the iodine industry. Nowadays seaweeds are harvested for their alginates, which are used in the cosmetic and pharmaceutical industries, for agricultural supply, water treatment, and for human food and health supplements (Bixler & Porse, 2010). There is little information on the collection of *Fucus spiralis.* However if there is collection of this characteristic species the effects are likely to be very similar to that caused by the removal of *Fucus vesiculosus.*

The commercial harvest removes seaweed canopies which will have important effects on the wider ecosystem. Stagnol *et al.* (2013) investigated the effects of commercial harvesting of intertidal fucoids on ecosystem biodiversity and functioning. The study found that the removal of the macroalgae canopy affected the metabolic flux of the area. Flows from primary production and community respiration were lower on the impacted area as the removal of the canopy caused changes in temperature and humidity conditions. Suspension feeders were the most affected by the canopy removal as canopy-forming algae are crucial habitats for these species, most of them being sessile organisms. Other studies confirm that loss of canopy had both short and long-term consequences for benthic communities in terms of diversity resulting in shifts in community composition and a loss of ecosystem functioning such as primary productivity (Lilley & Schiel, 2006; Gollety *et al.*, 2008). Due to the intolerance of macroalgae communities to human exploitation, the European Union put in place a framework to regulate the exploitation of algae establishing an organic label that implies that 'harvest shall not cause any impact on ecosystems' (no. 710/2009 and 834/2007).

Sensitivity assessment. The removal of *Fucus vesiculosus* 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. *Fucus vesiculosus* has a 'Low' resistance to removal as both of them are easy to locate and have no escape strategy. Resilience is 'Medium', however recovery will only be able to start when the pressure is removed from the shore i.e. harvesting is no longer occurring. A sensitivity of 'Medium' is recorded.

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

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

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

Bibliography

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. & 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.

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

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

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

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

Bäck, S., 1993. Morphological variation of northern Baltic *Fucus vesiculosus* along the exposure gradient. *Annales Botanici Fennici*, 275-283.

Bäck, S., Collins, J. & Russell, G., 1992. Effects of salinity on growth of Baltic and Atlantic *Fucus vesiculosus*. *British Phycological Journal*, **27** (1), 39-47.

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.

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

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

Bergström, L., Berger, R. & Kautsky, L., 2003. Negative direct effects of nutrient enrichment on the establishment of *Fucus vesiculosus* in the Baltic Sea. *European Journal of Phycology*, **38** (1), 41-46.

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.

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

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

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

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

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

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.

Burrows, E.M. & Lodge, S.M., 1950. Note on the inter-relationships of *Patella*, *Balanus* and *Fucus* on a semi-exposed coast. *Report of the Marine Biological Station, Port Erin*, **62**, 30-34.

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

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/

Coles, J.W., 1958. Nematodes parasitic on sea weeds of the genera *Ascophyllum* and *Fucus*. *Journal of the Marine Biological Association of the United Kingdom*, **37** (1), 145-155.

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

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

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

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

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

Eriksson, B.K. & Bergström, L., 2005. Local distribution patterns of macroalgae in relation to environmental variables in the northern Baltic Proper. *Estuarine, Coastal and Shelf Science*, **62** (1), 109-117.

Eriksson, B.K. & Johansson, G., 2003. Sedimentation reduces recruitment success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic Sea. *European Journal of Phycology*, **38** (3), 217-222.

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.

Fredersdorf, J., Müller, R., Becker, S., Wiencke, C. & Bischof, K., 2009. Interactive effects of radiation, temperature and salinity on different life history stages of the Arctic kelp *Alaria esculenta* (Phaeophyceae). *Oecologia*, **160** (3), 483-492.

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

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

Hammann, M., Buchholz, B., Karez, R. & Weinberger, F., 2013. Direct and indirect effects of *Gracilaria vermiculophylla* on native *Fucus vesiculosus*. *Aquatic Invasions*, **8** (2), 121-132.

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

Hawkins, S.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.

Henry, B.E. & Van Alstyne, K.L., 2004. Effects of UV radiation on growth and phlorotannins in *Fucus gardneri* (Phaeophyceae) juveniles and embryos. *Journal of Phycology*, **40** (3), 527-533.

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

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

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

Isaeus, M., 2004. Factors structuring *Fucus communities* at open and complex coastlines in the Baltic Sea. Department of Botany, Botaniska institutionen, Stockholm.

Jenkins, S.R., 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.

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

Johnson, W., Gigon, A., Gulmon, S. & Mooney, H., 1974. Comparative photosynthetic capacities of intertidal algae under exposed and submerged conditions. *Ecology*, **55**: 450-453.

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

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

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

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

Kautsky, N., Kautsky, H., Kautsky, U. & Waern, M., 1986. Decreased depth penetration of *Fucus vesiculosus* (L.) since the 1940s indicates eutrophication of the Baltic Sea. *Marine Ecology Progress Series*, **28**, 1-8.

Keser, M. & Larson, B., 1984. Colonization and growth dynamics of three species of *Fucus*. *Marine Ecology Progress Series*, **15** (1), 125-134.

Kinne, O., 1977. International Helgoland Symposium "Ecosystem research": summary, conclusions and closing. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **30**(1-4), 709-727.

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

Knight, M., 1947. A biological study of *Fucus vesiculosus* and *Fucus serratus*. *Proceedings of the Linnean Society of London*, Wiley Online Library, **159** (2) pp. 87-90.

Kõuts, T., Sipelgas, L. & Raudsepp, U., 2006. High resolution operational monitoring of suspended matter distribution during harbour dredging. *EuroGOOS Conference Proceedings*, pp. 108-115.

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

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

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

Lehvo, A., Bäck, S. & Kiirikki, M., 2001. Growth of *Fucus vesiculosus* L.(Phaeophyta) in the northern Baltic proper: energy and nitrogen storage in seasonal environment. *Botanica Marina*, **44** (4), 345-350.

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

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.

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.

Lüning, K., 1990. *Seaweeds: their environment, biogeography, and ecophysiology*: John Wiley & Sons.

Malm, T., 1999. Distribution patterns and ecology of *Fucus serratus* L. and *Fucus vesiculosus* L. in the Baltic Sea. PhD thesis, Stockholm University.

Malm, T. & Kautsky, L., 2003. Differences in life-history characteristics are consistent with the vertical distribution pattern of *Fucus serratus* and *Fucus vesiculosus* (Fucales, Phaeophyceae) in the central Baltic Sea. *Journal of Phycology*, **39** (5), 880-887.

Mann, K.H., 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. I. Zonation and biomass of seaweeds. *Marine Biology*, **12**, 1-10.

McCook, L. & Chapman, A., 1992. Vegetative regeneration of *Fucus* rockweed canopy as a mechanism of secondary succession on an exposed rocky shore. *Botanica Marina*, **35** (1), 35-46.

McLachlan, J. & Chen, L.-M., 1972. Formation of adventive embryos from rhizoidal filaments in sporelings of four species of *Fucus* (Phaeophyceae). *Canadian Journal of Botany*, **50** (9), 1841-1844.

Middelboe, A.L., Sand-Jensen, K. & Binzer, T., 2006. Highly predictable photosynthetic production in natural macroalgal communities from incoming and absorbed light. *Oecologia*, **150** (3), 464-476.

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

Nielsen, M., Krause-Jensen, D., Olesen, B., Thinggaard, R., Christensen, P. & Bruhn, A., 2014a. Growth dynamics of *Saccharina latissima* (Laminariales, Phaeophyceae) in Aarhus Bay, Denmark, and along the species' distribution range. *Marine Biology*, **161** (9), 2011-2022.

Nietsch, B., 2009. Messung der Zähigkeit der Makroalge *Fucus vesiculosus* an verschiedenen Standorten und Untersuchung der Auswirkungen auf die trophische Interaktion. Diploma Thesis, University of Kiel.

Nilsson, J., Engkvist, R. & Persson, L.-E., 2005. Long-term decline and recent recovery of *Fucus* populations along the rocky shores of southeast Sweden, Baltic Sea. *Aquatic Ecology*, **38** (4), 587-598.

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

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

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

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.

Powell, H., 1963. Speciation in the genus *Fucus* L., and related genera. In Harding, J. and Tebble, N. (eds.). *Speciation in the Sea*, London: Systematics Association, pp. 63–77.

Quadir, A., Harrison, P. & DeWreede, R., 1979. The effects of emergence and submergence on the photosynthesis and respiration of marine macrophytes. *Phycologia*, **18** (1), 83-88.

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

Schiel, D.R., Wood, S.A., Dunmore, R.A. & Taylor, D.I., 2006. Sediment on rocky intertidal reefs: effects on early post-settlement stages of habitat-forming seaweeds. *Journal of Experimental Marine Biology and Ecology*, **331** (2), 158-172.

Serrão, E.A., Kautsky, L. & Brawley, S.H., 1996a. Distributional success of the marine seaweed *Fucus vesiculosus* L. in the brackish Baltic Sea correlates with osmotic capabilities of Baltic gametes. *Oecologia*, **107** (1), 1-12.

Serrao, E.A., Kautsky, L., Lifvergren, T. & Brawley, S.H., 1997. Gamete dispersal and pre-recruitment mortality in Baltic *Fucus vesiculosus*. *Phycologia*, **36**, 101-102.

Serrão, E.A., Kautsky, L., Lifvergren, T. & Brawley, S.H., 2000. Gamete dispersal and pre-recruitment mortality in Baltic *Fucus vesiculosus* (Abstract only). *Phycologia*, **36** (Suppl.), 101-102.

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.

Staehr, 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.

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

Steen, H., 2004. Effects of reduced salinity on reproduction and germling development in *Sargassum muticum* (Phaeophyceae, Fucales). *European Journal of Phycology*, **39** (3), 293-299.

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

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

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

Tatarenkov, A., Jönsson, R.B., Kautsky, L. & Johannesson, K., 2007. Genetic structure in populations of *Fucus vesiculosus* (Phaeophyceae) over spatial scales from 10 m to 800 km. *Journal of Phycology*, **43** (4), 675-685.

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.

Torchin, M., Lafferty, K. & Kuris, A., 2002. Parasites and marine invasions. *Parasitology*, **124** (07), 137-151.

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

Wahl, M., Jormalainen, V., Eriksson, B.K., Coyer, J.A., Molis, M., Schubert, H., Dethier, M., Karez, R., Kruse, I., Lenz, M., Pearson, G., Rohde, S., Wikström, S.A. & Olsen, J.L., 2011. Chapter Two - Stress Ecology in Fucus: Abiotic, Biotic and Genetic Interactions. In Lesser, M. (ed.) *Advances in Marine Biology*. **59**, 37-105.

Wikström, S.A. & Kautsky, L., 2007. Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. *Estuarine, Coastal and Shelf Science*, **72** (1), 168-176.