



MarLIN

Marine Information Network

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

Barnacles and fucoids on moderately exposed shores

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

Frances Perry & Jacqueline Hill

2015-07-31

A report from:

The Marine Life Information Network, Marine Biological Association of the United Kingdom.

Please note. This MarESA report is a dated version of the online review. Please refer to the website for the most up-to-date version [<https://www.marlin.ac.uk/habitats/detail/33>]. All terms and the MarESA methodology are outlined on the website (<https://www.marlin.ac.uk>)

This review can be cited as:

Perry, F. & Hill, J.M., 2015. Barnacles and fucoids on moderately exposed shores. In Tyler-Walters H. and Hiscock K. (eds) *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*, [online]. Plymouth: Marine Biological Association of the United Kingdom.

DOI <https://dx.doi.org/10.17031/marlinhab.33.1>

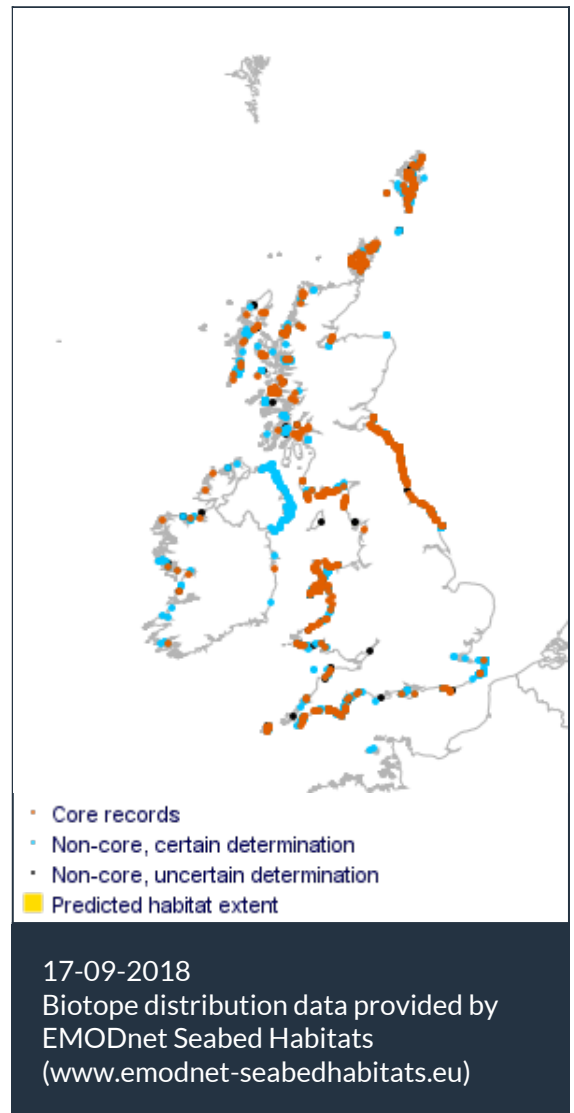


The information (TEXT ONLY) provided by the Marine Life Information Network (MarLIN) is licensed under a Creative Commons Attribution-Non-Commercial-Share Alike 2.0 UK: England & Wales License. Note that images and other media featured on this page are each governed by their own terms and conditions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

(page left blank)



Fucus serratus on moderately exposed lower eulittoral rock
 Photographer: Sue Scott
 Copyright: Joint Nature Conservation Committee (JNCC)



Researched by Frances Perry & Jacqueline Hill

Refereed by This information is not refereed.

Summary

☰ UK and Ireland classification

EUNIS 2008 A1.21 Barnacles and fucoids on moderately exposed shores

JNCC 2015 LR.MLR.BF Barnacles and fucoids on moderately exposed shores

JNCC 2004 LR.MLR.BF Barnacles and fucoids on moderately exposed shores

1997 Biotope LR.MLR.BF Barnacles and fucoids (moderately exposed shores)

🔍 Description

Moderately exposed rocky shores characterized by a mosaic of fucoids and barnacles on bedrock and boulders, where the extent of the fucoid cover is typically less than the blanket cover associated with sheltered shores. Other species are normally present as well in this habitat including the winkle *Littorina littorea*, the whelk *Nucella lapillus* and the red seaweed *Mastocarpus stellatus*. Beneath the band of yellow and grey lichens at the top of the shore is a zone dominated by the wrack *Pelvetia canaliculata*, scattered barnacles, while the black lichen *Verrucaria maura* covers

the rock surface (PelB). Below, on the mid shore the wrack *Fucus vesiculosus* generally forms a mosaic with the barnacle *Semibalanus balanoides* and the limpet *Patella vulgata* (FvesB). Finally, the wrack *Fucus serratus*, dominates the lower shore, while a variety of red seaweeds can be found underneath the *Fucus serratus* canopy (Fser). A number of variants have been described: lower shore bedrock and boulders characterised by mosaics of *Fucus serratus* and turf-forming red seaweeds (Fser.R); where the density of *Fucus serratus* is greater (typically Common to Superabundant) and the abundance of red seaweeds less Fserr.FS should be recorded. The presence of boulders and cobbles on the shore can increase the micro-habitat diversity, which often results in a greater species richness. Although the upper surface of the boulders may bear very similar communities to Fserr.FS there is often an increase in fauna (crabs, tube-forming polychaetes, sponges and bryozoans) and Fser.Bo should be recorded. Sand-influenced exposed to moderately exposed lower shore rock can be characterized by dense mats of *Rhodothamniella floridula* (Rho). (Information from Connor *et al.*, 2004; JNCC, 2015).

↓ Depth range

Upper shore, Mid shore, Lower shore

🏛️ Additional information

-

✓ Listed By

- none -

🔗 Further information sources

Search on:



Habitat review

Ecology

Ecological and functional relationships

Ecological relationships within this biotope are very complex resulting in dynamic communities with a mosaic of patches of furoid cover, dense barnacles and limpets subject to small scale temporal variations due to seasonal and non-seasonal factors. While physical factors clearly influence the distribution and abundance of species on rocky shores it is the interaction between physical and biological factors that is responsible for much of the structure and dynamics of rocky shore communities.

- The diversity of species within the MLR.BF biotope, and on rocky shores in general, increases towards the lower shore where the habitat is wet for longer. Macroalgal cover increases the structural complexity of the habitat providing refugia for a wide range of mobile and sessile animals. The MLR.BF biotope occurs in the eulittoral zone, extending from the upper shore where barnacles and limpets are present in quantity with furoids although often this belt has only sparse algal cover compared with the lower eulittoral.
- Grazing on rocky shores can exert significant controlling influences on the algal vegetation, particularly by patellid limpets and littorinid snails which are usually the most prominent grazers. There are probably also significant effects caused by 'mesograzers' - amphipods such as *Hyale prevostii* and isopods, which are much smaller but may occur in high densities.
- Predation can be an important force in the structuring of rocky shore communities. However, there are relatively few species or abundance of predators on rocky shores, a reflection of the species position at the top of the food web. The most obvious predator on rocky shores, particularly those exposed to wave action, is the whelk *Nucella lapillus*. At lower levels on the shore, starfish may become abundant and are predators especially of mussels. Crabs are more hidden from view on many rocky shores, often because they migrate up and down with the tides, or lurk in crevices at low tide. At low tide level the diversity of predators increases and nudibranch gastropods, polychaetes and nemertines may be abundant. Fish and birds, which invade the shore at high and low tide respectively, are also important predators on the shore.
- In addition to barnacles, other sessile suspension feeding animals may be abundant on the lower shore in barnacle-furoid biotopes. Organisms such as tunicates, sponges, bryozoans, hydroids and spirorbid worms are typically found on various parts of macroalgal plants or attached to the bedrock.
- The presence of a furoid canopy inhibits the settlement of barnacles by blocking larval recruitment mainly by 'sweeping' the rock of colonizers. However, the canopy offers protection against desiccation which promotes the clumping of adults and the recruitment of young in several species of mobile animals. The number of limpets increases with maturing furoid clumps.
- Limpets are the dominant grazers in the system and their home scars tend to be aggregated with a preference for mature algal patches. A spatially uneven pattern of grazing pressure is thought to lead to new algal patches in areas of low local limpet density (Hartnoll & Hawkins, 1985).
- A dense covering of barnacle species is effective in limiting the efficiency of limpet grazing which adversely affects limpet growth. The development of an increasing barnacle cover would contribute, together with decreased limpet grazing to the re-establishment of the

furoid canopy.

- The dense beds of furoid plants provide substratum and shelter for a very wide variety of species, including the tube worm *Spirorbis spirorbis*, herbivorous isopods, such as *Idotea*, and amphipods like *Hyale prevostii*, and surface grazing snails, such as *Littorina obtusata*, and also provide considerable substratum for epiphytic species. They may also act as nursery grounds for various species including *Nucella lapillus*.

Seasonal and longer term change

Furoid-barnacle mosaics on rocky shores are highly variable in space and time and considerable natural change is seen, especially in seaweed cover and number of limpets (Hartnoll & Hawkins, 1985). Natural changes can easily cause a given area to progress through a number of biotopes over time. Seasonal changes are also apparent on rocky shores with seasonal variation in growth and recruitment. *Fucus serratus* plants, for example, lose fronds in the winter, followed by regrowth from existing plants in late spring and summer, so that summer cover can be about 250% of the winter level (Hawkins & Hartnoll, 1980). The barnacle population can be depleted by the foraging activity of the dog whelk *Nucella lapillus* from spring to early winter and replenished by settlement of *Semibalanus balanoides* in the spring and *Chthamalus* spp. in the summer and autumn.

Habitat structure and complexity

Barnacle-furoid shores provide a variety of habitats and refugia for other species. Macroalgae increases the structural complexity of the habitat providing a variety of resources that are not available on bare rock. Fronds provide space for attachment of encrusting or sessile epifauna and epiphytic algae and provide shelter from wave action, desiccation and heat for invertebrates. Empty barnacle shells provide shelter for small littorinids such as *Littorina neglecta* and *Littorina saxatilis*.

The littoral community of furoids, barnacles and limpets on moderately exposed shores is relatively unstable, existing in a state of dynamic equilibrium in which biological or physical changes can create quite drastic effects on the pattern of the community (Southward & Southward, 1978) and so the biotope itself is subject to change and may cycle between different biotopes or sub-biotopes.

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). Macroalgae exude considerable amounts of dissolved organic carbon which are taken up readily by bacteria and may even be taken up directly by some larger invertebrates. Only about 10% of the primary production is directly cropped by herbivores (Raffaelli & Hawkins, 1999). Dissolved organic carbon, algal fragments and microbial film organisms are continually removed by the sea. This may enter the food chain of local, subtidal ecosystems, or be exported further offshore. Rocky shores make a contribution to the food of many marine species through the production of planktonic larvae and propagules which contribute to pelagic food chains.

Recruitment processes

Many rocky shore species, plant and animal, possess a planktonic stage: gamete, spore or larvae which float in the plankton before settling and metamorphosing into adult form. This strategy allows species to rapidly colonize new areas that become available such as in the gaps often

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.

- Community structure and dynamics on barnacle-furoid shores are strongly influenced by larval supply. Annual variation in recruitment success, of algae and barnacles particularly, can have a significant impact on the patchiness of the shore. For example, a low recruitment of limpets, or high recruitment of barnacles might lead to reduced limpet grazing and, therefore, more *Fucus* spp. escapes resulting in a furoid dominated community.
- Recruitment of *Fucus serratus* from minute pelagic sporelings takes place from late spring until October. There is a reproductive peak in the period August - October and plants can be dispersed long distances (up to 10km). Germlings have a high mortality during winter due to storms and heavy wave action with up to 83% being recorded lost in 77 days on the Isle of Man.
- *Ascophyllum nodosum* is also recruited from pelagic sporelings, but recruitment is generally poor with few germlings found on the shore.
- 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.
- Recruitment of *Patella vulgata* fluctuates from year to year and from place to place. Fertilization is external and the larvae is pelagic for up to two weeks before settling on rock at a shell length of about 0.2mm. Winter breeding occurs only in southern England: in the north of Scotland it breeds in August and in north-east England in September.
- Among sessile organisms, patterns fixed at settlement, though potentially altered by post settlement mortality, obviously cannot be influenced by dispersal of juveniles or adults.

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, many whelks such as *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 than species with a pelagic larvae.

Time for community to reach maturity

Although the recruitment of many species in the barnacle-furoid mosaics is rapid, the time scale for recovery of rocky shore communities following mass mortalities caused by oil dispersants used in the *Torrey Canyon* oil spill clean-up was at least 10 years. However, when considering limpet population structure and barnacle densities then the time to return to levels of spatial and temporal variation normally seen on barnacle-furoid shores was closer to 15 years. (Hill *et al.*, 1998).

Additional information

Moderately exposed rocky shores are often made up of a mosaic of communities, each cycling through a number of successional stages and structured by a number of positive and negative interactions between the main species but with fluctuations generated by recruitment variation. These communities are each dominated by a particular group of species, which may give way to others and sometimes to bare rock over time so that the MLR.BF biotopes may represent one stage in a progression of biotopes.

Preferences & Distribution

Habitat preferences

Depth Range	Upper shore, Mid shore, Lower shore
Water clarity preferences	
Limiting Nutrients	Nitrogen (nitrates), Phosphorus (phosphates)
Salinity preferences	Full (30-40 psu)
Physiographic preferences	Open coast
Biological zone preferences	Eulittoral
Substratum/habitat preferences	Bedrock, Large to very large boulders, Small boulders
Tidal strength preferences	
Wave exposure preferences	Moderately exposed
Other preferences	None found

Additional Information

Changes in the relative abundance of the cold-water barnacle *Semibalanus balanoides* and its warm-water counterparts *Chthamalus stellatus* and *Chthamalus montagui* show strong links with climatic conditions (Southward *et al.*, 1995).

Species composition

Species found especially in this biotope

Rare or scarce species associated with this biotope

-

Additional information

No text entered.

Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

Fucus vesiculosus and *Semibalanus balanoides* are the characterizing species of this biotope. However *Patella vulgata* can play a very important role in structuring the biological community. The complex interactions between these species create the mosaics which are characteristic of this biotope. In mid shore locations, where this biotope is found, *Fucus vesiculosus* is the dominant furoid species. The dominant barnacle species is *Semibalanus balanoides*. The limpet species *Patella vulgata* also plays an important role as a grazer on the shore and contributes to the regulation of algal patches. Ecological relationships within these biotopes are very complex resulting in dynamic and patchy communities.

As ecosystem engineers furoid algal canopies modify habitat conditions. This facilitates the existence and survival of other intertidal species and therefore strongly influencing the structure and functioning of intertidal ecosystems (Jenkins *et al.*, 2008). The dominant grazing species is *Patella vulgata*, which strongly affects the distribution of the furoid canopies. Other important grazing species include littorinid snails which can be prominent on algae fronds. The filter feeding barnacle *Semibalanus balanoides* can be very common within this biotope; its distribution can be highly patchy. Both the mussel *Mytilus edulis* and the anemone *Actinia equina* can be found in crevices and fissures in the bed rock and boulders. The most obvious predator in this biotope is the dogwhelk *Nucella lapillus*. A number of other algae species can be found within this biotope including; *Corallina officinalis*, *Mastocarpus stellatus* and *Osmundea pinnatifida*.

Resilience and recovery rates of habitat

Furoids dominate sheltered intertidal rocky shores due to the lack of damage from wave action (Jonsson *et al.*, 2006), good recruitment (Southward & Southward, 1978) and the limited recruitment of grazers (Jenkins *et al.*, 1999). An increase to moderate wave exposure destabilizes the balance between furoids, limpets and barnacles (Hartnoll & Hawkins, 1985), and results in a dynamic equilibrium between furoid and barnacle dominance, mediated by physical wave action, and natural variation in grazing and recruitment. For example, limpets graze on algae and prevent algal growth but furoid patches encourage the recruitment of juvenile limpets. Newly settled barnacles are reduced in number by limpets but are able to settle due to the removal of fast growing, and competitively superior ephemeral algae. Barnacles reduce limpet foraging efficiency allowing algal escapes. Dogwhelks thin-out barnacles, allowing limpets to more effectively reduce algal cover. The sweeping by furoid fronds reduces barnacle settlement (Raffaelli & Hawkins, 1996). Hence, these biotopes exist in a state of dynamic equilibrium in which biological or physical changes can create quite drastic effects on the pattern of the community (Southward & Southward, 1978) and so biotopes are subject to change and may cycle between different biotopes or sub-biotopes. In addition there is also natural variation, and patchiness within intertidal rocky shores (Burrow & Lodge, 1950, Raffaelli & Hawkins, 1996).

Hartnoll & Hawkins (1985) found that within test areas on a moderately exposed intertidal rocky shore a natural cycling of species on the mid shore took 6 – 7 years. Southward (1956) recorded a similar cycle taking five years.

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 large scale 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 underlying fauna and flora to environmental conditions with which they would be intolerant of resulting in mortality events.

Hartnoll & Hawkins (1985) reported that *Fucus vesiculosus* recruits readily to cleared areas of the shore and full recovery takes 1-3 years in British waters. Keser & Larson (1984) investigated the recovery of *Fucus vesiculosus* after clearance experiments where plots were 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 furoids have the ability to rapidly recolonize all areas of the shore, even those which in a balanced ecosystem they do not normally occur (Burrows & Lodge, 1950, Southward & Southward, 1978). Furoid 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 furoids 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 (Strömngren, 1977, Knight & Parke, 1950, Middelboe *et al.*, 2006). Strömngren (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 (Strömngren 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 found 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 furoid algae as only considering fully developed adult specimens may lead to false conclusions (Nielsen *et al.*, 2014).

Genetic diversity can influence the resilience of furoids in particular when pressure persists over a long period of time. Genetically diverse population 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 furoid 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).

Semibalanus balanoides is a small but long lived barnacle with a life expectancy of 3 – 6 years depending on shore height. Individuals on the low shore typically die in their third year, whereas those found from mean high water neaps downwards may live for five or six years. Individuals are hermaphrodites and reach sexual maturity between 1 – 2 years. Fertilization occurs between November – December in the British Isles. Fertilized eggs are retained brooded over winter for dispersal in the spring plankton bloom. The planktonic stage of these organisms is 2 months long during which they can disperse up to 10 km. Reproductive success is affected by temperature, latitude, light, food availability, age, size, crowding, seaweed cover and pollution. High shore *Semibalanus balanoides* breed first and low shore specimens last (up to 12 days difference) (Barnes, 1989). Fertilization is prevented by temperatures above 10 °C and continuous light.

Local environmental conditions, including surface roughness (Hills & Thomason, 1998), wind direction (Barnes, 1956), shore height, wave exposure (Bertness *et al.*, 1991) and tidal currents (Leonard *et al.*, 1998) have been identified, among other factors, as factors affecting settlement of *Semibalanus balanoides*. Biological factors such as larval supply, competition for space, presence of adult barnacles (Prendergast *et al.*, 2009) and the presence of species that facilitate or inhibit

settlement (Kendall, *et al.*, 1985, Jenkins *et al.*, 1999) also play a role in recruitment. Mortality of juveniles can be high but highly variable, with up to 90% of *Semibalanus balanoides* dying within ten days (Kendall *et al.*, 1985).

Successful recruitment of high number of *Semibalanus balanoides* individuals to replenish the population may be episodic (Kendall *et al.*, 1985). After settlement the juveniles are subject to high levels of predation as well as dislodgement from waves and sand abrasion depending on the area of settlement. *Semibalanus balanoides* may live up to 4 years in higher areas of the shore (Wethey, 1985). Predation rates are variable (see Petraitis *et al.*, 2003) and are influenced by a number of factors including the presence of algae (that shelters predators such as the dog whelk, *Nucella lapillus*, and the shore crab, *Carcinus maenas* and the sizes of clearings (as predation pressure is higher near canopies (Petraitis *et al.*, 2003).

On rocky shores, barnacles are often quick to colonize available gaps. 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 previously been dominated by *Ascophyllum nodosum*. However, barnacle densities were fairly low (on average 7.6 % cover), predation levels in smaller patches were high (Petraitis *et al.*, 2003). The success of recruitment and settlement of *Semibalanus balanoides* to an intertidal shore can be affected by the components of the community itself (Beermann *et al.*, 2013). Barnacles are gregarious and larvae settle within areas where adults are present (Knight-Jones & Stevenson, 1950). The mechanism by which they are able to sense adults is chemosensory (Knight-Jones, 1953). Adults exude a protein named arthropodin, which the larvae can sense when they are searching for suitable substrates to settle on (Crisp & Meadows, 1962). The mortality rates for larvae who settle within an area containing a mosaic of adults is less than those who settle in areas without adults (Jenkins *et al.*, 1999). Macroalgae can have both positive and negative impacts on the success of barnacle larvae. Jenkins *et al.* (1999) investigated settlement and post settlement impacts of three macroalgae on *Semibalanus balanoides* cyprid larvae. The investigation found that *Fucus spiralis*, *Ascophyllum nodosum* and *Fucus serratus* all have negative impacts on the ability of larvae to settle due to the sweeping action of their fronds. Larvae which had settled underneath *Fucus serratus* had a mortality rate of 82 – 97% within a single high tide (Jenkins *et al.*, 1999). *Fucus serratus* also inhibited the settlement ability of larvae due to the dense low lying fronds. Although larvae which settle below a furoid canopy have a low chance of survival, mortality of barnacle spat is significantly lower under furoid canopies than in unprotected areas (Jenkins *et al.*, 1999, Beermann *et al.*, 2013).

The life expectancy of *Patella vulgata* depends on location. Those found under furoid canopies may only live for 2 – 3 years. In contrast, those which are found on bare rocks and have slower growth rates due to food limitations can live for 15 – 16 years. Maximum life expectancies have been estimated at 20 years. This species is a protandrous hermaphrodite, male sex organs can mature at nine months. However in northern England, limpets reach sexual maturity in their second year (Blackmore, 1969) and thereafter reproduce annually. The female reproductive organs can mature most often between 2 – 3 years, but in some situations they never mature. In Robin Hood's Bay, Lewis & Bowman (1975) observed spawning of *Patella vulgata* in the Autumn, with spatfall occurring in winter when desiccation pressures were lower.

Patella vulgata is mobile and can relocate to avoid the negative impacts of a pressure. Lewis (1954) found that on particular shores seasonal variations in temperature induced *Patella vulgata* to

migrate further down rocky intertidal shores in the warmer months and further up the shore in winter months. However the ability to relocate depends on the shore type and roughness. *Patella vulgata* individuals also create home scars these are areas of rock where the limpet returns to repeatedly to rest when not feeding. The shell of the organism slowly wears down the rock to create a home scar which can reduce the level of desiccation (Davies, 1969) and the level of predation (Garrity & Levings, 1983). Mortality of these species can increase if they are unable to return to a home scar.

Re-colonization of *Patella vulgata* on rocky shores is rapid as seen by the appearance of limpet spat 6 months after the *Torrey Canyon* oil spill reaching peak numbers 4-5 years after the spill. However, although re-colonization was rapid, the alteration to the population structure (size and age class) persisted for about 15 years because of the complex cycles of dominance (see below) involving limpets, barnacles and algae (Hawkins & Southward, 1992, Lewis & Bowman, 1975). Hence the establishment of furoids if *Patella vulgata* and other grazers are absent.

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. *Semibalanus balanoides* exhibits episodic and patchy recruitment. The evidence suggests that the size of the footprint of an impact and the magnitude will influence the recovery rates by mediating settlement and post-settlement recruitment. Barnacles are attracted to settle in the presence of adults of the same species (Prendergast *et al.*, 2009); so that the presence of adults will facilitate recovery. Resilience is assessed as 'High' (within 2 years) where resistance is 'High' (no significant impact). Recovery of *Patella vulgata* will depend on recolonization by larvae which have pelagic life stage. As *Patella vulgata* is a common, widespread species. Where the footprint of the impact is relatively small, larval supply from adjacent populations should support recolonization. Where source populations are very distant due to regional impacts or habitat discontinuities, larval supply and recovery could be affected.

However, changes and recovery trajectories following the removal of key species are unpredictable and interactions between the key species may be positive or negative. Limpets may enhance barnacle settlement by removing algae (Little *et al.*, 2009) or by depositing pedal mucus trails that attract larvae (Holmes *et al.*, 2005), or they may crush and displace newly settled individuals (Denley & Underwood, 1979). Barnacles may enhance survival of small limpets by moderating environmental stresses but they may also have negative effects on recruitment by occupying space and by limiting access to grazing areas. On the moderately wave exposed shores on which this biotope occurs, grazing may limit initial settlement of macroalgae but wave action will limit the presence of adults and larger species through, breakage and drag effects leading to loss. Mrowicki *et al.*, (2014) found that limpet and barnacle removal allowed ephemeral and furoid macroalgae to establish on sheltered and wave exposed shores in Ireland. Unlike the characteristic animal species macroalgae have short dispersal distances, over tens of metres (Dudgeon *et al.*, 2001) and therefore rapid recovery will require the presence of adults.

Overall, where populations of the characterizing species remain after disturbance, then recovery is likely to be rapid (Hartnoll & Hawkins 1985) within 1-3 years. Similarly, if the natural cycle in species abundance (from furoid to barnacle dominance) takes 5-7 years (Southward, 1956; Hartnoll & Hawkins, 1985) then resilience would be considered to be 'High' to 'Medium' depending on the degree of disturbance. However, where the disturbance causes a severe decline in the characteristic species (resistance is 'None') then recovery is likely to be prolonged (resilience is

'Low'). Southward & Southward (1978) recorded that after the *M.V. Torrey Canyon* oil spill recovery of intertidal shores to their previous ecosystem function recovery can take 10 – 15 years.

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

Hydrological Pressures

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

In Europe *Fucus vesiculosus* occurs from Northern Russia to Morocco (Powell, 1963) withstanding a wide range 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).

Semibalanus balanoides is a 'northern' species, with a range which extends from Portugal or Northern Spain to the Arctic circle. Populations in the southern part of England are therefore relatively close to the southern edge of its geographic range. As this species is found in the intertidal it is exposed to extremes of high and low air temperatures during periods of emersion. Individuals must also be able to cope with sharp temperature fluctuations over a short period of time during the tidal cycle. In winter air temperatures are colder than the sea, conversely in summer air temperatures are much warmer than the sea.

Semibalanus balanoides are found on the mid-shore but are less resistant to desiccation than the 'southern' *Chthamalus* species. Long-term time series show that successful recruitment of *Semibalanus balanoides* is correlated to sea temperatures (Mieszkowska, *et al.*, 2014) and that due to recent warming its range has been contracting northwards. Temperatures above 10 to 12°C inhibit reproduction (Barnes, 1957, 1963, Crisp & Patel, 1969) and laboratory studies suggest that temperatures at or below 10°C for 4-6 weeks are required in winter for reproduction, although the precise threshold temperatures for reproduction are not clear (Rognstad *et al.*, 2014). Observations of recruitment success in *Semibalanus balanoides* throughout the South West of England, strongly support the hypothesis that an extended period (4-6 weeks) of sea temperatures <10°C is required to ensure a good supply of larvae (Rognstad *et al.*, 2014, Jenkins *et al.*, 2000). During periods of high reproductive success, linked to cooler temperatures, the range of barnacles has been observed to increase, with range extensions in the order of 25 km (Wethey *et al.*, 2011), and 100 km (Rognstad *et al.*, 2014).

Sensitivity assessment. *Fucus vesiculosus* is found in the middle of its 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. However *Semibalanus balanoides* is found closer to the southern extent of its range in the British Isles and higher temperatures could reduce its reproductive capacity. A reduction in barnacles present may mean that this biotope is no longer present and another biotope has emerged. Consequently, the resistance and resilience are 'Medium'. The biotope has 'Medium' sensitivity to this pressure at the pressure benchmark.

Temperature decrease (local)

High

Q: High A: High C: Medium

High

Q: High A: High C: High

Not sensitive

Q: High A: High C: Medium

In Europe *Fucus vesiculosus* occurs from Northern Russia to Morocco (Powell, 1963) withstanding a wide range 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).

Semibalanus balanoides is found towards the southern limit of its range in the British Isles, its northern limit extends up into the Arctic circle. A decrease in temperature will not have a negative impact on the barnacle population. This statement is backed up by evidence collected by Crisp *et al.* (1964) after the particularly cold UK winter 1962 – 1963.

Sensitivity assessment. Both *Semibalanus balanoides* and *Fucus vesiculosus* have natural northern range limits in the Arctic circle and a decrease in temperature is unlikely to have a negative impact. 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.

Salinity increase (local)

Medium

Q: Medium A: Medium C: Medium

Medium

Q: High A: High C: Medium

Medium

Q: Medium A: Medium 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 a wide range of salinities in laboratory cultures, yet some differences were recorded. The Atlantic population showed better growth in higher salinities and virtually no growth was recorded for specimens kept at 5 ppt and mortality occurred after 7 weeks. In contrast, the Baltic wracks grew better in the lower range of salinity with growth negligible in the highest salinity (45 ppt). Bäck *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 furoids. However, there is also some evidence suggesting that reduced salinities can influence the rate of receptacle maturation in furoids (Munda, 1964). The rate of fructification in both *Ascophyllum nodosum* and *Fucus vesiculosus* has been measured to increase in diluted seawater (Munda, 1964).

Sensitivity assessment. This biotope is found in fully marine conditions, and an increase in salinity, would create a hyper-saline environment. There are no records of this biotope being found in hyper-saline conditions. However, a number of the species which are present within this biotope

can be found in rock pools where they must be able to survive increased salinities. Therefore, an increase in salinity may decrease the biodiversity of the biotope, and may even cause a shift in the biotope. Both resistance and resilience are thus assessed as 'Medium'. The biotope is 'Medium' to this pressure at the pressure benchmark.

Salinity decrease (local)

High

Q: High A: High C: Medium

High

Q: High A: High C: High

Not sensitive

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 was recorded for specimens kept at 5 ppt and mortality occurred after 7 weeks. In contrast, the Baltic wracks grew better in the lower range of salinity with growth negligible in the highest salinity (45 ppt). Bäck *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 furoids. However, there is also some evidence suggesting that reduced salinities can influence the rate of receptacle maturation in furoids (Munda, 1964). The rate of fructification in both *Ascophyllum nodosum* and *Fucus vesiculosus* has been measured to increase in diluted seawater (Munda, 1964).

Semibalanus balanoides are tolerant of a wide range of salinities and can survive periodic emersion in freshwater, e.g. from rainfall or freshwater run-off, by closing their opercular valves (Foster, 1971b). They can also withstand large changes in salinity over moderately long periods of time by falling into a "salt sleep" and can be found on shores (example from Sweden) with large fluctuations in salinity around a mean of 24 (Jenkins *et al.*, 2001).

Similarly, most of the associated species (e.g. *Mytilus edulis*) are found in a wide range of salinities and are probably tolerant of a variable or reduced salinity. The intertidal interstitial invertebrates and epifauna probably experience short-term fluctuating salinities, with reduced salinities due to rainfall and freshwater runoff when emersed. Prolonged reduction in salinity, e.g. from full to reduced due to e.g. freshwater runoff, is likely to reduce the species richness of the biotope due to loss of less tolerant red algae and some intolerant invertebrates. However, the dominant species will probably survive and the integrity of the biotope is likely to be little affected. Areas of freshwater runoff in the intertidal promote the growth of ephemeral greens, probably due to their tolerance of low salinities and inhibition of grazing invertebrates.

Sensitivity assessment. The highly variable conditions found on temperate intertidal rocky shores means that most species are tolerant of a range of environmental factors. However a change in a salinity category could cause enough of a change to the community composition to change the biotope. Both resistance and resilience are thus assessed as 'Medium'. The biotope has 'Medium' sensitivity to this pressure at the benchmark.

Water flow (tidal current) changes (local)**Medium**

Q: Medium A: Medium C: Medium

Medium

Q: High A: High C: Medium

Medium

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. Furoids are however highly flexible and are able to re-orientate their position in the water column to become more streamlined. This ability allows furoids 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* and *Fucus spiralis* 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. Indeed if the substratum is less stable, such as a small stone or mussel shell, 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 (Isaacs, 2004).

Propagule dispersal, fertilization, settlement, and recruitment are also influenced by water movement (Pearson & Brawley, 1996). In addition, increased water flow increases scour though 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 & Vorse, 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 CO₂ by the macroalgae. Slower water movement can also cause oxygen deficiency directly impacting the fitness of algae (Olsenz, 2011).

Growth and reproduction of *Semibalanus balanoides* is influenced by food supply and water velocity (Bertness *et al.*, 1991). Laboratory experiments demonstrated that barnacle feeding behaviour altered over different flow rates but that barnacles fed at a variety of flow speeds (Sanford *et al.*, 1994). Flow tank experiments using velocities of 0.03, 0.07 and 0.2 m/s showed that a higher proportion of barnacles fed at higher flow rates (Sanford *et al.*, 1994). Feeding was passive, meaning the cirri were held out to the flow to catch particles; although active beating of the cirri to generate feeding currents occurs in still water (Crisp & Southward, 1961). Field observations at sites in southern New England (USA) that experience a number of different measured flow speeds, found that *Semibalanus balanoides* from all sites responded quickly to higher flow speeds, with a higher proportion of individuals feeding when current speeds were higher. Barnacles were present at a range of sites, varying from sheltered sites with lower flow rates (maximum observed flow rates <0.06- 0.1 m/s), a bay site with higher flow rates (maximum observed flows 0.2-0.3 m/s) and open coast sites (maximum observed flows 0.2-0.4 m/s). Recruitment was higher at the site with flow rates of 0.2-0.3 m/s (although this may be influenced by supply) and at higher flow microhabitats within all sites. Both laboratory and field observations indicate that flow is an important factor with effects on feeding, growth and recruitment in *Semibalanus balanoides* (Sanford *et al.*, 1994, Leonard *et al.*, 1998), however, the results suggest that flow is not a limiting factor determining the overall distribution of barnacles as they can adapt to a variety of flow

speeds.

Sensitivity assessment. This biotope is characteristic of exposed to moderately wave exposed conditions where water movement from wave action will greatly exceed the strength of any possible tidal flow. Based on the available evidence the characterizing species *Fucus vesiculosus* and *Semibalanus balanoides* are able to 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 characterizing species. Changes in emergence can lead to; greater exposure to desiccation and reduced feeding 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 CO₂ 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 CO₂ (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 & Johnson (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 components 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.

Semibalanus balanoides is less tolerant of desiccation stress than *Chthamalus* barnacle species and consequently appears in zones lower on the shore. However, the presence of a furoid canopy within this biotope means desiccation stress is less severe on the underlying population and enables them to survive (Raffaelli & Hawkins, 1996). An increase in desiccation may lead to a

change in the furoid canopy, but as long as there is a canopy to moderate the physical environmental factors then *Semibalanus balanoides* can prevail. The presence of a version on this biotope further up the shore gives credence to this theory (Connor *et al.*, 2004).

Decreased emergence would reduce desiccation stress and allow the attached suspension feeders more feeding time. However, predation pressure on barnacles is likely to increase where these are submerged for longer periods and may prevent colonization of lower zones. *Semibalanus balanoides* is able to extend its range into lower zones when protected from predation by the dogwhelk, *Nucella lapillus* (Connell, 1961). Competition from large furoids and red algal turfs can also prevent *Semibalanus balanoides* from extending into lower shore levels (Hawkins, 1983). Decreased emergence is likely to lead to the habitat the biotope is found in becoming more suitable for the lower shore species generally found below the biotope, leading to replacement.

The mobile species present within the biotope, including *Nucella lapillus*, *Patella vulgata*, and the littorinids would be able to relocate to preferred shore levels.

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. *Semibalanus balanoides* requires protection from the more extreme elements if it is found in areas with greater emergence. A change in emergence is likely to cause a change in the 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). Furoids 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. Furoids 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 furoids (Blanchette, 1997) as smaller individuals create less resistance to waves.

As exposure increases the furoid population will become dominated by small juvenile algae, and dwarf forms of macroalgae 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 furoids 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, 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* may be better adapted to more exposed positions compared to other furoids by its ability to regenerate from holdfasts, an ability that *Fucus serratus* lacks (Malm & Kautsky, 2003).

No direct evidence was found to assess the sensitivity of *Semibalanus balanoides* to changes in wave exposure at the pressure benchmark.

This biotope occurs in wave exposed and moderately exposed 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 may lead to an increase in the dominance of *Fucus vesiculosus*, which would, in turn, reduce the abundance of *Semibalanus balanoides*, resulting in a different biotope.

Sensitivity assessment. *Fucus vesiculosus* is sensitive to a change in wave action which would have 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 but could be rapid once conditions return to normal. Overall this biotope group 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	No evidence (NEv) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR
-----------------------------------	--	--	--

No evidence.

Introduction of other substances

Not Assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

This pressure is **Not assessed**.

De-oxygenation

High

Q: 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 2mg/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. No specific information about the effects of deoxygenation on the characteristic species was found. *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 within this biotope may be negatively impacted by reduced dissolved oxygen level at the level of the benchmark (2 mg/l for 1 week) resulting in direct mortalities. However, the biotope in question occurs in the eulittoral and consequently 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. Also, the moderately exposed and exposed locations where this biotope is found means that there will always be high levels of water mixing created by tidal streams, currents and waves. All of these factors are likely to maintain high oxygen levels. Therefore, resistance is assessed as 'High'. Hence, resilience is assessed as 'High', and the biotope as 'Not sensitive'.

Nutrient enrichment

High

Q: High A: High C: Medium

High

Q: High A: High C: Medium

Not sensitive

Q: High A: High 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, 2007, Kraufvelin *et al.*, 2006b).

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, 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 (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 cannot 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). Bellgrove *et al.* (2010) found that coralline turfs out-competed fucoids at a site associated with organic enrichment caused by an ocean sewage outfall.

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

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'.

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, a change towards a sedimentary or soft rock substratum would lead to the direct loss of suitable attachment areas resulting in the loss of the characterizing species *Fucus vesiculosus* and *Semibalanus balanoides* 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 a suitable substratum for furoids is lacking. Consequently, resilience is assessed as 'None'. 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
---	---	---	---

The benchmark for this pressure refers to a change in one Folk class. The pressure benchmark originally developed by Tillin *et al.* (2010) used the modified Folk triangle developed by Long (2006) which simplified sediment types into four categories: mud and sandy mud, sand and muddy sand, mixed sediments and coarse sediments. The change referred to is, therefore, a change in sediment classification rather than a change in the finer-scale original Folk categories (Folk, 1954). For mixed sediments and sand and muddy sand habitats, a change in one folk class may refer to a change to any of the sediment categories. However, for coarse sediments resistance is assessed based on a change to either mixed sediments or sand and muddy sands but not mud and sandy muds. Similarly, muds and sandy muds are assessed based on a change to either mixed sediments or sand and muddy sand but not coarse sediment.

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 are epifauna or epiflora occurring 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' on 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: Medium

Medium

Q: High A: High C: High

These biotope groups are found in the mid intertidal shore. An area easily accessible by humans especially at low tide. Individual *Fucus* specimens are very flexible but not physically robust. Furoids 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 understory species, while promoting the colonization 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 distichus*, 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 / m² on stations on an intertidal rocky shore in the north east of England were sufficient to reduce the abundance of furoids (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 furoids, but had greater abundances of crustose and ephemeral species (Pinn & Rodgers, 2005). The densities of furoids 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 furoids 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 month 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).

Semibalanus balanoides typically occur on the rock surfaces where they will be exposed to abrasion. Although they are protected by hard shells or plates, abrasion may damage and kill individuals or detach these. All removed barnacles would be expected to die as there is no mechanism for these

to reattach. The effects of trampling on barnacles appears to be variable with some studies not detecting significant differences between trampled and controlled areas (Tyler-Walters & Arnold, 2008). However, this variability may be related to differences in trampling intensities and abundance of populations studied. The worst case incidence was reported by Brosnan and Crumrine (1994) who reported that a trampling pressure of 250 steps in a 20x20 cm plot one day a month for a period of a year significantly reduced barnacle cover at two study sites. Barnacle cover reduced from 66% to 7% cover in 4 months at one site and from 21% to 5% within 6 months at the second site. Overall barnacles were crushed and removed by trampling. Barnacle cover remained low until recruitment the following spring. Long *et al.* (2011) also found that heavy trampling (70 humans/km shoreline/hr) led to reductions in barnacle cover. Single step experiments provide a clearer, quantitative indication of sensitivity to direct abrasion. Povey & Keough (1991) in experiments on shores in Mornington peninsula, Victoria, Australia, found that in single step experiments 10 out of 67 barnacles, (*Chthamalus antennatus* about 3mm long), were crushed. However, on the same shore, the authors found that limpets may be relatively more resistant to abrasion from trampling. Following step and kicking experiments, few individuals of the limpet *Cellana trasomerica*, (similar size to *Patella vulgata*) suffered damage or relocated (povey & Keough, 1991). One kicked limpet (out of 80) was broken and 2 (out of 80) limpets that were stepped on could not be relocated the following day (Povey & Keough, 1991). Trampling may lead to indirect effects on limpet populations, Bertocci *et al.* (2011) found that the effects of trampling on *Patella* sp. increased temporal and spatial variability of in abundance. The experimental plots were sited on a wave-sheltered shore dominated by *Ascophyllum nodosum*. On these types of shore, trampling in small patches, that removes macroalgae and turfs, will indirectly enhance habitat suitability for limpets by creating patches of exposed rock for grazing. Pinn & Rodgers (2005) compared abundances of *Patella* sp. on frequently visited rocky ledges and less visited ledges. They found that limpet abundances on the ledge which was visited more frequently by humans had lower abundances of limpets. The use of 'limpet protection zones', where trampling was minimised, helped populations of limpets recover. Also strengthening the evidence that human trampling was the cause of the population reduction in the first instance.

Shanks & Wright (1986), found that even small pebbles (<6 cm) that were thrown by wave action in Southern California shores could create patches in *Chthamalus fissus* aggregations and could smash owl limpets (*Lottia gigantea*). Average, estimated survivorship of limpets at a wave exposed site, with many loose cobbles and pebbles allowing greater levels of abrasion was 40% lower than at a sheltered site. Severe storms were observed to lead to almost total destruction of local populations of limpets through abrasion by large rocks and boulders.

Sensitivity assessment. Abrasion of the substratum will cause a reduction in furoid (e.g. *Fucus vesiculosus*) and *Semibalanus balanoides* abundance. Although barnacles may be more resistant to this pressure the biotope will still be damaged or altered if *Fucus vesiculosus* is removed, consequently 'Low' resistance has been allocated. Several studies however found that the seaweed is able to quickly recolonize disturbed area, outcompeting other macroalgae such as *Ascophyllum nodosum*. Although *Fucus vesiculosus* may return quickly, an equilibrium 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 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* (Rhode *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).

Semibalanus balanoides may be adversely affected. As a filter feeding organism their feeding apparatus can become 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. Seapy & Littler (1982) found that a sediment inundation on an intertidal rocky shore caused a decrease in species diversity. One of the species on which the deposition of sediment was noted to have a notable negative impact was on the barnacle species *Tetraclita rubescens*.

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 group scores a 'Medium' sensitivity.

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 spiralis* and *Fucus vesiculosus* attach to the substratum by a holdfast. These species are thus 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 & Vorse, 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 group to this pressure may thus 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)

Semibalanus balanoides is found permanently attached to hard substrata and is a suspension feeder. This species, therefore, has no ability to escape from silty sediments which would bury individuals and prevent feeding and respiration. However, no direct evidence for sensitivity to siltation was found.

The biotope group occurs in moderately exposed to exposed 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. No evidence for the impact of burial on *Semibalanus balanoides* can be found. However considering that the benchmark of this pressure is 5 cm of sediment deposition and this species never exceeds 1.5 cm in height, even the largest individual would be entirely smothered. Consequently inhibiting filter feeding and respiration entirely. Therefore this pressure could lead to mortality if the sediment is not removed within a few tidal cycles.

This pressure will have different impacts on the biotopes within this group 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. This biotope is found in moderately exposed to exposed conditions, the wave action within these conditions will allow sediment to be removed relatively quickly from the intertidal shore. Resistance and resilience are assessed as 'Medium'. Recovery could be rapid if sediment is removed from the shore by wave energy before organisms begin to die. Overall the biotope group 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: 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 understory algae, invertebrate grazers and young (germling) fucoids. Even in the moderately exposed to exposed conditions within which this biotope is found it would take longer for the sediment to be removed from the shore. The longer the sediment is on the shore the greater the negative impact on the biotope. 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

Thompson *et al.* (2004) demonstrated that *Semibalanus balanoides*, kept in aquaria, ingested microplastics within a few days. However, the effects of the microplastics on the health of exposed individuals have not been identified. There is currently no evidence to assess the level of impact.

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 assessed.

Underwater noise changes

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

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

Introduction of light or shading

No evidence (NEv)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

No evidence (NEv)

Q: NR A: NR C: NR

Increased levels of diffuse irradiation correlate with increased growth in macroalgae (Aguilaria *et al.*, 1999). Levels of diffuse irradiation increase in summer, and with a decrease in latitude. As *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.

Semibalanus balanoides sheltered from the sun grew bigger than unshaded individuals (Hatton, 1938; cited in Wethey, 1984), although the effect may be due to indirect cooling effects rather than shading. Barnacles are also frequently found under algal canopies suggesting that they are tolerant of shading. Light levels have also been demonstrated to influence a number of phases of the reproductive cycle in *Semibalanus balanoides*. In general light inhibits aspects of the breeding cycle. Penis development is inhibited by light (Barnes & Stone, 1972) while Tighe-Ford (1967) showed that constant light inhibited gonad maturation and fertilization. Davenport & Crisp

(unpublished data from Menai Bridge, Wales, cited from Davenport *et al.*, 2005) found that experimental exposure to either constant darkness, or 6 h light: 18 h dark photoperiods induced autumn breeding in *Semibalanus*. They also confirmed that very low continuous light intensities (little more than starlight) inhibited breeding. Latitudinal variations in the timing of the onset of reproductive phases (egg mass hardening) have been linked to the length of darkness (night) experienced by individuals rather than temperature (Davenport *et al.*, 2005). Changes in light levels associated with climate change (increased cloud cover) were considered to have the potential to alter the timing of reproduction (Davenport *et al.*, 2005) and to shift the range limits of this species southward. 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

Not relevant – 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. NB. Collision by grounding vessels is addressed under 'surface abrasion'.

Visual disturbance

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant to most receptors.

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

High

Q: High A: Medium C: Medium

High

Q: High A: Medium C: Medium

Not sensitive

Q: High A: Medium C: Medium

Thompson & Schiel (2012) found that native furoids 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 a 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 resources, 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 furoids, and could become relevant to this specific biotope.

The Australasian barnacle *Austrominius* (previously *Elminius*) *modestus* was introduced to British waters on ships during the second world war. However, its overall effect on the dynamics of rocky shores has been small as *Austrominius modestus* has simply replaced some individuals of a group of co-occurring barnacles (Raffaelli & Hawkins, 1999). Although present, monitoring indicates it has not outnumbered native barnacles in the Isle of Cumbrae (Gallagher *et al.*, 2015) although it may dominate in estuaries where it is more tolerant of lower salinities than *Semibalanus balanoides* (Gomes-Filho, *et al.*, 2010).

Sensitivity assessment. Although evidence often indicates that invasive non-native species (INNS) 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 furoids indicate that some mortality of characterizing species can occur through direct and indirect consequences of INNS being present. Due to the current lack of INNS 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 NIS 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)	Not relevant (NR)	No evidence (NEv)
	Q: NR A: NR C: NR	Q: NR A: NR C: NR	Q: NR A: NR C: NR

No evidence.

Removal of target species	High	High	Not sensitive
	Q: Low A: NR C: NR	Q: Low A: NR C: NR	Q: Low A: NR C: NR

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. Currently, 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). Removal of the canopy caused bleaching and death of the understory of red algal turf. Stagnol *et al.* (2013) observed *Patella vulgata* recruiting in bare patches of disturbed plots. Experimental studies have shown that limpets control the development of macroalgae by consuming microscopic phases (Jenkins *et al.*, 2005) or the adult stages (Davies *et al.*, 2007). The increase in *Patella vulgata* abundance could thus limit the recruitment and growth of *F. serratus* on the impact zone.

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).

Semibalanus balanoides is not a targeted species. *Patella vulgata*, however, is an important characterizing and structuring species within this biotope. *Patella vulgata* grazing can control the character of the shore by grazing algae and newly settled barnacle larvae. Even a small, localised temporary absence of limpets (Southward, 1956; Southward, 1964; Hawkins, 1981; Hawkins *et al.*, 1983) can alter the biological assemblage. Significant limpet kills resulting from the widespread use of dispersants after the *Torrey Canyon* oil spill dramatically altered rocky shore communities. *Laminaria digitata*, for example, was able to extend 2m up shore in the absence of limpets and there were dense growths of ephemeral green seaweeds followed by equally dense growth of fucoids (Southward & Southward, 1978; Hawkins & Southward, 1992).

Sensitivity assessment. The removal of *Fucus vesiculosus* canopy will significantly change the community composition of the biotope. As will the targeted removal of the important grazing species *Patella vulgata*. 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. Both *Fucus vesiculosus* and *Patella vulgata* have 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

- Berndt, M.-L., Callow, J.A. & Brawley, S.H., 2002. Gamete concentrations and timing and success of fertilization in a rocky shore seaweed. *Marine Ecology Progress Series*, **226**, 273-285.
- Alvera-Azcárate, A., Ferreira, J. & Nunes, J., 2003. Modelling eutrophication in mesotidal and macrotidal estuaries. The role of intertidal seaweeds. *Estuarine, Coastal and Shelf Science*, **57** (4), 715-724.
- Eklund, B.T. & Kautsky, L., 2003. Review on toxicity testing with marine macroalgae and the need for method standardization—exemplified with copper and phenol. *Marine Pollution Bulletin*, **46** (2), 171-181.
- Coyer, J.A., Hoarau, G., Pearson, G.A., Serrao, E.A., Stam, W.T. & Olsen, J.L., 2006b. Convergent adaptation to a marginal habitat by homoploid hybrids and polyploid ecads in the seaweed genus *Fucus*. *Biology Letters*, **2** (3), 405-408.
- Worm, B. & Lotze, H.K., 2006. Effects of eutrophication, grazing, and algal blooms on rocky shores. *Limnology and Oceanography*, **51** (1part2), 569-579.
- Korpinen, S. & Jormalainen, V., 2008. Grazing and nutrients reduce recruitment success of *Fucus vesiculosus* L. (Fucales: Phaeophyceae). *Estuarine, Coastal and Shelf Science*, **78** (2), 437-444.
- Brinza, L., Nygård, C.A., Dring, M.J., Gavrilesco, M. & Benning, L.G., 2009. Cadmium tolerance and adsorption by the marine brown alga *Fucus vesiculosus* from the Irish Sea and the Bothnian Sea. *Bioresource technology*, **100** (5), 1727-1733.
- Kosenius, A.-K., 2010. Heterogeneous preferences for water quality attributes: the case of eutrophication in the Gulf of Finland, the Baltic Sea. *Ecological Economics*, **69** (3), 528-538.
- Lago-Lestón, A., Mota, C., Kautsky, L. & Pearson, G.A., 2010. Functional divergence in heat shock response following rapid speciation of *Fucus* spp. in the Baltic Sea. *Marine Biology*, **157** (3), 683-688.
- Schagerl, M. & Möstl, M., 2011. Drought stress, rain and recovery of the intertidal seaweed *Fucus spiralis*. *Marine Biology*, **158** (11), 2471-2479.
- Harley, C.D., Anderson, K.M., Demes, K.W., Jorve, J.P., Kordas, R.L., Coyle, T.A. & Graham, M.H., 2012. Effects of climate change on global seaweed communities. *Journal of Phycology*, **48** (5), 1064-1078.
- Abou-Aisha, K.M., Kobbia, I., El Abyad, M., Shabana, E.F. & Schanz, F., 1995. Impact of phosphorus loadings on macro-algal communities in the Red Sea coast of Egypt. *Water, Air, and Soil Pollution*, **83** (3-4), 285-297.
- Aguilera, J., Karsten, U., Lippert, H., Voegelé, B., Philipp, E., Hanelt, D. & Wiencke, C., 1999. Effects of solar radiation on growth, photosynthesis and respiration of marine macroalgae from the Arctic. *Marine Ecology Progress Series*, **191**, 109-119.
- Anderson, C.I.H. & Scott, G.W., 1998. The occurrence of distinct morphotypes within a population of *Fucus spiralis*. *Journal of the Marine Biological Association of the United Kingdom*, **78**, 1003-1006.
- 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., Collins, J. & Russell, G., 1992. Effects of salinity on growth of Baltic and Atlantic *Fucus vesiculosus*. *British Phycological Journal*, **27** (1), 39-47.
- Baardseth, E., 1970. Synopsis of the biological data on knotted wrack *Ascophyllum nodosum* (L.) Le Jolis. *FAO Fisheries Synopsis*, no. 38, Rev. 1.
- Bäck, S., Collins, J.C. & Russell, G., 1991. Aspects of the reproductive biology of *Fucus vesiculosus* from the coast of south west Finland. *Ophelia*, **34**, 129-141.
- Barnes, H. & Stone, R., 1972. Suppression of penis development in *Balanus balanoides* (L.). *Journal of Experimental Marine Biology and Ecology*, **9** (3), 303-309.
- Barnes, H., 1957. Processes of restoration and synchronization in marine ecology. The spring diatom increase and the 'spawning' of the common barnacle *Balanus balanoides* (L.). *Année Biologique. Paris*, **33**, 68-85.
- Barnes, H., 1963. Light, temperature and the breeding of *Balanus balanoides*. *Journal of the Marine Biological Association of the United Kingdom*, **43** (03), 717-727.
- Barnes, M., 1989. Egg production in Cirripedia. *Oceanography and Marine Biology: an Annual Review*, **27**, 91-166.
- 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.
- Beermann, A.J., Ellrich, J.A., Molis, M. & Scrosati, R.A., 2013. Effects of seaweed canopies and adult barnacles on barnacle recruitment: the interplay of positive and negative influences. *Journal of Experimental Marine Biology and Ecology*, **448**, 162-170.

- Bellgrove, A., McKenzie, P.F., McKenzie, J.L. & Sfiligoj, B.J., 2010. Restoration of the habitat-forming furoid alga *Hormosira banksii* at effluent-affected sites: competitive exclusion by coralline turfs. *Marine Ecology Progress Series*, **419**, 47-56.
- Bennell, S.J., 1981. Some observations on the littoral barnacle populations of North Wales. *Marine Environmental Research*, **5**, 227-240.
- Berger, R., Bergström, L., Granéli, E. & Kautsky, L., 2004. How does eutrophication affect different life stages of *Fucus vesiculosus* in the Baltic Sea? - a conceptual model. *Hydrobiologia*, **514** (1-3), 243-248.
- Berger, R., Henriksson, E., Kautsky, L. & Malm, T., 2003. Effects of filamentous algae and deposited matter on the survival of *Fucus vesiculosus* L. germlings in the Baltic Sea. *Aquatic Ecology*, **37** (1), 1-11.
- Berger, R., Malm, T. & Kautsky, L., 2001. Two reproductive strategies in Baltic *Fucus vesiculosus* (Phaeophyceae). *European Journal of Phycology*, **36**, 265-273.
- Bergström, L., Berger, R. & Kautsky, L., 2003. Negative direct effects of nutrient enrichment on the establishment of *Fucus vesiculosus* in the Baltic Sea. *European Journal of Phycology*, **38** (1), 41-46.
- Bertness, M.D., Gaines, S.D., Bermudez, D. & Sanford, E., 1991. Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series*, **75**, 91-100.
- Bertocci, I., Araujo, R., Vaselli, S. & Sousa-Pinto, I., 2011. Marginal populations under pressure: spatial and temporal heterogeneity of *Ascophyllum nodosum* and associated assemblages affected by human trampling in Portugal. *Marine Ecology Progress Series*, **439**, 73-82.
- Bishop, J. 2012c. Carpet Sea-squirt, *Didemnum vexillum*. *Great Britain Non-native Species Secretariat* [On-line]. [cited 30/10/2018]. Available from: <http://www.nonnativespecies.org/factsheet/factsheet.cfm?speciesId=1209>
- Bixler, H.J. & Porse, H., 2010. A decade of change in the seaweed hydrocolloids industry. *Journal of Applied Phycology*, **23** (3), 321-335.
- Blackmore, D.T., 1969. Growth, reproduction and zonation of *Patella vulgata*. *Journal of Experimental Marine Biology and Ecology*, **3**, 200-213.
- 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.
- Boisson, F., Hutchins, D.A., Fowler, S.W., Fisher, N.S. & Teyssie, J.-L., 1997. Influence of temperature on the accumulation and retention of 11 radionuclides by the marine alga *Fucus vesiculosus* (L.). *Marine Pollution Bulletin*, **35**, 313-321.
- Bokn, T.L., Duarte, C.M., Pedersen, M.F., Marba, N., Moy, F.E., Barrón, C., Bjerkgeng, 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.
- Bond, P.T., Brown, M.T., Moate, R.M., Gledhill, M., Hill, S.J. & Nimmo, M., 1999. Arrested development in *Fucus spiralis* (Phaeophyceae) germlings exposed to copper. *European Journal of Phycology*, **34**, 513-521.
- Brawley, S.H. & Johnson, L.E., 1991. Survival of furoid embryos in the intertidal zone depends upon developmental stages and microhabitat. *Journal of Phycology*, **27** (2), 179-186.
- 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.
- 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.]
- Bulleri, F. & Benedetti-Cecchi, L., 2008. Facilitation of the introduced green alga *Caulerpa racemosa* by resident algal turfs: experimental evaluation of underlying mechanisms. *Marine Ecology Progress Series*, **364**, 77-86.
- 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.
- Burrows, E.M. & Lodge, S.M., 1951. Autecology and the species problem in *Fucus*. *Journal of the Marine Biological Association of the United Kingdom*, **30**, 161-176.
- Carlson, L., 1991. Seasonal variation in growth, reproduction and nitrogen content of *Fucus vesiculosus* in the Öresund, Southern Sweden. *Botanica Marina*, **34**, 447-453.

- 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.
- Chapman, A.S. & Fletcher, R.L., 2002. Differential effects of sediments on survival and growth of *Fucus serratus* embryos (Fucales, Phaeophyceae). *Journal of Phycology*, **38** (5), 894-903.
- 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.
- Connell, J.H., 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs*, **31**, 61-104.
- 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/>
- Connor, D.W., Brazier, D.P., Hill, T.O., & Northen, K.O., 1997b. Marine biotope classification for Britain and Ireland. Vol. 1. Littoral biotopes. *Joint Nature Conservation Committee, Peterborough, JNCC Report no. 229, Version 97.06.*, *Joint Nature Conservation Committee, Peterborough, JNCC Report No. 230, Version 97.06.*
- Crisp, D. & Meadows, P., 1962. The chemical basis of gregariousness in cirripedes. *Proceedings of the Royal Society of London B: Biological Sciences*, **156** (965), 500-520.
- Crisp, D. & Patel, B., 1969. Environmental control of the breeding of three boreo-arctic cirripedes. *Marine Biology*, **2** (3), 283-295.
- Crisp, D.J. & Southward, A.J., 1961. Different types of cirral activity *Philosophical Transactions of the Royal Society of London, Series B*, **243**, 271-308.
- 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.
- Davenport, J., Berggren, M.S., Brattegard, T., Brattenborg, N., Burrows, M., Jenkins, S., McGrath, D., MacNamara, R., Sneli, J.-A. & Walker, G., 2005. Doses of darkness control latitudinal differences in breeding date in the barnacle *Semibalanus balanoides*. *Journal of the Marine Biological Association of the United Kingdom*, **85** (01), 59-63.
- Davies, A.J., Johnson, M.P. & Maggs, C.A., 2007. Limpet grazing and loss of *Ascophyllum nodosum* canopies on decadal time scales. *Marine Ecology Progress Series*, **339**, 131-141.
- Davies, P.S., 1969. Physiological ecology of *Patella* III. Desiccation effects. *Journal of the Marine Biological Association of the United Kingdom*, **49**, 291-304.
- Denley, E. & Underwood, A., 1979. Experiments on factors influencing settlement, survival, and growth of two species of barnacles in New South Wales. *Journal of Experimental Marine Biology and Ecology*, **36** (3), 269-293.
- 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.
- Devlin, 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.
- Duggins, D., Eckman, J.E., Siddon, C.E. & Klinger, T., 2001. Interactive roles of mesograzers and current flow in survival of kelps. *Marine Ecology Progress Series*, **223**, 143-155.
- 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.
- 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.
- Floc'h, J. H. & Diouris, M., 1980. Initial effects of Amoco Cadiz oil on intertidal algae. *Ambio*, **9**, 284-286.
- Folk, R.L., 1954. The distinction between grain size and mineral composition in sedimentary-rock nomenclature. **62**, *The Journal of Geology*, 344-359.
- Foster, B.A., 1971b. On the determinants of the upper limit of intertidal distribution of barnacles. *Journal of Animal Ecology*, **40**, 33-48.
- 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.
- Gallagher, M.C., Davenport, J., Gregory, S., McAllen, R. & O'Riordan, R., 2015. The invasive barnacle species, *Austrominius modestus*: Its status and competition with indigenous barnacles on the Isle of Cumbrae, Scotland. *Estuarine, Coastal and Shelf Science*, **152**, 134-141.
- Garrity, S. & Levings, S., 1983. Homing to scars as a defense against predators in the pulmonate limpet *Siphonaria gigas* (Gastropoda). *Marine Biology*, **72** (3), 319-324.
- 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.
- Gomes-Filho, J., Hawkins, S., Aquino-Souza, R. & Thompson, R., 2010. Distribution of barnacles and dominance of the introduced species *Elminius modestus* along two estuaries in South-West England. *Marine Biodiversity Records*, **3**, e58.
- Guiry, M.D. & Blunden, G., 1991. *Seaweed Resources in Europe: Uses and Potential*. Chichester: John Wiley & Sons.
- Guiry, M.D. & Nic Dhonncha, E., 2002. AlgaeBase. World Wide Web electronic publication <http://www.algaebase.org>,
- Gylle, A.M., Nygård, C.A. & Ekelund, N.G.A., 2009. Desiccation and Salinity Effects on Marine and Brackish *Fucus vesiculosus* L. (Phaeophyceae). *Phycologia*, **48** (3), 156-164.
- Hamann, 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.
- Hardy, F.G. & Guiry, M.D., 2003. *A check-list and atlas of the seaweeds of Britain and Ireland*. London: British Phycological Society
- Haring, R.N., Dethier, M.N. & Williams, S.L., 2002. Desiccation facilitates wave-induced mortality of the intertidal alga *Fucus gardneri*. *Marine Ecology Progress Series*, **232**, 75-82.
- Hariot, M.P., 1909. Sur la crissance des *Fucus*. *Comptes rendus hebdomadaires des seances de l'Academie des sciences Paris*, **149**, 352 - 354.
- Hartnoll, R.G. & Hawkins, S.J., 1980. Monitoring rocky shore communities: a critical look at spatial and temporal variation. *Helgolander Meeresuntersuchungen*, **33**, 484-495.
- Hartnoll, R.G. & Hawkins, S.J., 1985. Patchiness and fluctuations on moderately exposed rocky shores. *Ophelia*, **24**, 53-63.
- Hatton, H., 1938. Easelsde bionomie explicative surquelques especesintercotidalesd'algues et d'animaux. *Annales de l'Institut Oceanographique* **17**: 241-348
- Hawkins, S., 1983. Interactions of *Patella* and macroalgae with settling *Semibalanus balanoides* (L.). *Journal of Experimental Marine Biology and Ecology*, **71** (1), 55-72.
- Hawkins, S.J. & Harkin, E., 1985. Preliminary canopy removal experiments in algal dominated communities low on the shore and in the shallow subtidal on the Isle of Man. *Botanica Marina*, **28**, 223-30.
- Hawkins, S.J. & Southward, A.J., 1992. The *Torrey Canyon* oil spill: recovery of rocky shore communities. In *Restoring the Nations Marine Environment*, (ed. G.W. Thorpe), Chapter 13, pp. 583-631. Maryland, USA: Maryland Sea Grant College.
- Hawkins, S.J., 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.
- Hawkins, S.J., Sugden, H.E., Mieszkowska, N., Moore, P.J., Poloczanska, E., Leaper, R., Herbert, R.J.H., Genner, M.J., Moschella, P.S., Thompson, R.C., Jenkins, S.R., Southward, A.J., Burrows, M.T., 2009. Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. *Marine Ecology Progress Series*, **396**, 245-259.
- Hazlett, A. & Seed, R., 1976. A study of *Fucus spiralis* and its associated fauna in Strangford Lough, Co. Down. *Proceedings of the Royal Irish Academy*, **76**, 607-618.
- 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).
- Hills, J. & Thomason, J., 1998. The effect of scales of surface roughness on the settlement of barnacle (*Semibalanus balanoides*) cyprids. *Biofouling*, **12** (1-3), 57-69.
- Hiscock, S., 1979. A field key to the British brown seaweeds (Phaeophyta). *Field Studies*, **5**, 1- 44.
- Hoare, R. & Hiscock, K., 1974. An ecological survey of the rocky coast adjacent to the effluent of a bromine extraction plant. *Estuarine and Coastal Marine Science*, **2** (4), 329-348.
- Holmes, S.P., Walker, G. & van der Meer, J., 2005. Barnacles, limpets and periwinkles: the effects of direct and indirect interactions on cyprid settlement and success. *Journal of Sea Research*, **53** (3), 181-204.

- 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*.
- Howson, C.M. & Picton, B.E., 1997. *The species directory of the marine fauna and flora of the British Isles and surrounding seas*. Belfast: Ulster Museum. [Ulster Museum publication, no. 276.]
- 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., Åberg, P., Cervin, G., Coleman, R., Delany, J., Della Santina, P., Hawkins, S., LaCroix, E., Myers, A. & Lindegarth, M., 2000. Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. *Journal of Experimental Marine Biology and Ecology*, **243** (2), 209-225.
- Jenkins, S., Coleman, R., Della Santina, P., Hawkins, S., Burrows, M. & Hartnoll, R., 2005. Regional scale differences in the determinism of grazing effects in the rocky intertidal. *Marine Ecology Progress Series*, **287**, 77-86.
- Jenkins, S.R., Beukers-Stewart, B.D. & Brand, A.R., 2001. Impact of scallop dredging on benthic megafauna: a comparison of damage levels in captured and non-captured organisms. *Marine Ecology Progress Series*, **215**, 297-301.
- Jenkins, S.R., Hawkins, S.J. & Norton, T.A., 1999. Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community. *Marine Ecology Progress Series*, **188**, 81-92.
- Jenkins, S.R., Moore, P., Burrows, M.T., Garbary, D.J., Hawkins, S.J., Ingólfsson, A., Sebens, K.P., Snelgrove, P.V., Wetthey, D.S. & Woodin, S.A., 2008. Comparative ecology of North Atlantic shores: do differences in players matter for process? *Ecology*, **89** (11), 3-523.
- JNCC, 2015. The Marine Habitat Classification for Britain and Ireland Version 15.03. (20/05/2015). Available from <https://mhc.jncc.gov.uk/>
- JNCC, 2015. The Marine Habitat Classification for Britain and Ireland Version 15.03. (20/05/2015). Available from <https://mhc.jncc.gov.uk/>
- JNCC (Joint Nature Conservation Committee), 1999. *Marine Environment Resource Mapping And Information Database (MERMAID): Marine Nature Conservation Review Survey Database*. [on-line] <http://www.jncc.gov.uk/mermaid>
- 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, H., 1992. The impact of pulp-mill effluents on phytobenthic communities in the Baltic Sea. *Ambio*, **21**, 308-313.
- Kautsky, N., Kautsky, H., Kautsky, U. & Waern, M., 1986. Decreased depth penetration of *Fucus vesiculosus* (L.) since the 1940s indicates eutrophication of the Baltic Sea. *Marine Ecology Progress Series*, **28**, 1-8.
- Kendall, M.A., Bowman, R.S., Williamson, P. & Lewis, J.R., 1985. Annual variation in the recruitment of *Semibalanus balanoides* on the North Yorkshire coast 1969-1981. *Journal of the Marine Biological Association of the United Kingdom*, **65**, 1009-1030.
- Keser, M. & Larson, B., 1984. Colonization and growth dynamics of three species of *Fucus*. *Marine Ecology Progress Series*, **15** (1), 125-134.
- Kinne, O. (ed.), 1970. *Marine Ecology: A Comprehensive Treatise on Life in Oceans and Coastal Waters. Vol. 1 Environmental Factors Part 1*. Chichester: John Wiley & Sons
- Kinne, O., 1977. International Helgoland Symposium "Ecosystem research": summary, conclusions and closing. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **30**(1-4), 709-727.
- Knight, M. & Parke, M., 1950. A biological study of *Fucus vesiculosus* L. and *Fucus serratus* L. *Journal of the Marine Biological Association of the United Kingdom*, **29**, 439-514.
- Knight, M., 1947. A biological study of *Fucus vesiculosus* and *Fucus serratus*. *Proceedings of the Linnean Society of London*, Wiley Online Library, **159** (2) pp. 87-90.
- Knight-Jones, E. & Stevenson, J., 1950. Gregariousness during settlement in the barnacle *Elminius modestus* Darwin. *Journal of the Marine Biological Association of the United Kingdom*, **29** (02), 281-297.
- Knight-Jones, E., 1953. Laboratory experiments on gregariousness during setting in *Balanus balanoides* and other barnacles. *Journal of Experimental Biology*, **30** (4), 584-598.
- Köuts, T., Sipelgas, L. & Raudsepp, U., 2006. High resolution operational monitoring of suspended matter distribution during harbour dredging. *EuroGOOS Conference Proceedings*, pp. 108-115.

- Kraufvelin, P., 2007. Responses to nutrient enrichment, wave action and disturbance in rocky shore communities. *Aquatic Botany*, **87** (4), 262-274.
- Kraufvelin, P., Moy, F.E., Christie, H. & Bokn, T.L., 2006. Nutrient addition to experimental rocky shore communities revisited: delayed responses, rapid recovery. *Ecosystems*, **9** (7), 1076-1093.
- Kraufvelin, P., Ruuskanen, A., Nappu, N. & Kiirikki, M., 2007. Winter colonisation and succession of filamentous algae and possible relationships to *Fucus vesiculosus* settlement in early summer. *Estuarine Coastal and Shelf Science*, **72**, 665-674.
- Ladah, L., Feddersen, F., Pearson, G. & Serrão, E., 2008. Egg release and settlement patterns of dioecious and hermaphroditic furoid 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.
- Leonard, G.H., Levine, J.M., Schmidt, P.R. & Bertness, M.D., 1998. Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology*, **79** (4), 1395-1411.
- 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., 1954. Observations on a high-level population of limpets. *Journal of Animal Ecology*, **23**, 85-100.
- 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.
- Little, C. & Kitching, J.A., 1996. *The Biology of Rocky Shores*. Oxford: Oxford University Press.
- Little, C., Morrill, D. & Stirling, P., 1992. Changes in the shore fauna and flora of Lough Hyne. *The Irish Naturalists' Journal*, **87-95**.
- Little, C., Williams, G.A. & Trowbridge, C.D., 2009. *The biology of rocky shores*: Oxford University Press New York.
- 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.
- Long, J.D., Cochrane, E. & Dolecal, R., 2011. Previous disturbance enhances the negative effects of trampling on barnacles. *Marine Ecology Progress Series*, **437**, 165-173.
- 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.
- Malm, T., Kautsky, L. & Engkvist, R., 2001. Reproduction, recruitment and geographical distribution of *Fucus serratus* L. in the Baltic Sea. *Botanica Marina*, **44** (2), 101-108.
- Mann, K.H., 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. I. Zonation and biomass of seaweeds. *Marine Biology*, **12**, 1-10.
- McCook, L. & Chapman, A., 1992. Vegetative regeneration of *Fucus* rockweed canopy as a mechanism of secondary succession on an exposed rocky shore. *Botanica Marina*, **35** (1), 35-46.
- McLachlan, J. & Chen, L.-M., 1972. Formation of adventive embryos from rhizoidal filaments in sporelings of four species of *Fucus* (Phaeophyceae). *Canadian Journal of Botany*, **50** (9), 1841-1844.
- Middelboe, A.L., Sand-Jensen, K. & Binzer, T., 2006. Highly predictable photosynthetic production in natural macroalgal communities from incoming and absorbed light. *Oecologia*, **150** (3), 464-476.
- Mieszkowska, N., Burrows, M.T., Pannacciulli, F.G. & Hawkins, S.J., 2014. Multidecadal signals within co-occurring intertidal barnacles *Semibalanus balanoides* and *Chthamalus* spp. linked to the Atlantic Multidecadal Oscillation. *Journal of Marine Systems*, **133**, 70-76.
- Miossec, L., Le Deuff, R.-M. & Gouletquer, P., 2009. Alien species alert: *Crassostrea gigas* (Pacific oyster). *ICES Cooperative Research Report*, 299
- Morrissey, J., Kraan, S. & Guiry, M.D., 2001. *A guide to commercially important seaweeds on the Irish coast*. Bord Iascaigh Mhara: Dun Laoghaire.
- Moschella, P., Abbiati, M., Åberg, P., Airoidi, L., Anderson, J., Bacchiocchi, F., Bulleri, F., Dinesen, G.E., Frost, M. & Gacia, E., 2005. Low-crested coastal defence structures as artificial habitats for marine life: using ecological criteria in design. *Coastal Engineering*, **52** (10), 1053-1071.
- Mrowicki, R.J., Maggs, C.A. & O'Connor, N.E., 2014. Does wave exposure determine the interactive effects of losing key grazers and ecosystem engineers? *Journal of Experimental Marine Biology and Ecology*, **461** (0), 416-424.
- Munda, I., 1964. *The influence of salinity on the chemical composition, growth and fructification of some Fucaceae*. New York: Pergamon Press.
- Munda, I.M., 1997. Combined effects of temperature and salinity on growth rates of germlings of three *Fucus* species from Iceland, Helgoland and the North Adriatic Sea. *Helgoländer Wissenschaftliche Meeresunters*, **29**, 302-310.

- Newell, R.C., 1979. *Biology of intertidal animals*. Faversham: Marine Ecological Surveys Ltd.
- Newey, S. & Seed, R., 1995. The effects of the *Braer* oil spill on rocky intertidal communities in south Shetland, Scotland. *Marine Pollution Bulletin*, **30**, 274-280.
- 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.
- Niemeck, R.A. & Mathieson, A.C., 1976. An ecological study of *Fucus spiralis*. *Journal of Experimental Marine Biology and Ecology*, **24**, 33-48.
- 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.
- Norton, T.A. (ed.), 1985. *Provisional Atlas of the Marine Algae of Britain and Ireland*. Huntingdon: Biological Records Centre, Institute of Terrestrial Ecology.
- Olsenz, J.L., 2011. Stress ecology in *Fucus*: abiotic, biotic and genetic interactions. *Advances in Marine Biology*, **59** (57), 37.
- Pearson, G.A. & Brawley, S.H., 1996. Reproductive ecology of *Fucus distichus* (Phaeophyceae): an intertidal alga with successful external fertilization. *Marine Ecology Progress Series*. Oldendorf, **143** (1), 211-223.
- Pearson, G.A., Lago-Leston, A. & Mota, C., 2009. Frayed at the edges: selective pressure and adaptive response to abiotic stressors are mismatched in low diversity edge populations. *Journal of Ecology*, **97** (3), 450-462.
- Perrin, C., Daguin, C., Vliet, M.V.D., Engel, C.R., Pearson, G.A. & Serrão, E.A., 2007. Implications of mating system for genetic diversity of sister algal species: *Fucus spiralis* and *Fucus vesiculosus* (Heterokontophyta, Phaeophyceae). *European Journal of Phycology*, **42** (3), 219-230.
- Petratis, 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.
- Petratis, P.S., Rhile, E.C. & Dudgeon, S., 2003. Survivorship of juvenile barnacles and mussels: spatial dependence and the origin of alternative communities. *Journal of Experimental Marine Biology and Ecology*, **293** (2), 217-236.
- 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.
- Pinn, E.H., Mitchell, K. & Corkill, J., 2005. The assemblages of groynes in relation to substratum age, aspect and microhabitat. *Estuarine, Coastal and Shelf Science*, **62** (1), 271-282.
- Povey, A. & Keough, M.J., 1991. Effects of trampling on plant and animal populations on rocky shores. *Oikos*, **61**: 355-368.
- 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.
- Prendergast, G.S., Zurn, C.M., Bers, A.V., Head, R.M., Hansson, L.J. & Thomason, J.C., 2009. The relative magnitude of the effects of biological and physical settlement cues for cypris larvae of the acorn barnacle, *Semibalanus balanoides* L. *Biofouling*, **25** (1), 35-44.
- 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.
- Raffaelli, D. & Hawkins, S., 1999. *Intertidal Ecology* 2nd edn.. London: Kluwer Academic Publishers.
- Raffaelli, D.G. & Hawkins, S.J., 1996. *Intertidal Ecology* London: Chapman and Hall.
- Robertson, B.L., 1985. Reproductive ecology and canopy structure of *Fucus spiralis* (L.) *Botanica Marina*, **30**, 475-482.
- Rognstad, R.L., Wethey, D.S. & Hilbish, T.J., 2014. Connectivity and population repatriation: limitations of climate and input into the larval pool. *Marine Ecology Progress Series*, **495**, 175-183.
- 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.
- Ryan, T.P., McMahon, C.A., Dowdall, A., Fegan, M., Sequeira, S., Murray, M., McKittrick, L., Hayden, E., Wong, J. & Colgan, P.A., 2003. Radioactivity monitoring of the marine environment 2000 and 2001. , Radiological Protection Institute of Ireland., <http://www.rpii.ie/reports/2003/MarineReport20002001final.pdf>
- Sanford, E., Bermudez, D., Bertness, M.D. & Gaines, S.D., 1994. Flow, food supply and acorn barnacle population dynamics. *Marine Ecology Progress Series*, **104**, 49-49.
- 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., 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.
- Scott, G.W., Shaw, J.H., Hull, S.L., Pickaert, C. & Burlak, A.M., 1999. Some implications of plant size in monotypic and polytypic populations of *Fucus spiralis*. *Journal of the Marine Biological Association of the United Kingdom*, **80**, 359-360.
- Seapy, R.R. & Littler, M.M., 1982. Population and Species Diversity Fluctuations in a Rocky Intertidal Community Relative to

- Severe Aerial Exposure and Sediment Burial. *Marine Biology*, **71**, 87-96.
- Serrão, E.A., Kautsky, L. & Brawley, S.H., 1996a. Distributional success of the marine seaweed *Fucus vesiculosus* L. in the brackish Baltic Sea correlates with osmotic capabilities of Baltic gametes. *Oecologia*, **107** (1), 1-12.
- Serrão, E.A., Pearson, G., Kautsky, L. & Brawley, S.H., 1996b. Successful external fertilization in turbulent environments. *Proceedings of the National Academy of Sciences*, **93** (11), 5286-5290.
- 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.
- Shanks, A.L. & Wright, W.G., 1986. Adding teeth to wave action- the destructive effects of wave-bourne rocks on intertidal organisms. *Oecologia*, **69** (3), 420-428.
- Shields, M.A., Woolf, D.K., Grist, E.P., Kerr, S.A., Jackson, A., Harris, R.E., Bell, M.C., Beharie, R., Want, A. & Osalusi, E., 2011. Marine renewable energy: the ecological implications of altering the hydrodynamics of the marine environment. *Ocean & Coastal Management*, **54**, 2-9.
- 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.
- Southward, A.J., 1956. The population balance between limpets and seaweeds on wave-beaten rocky shores. *Report of the Marine Biological Station, Port Erin*, 68, 20-29.
- Southward, A.J., 1964. Limpet grazing and the control of vegetation on rocky shores. In *Grazing in Terrestrial and Marine Environments*, *British Ecological Society Symposium No. 4* (ed. D.J. Crisp), 265-273.
- Southward, A.J., Hawkins, S.J. & Burrows, M.T., 1995. Seventy years observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology*, **20**, 127-155.
- 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.
- Stecher, A., 2011. *Combined effects of ocean acidification and tidal emergence on the performance and gene expression in the intertidal brown seaweed Fucus serratus*. Universität Bremen.
- 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.
- Strömberg, T., 1977. Short-term effect of temperature upon the growth of intertidal Fucales. *Journal of Experimental Marine Biology and Ecology*, **29**, 181-195.
- Subrahmanyam, R., 1961. Ecological studies on the Fucales. II. *Fucus spiralis* L. *Journal of the Indian Botanical Society*, **40**, 335-354.
- 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.
- Tatarenkov, A., Bergström, L., Jönsson, R.B., Serrão, E.A., Kautsky, L. & Johannesson, K., 2005. Intriguing asexual life in marginal populations of the brown seaweed *Fucus vesiculosus*. *Molecular Ecology*, **14** (2), 647-651.
- 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.
- Thompson, N., Cross, J.E., Miller, R.M. & Day, J.P., 1982. Alpha and gamma radioactivity in *Fucus vesiculosus* from the Irish Sea. *Environmental Pollution (Series B)*, **3**, 11-19.
- Thompson, R.C., Olsen, Y., Mitchell, R.P., Davis, A., Rowland, S.J., John, A.W., McGonigle, D. & Russell, A.E., 2004. Lost at sea: where is all the plastic? *Science*, **304** (5672), 838-838.
- Tighe-Ford, D., 1967. Possible mechanism for the endocrine control of breeding in a cirripede. *Nature*, **216**, 920-921.
- Tillin, H.M., Hull, S.C. & Tyler-Walters, H., 2010. Development of a sensitivity matrix (pressures-MCZ/MPA features). *Report to the Department of the Environment, Food and Rural Affairs from ABPmer, Southampton and the Marine Life Information Network (MarLIN) Plymouth: Marine Biological Association of the UK., Defra Contract no. MB0102 Task 3A, Report no. 22., London, 145 pp.*
- 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>
- Tyler-Walters, H. & Arnold, C., 2008. Sensitivity of Intertidal Benthic Habitats to Impacts Caused by Access to Fishing Grounds. *Report to Cynfor Cefn Gwlad Cymru / Countryside Council for Wales from the Marine Life Information Network (MarLIN) [Contract no. FC 73-03-327]*, Marine Biological Association of the UK, Plymouth, 48 pp. Available from: www.marlin.ac.uk/publications

- van der Ben, D. & Bonotto, S., 1991. Utilization of brown algae for monitoring the radioactive contamination of the marine environment. *Oebalia*, **17**, 143 - 153.
- Vernet, P. & Harper, J.L., 1980. The costs of sex in seaweeds. *Biological Journal of the Linnean Society*, **13**, 129-138.
- Viñebla, B., Segovia, M. & Figueroa, F.L., 2006. Effect of artificial UV radiation on carbon and nitrogen metabolism in the macroalgae *Fucus spiralis* L. and *Ulva olivascens* Dangeard. *Hydrobiologia*, **560** (1), 31-42.
- 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.
- Wethey, D.S., 1985. Catastrophe, Extinction, and Species Diversity: A Rocky Intertidal Example. *Ecology*, **66** (2), 445-456.
- Wethey, D.S., 1984. Sun and shade mediate competition in the barnacles *Chthamalus* and *Semibalanus*: a field experiment. *The Biological Bulletin*, **167** (1), 176-185.
- Wethey, D.S., Woodin, S.A., Hilbish, T.J., Jones, S.J., Lima, F.P. & Brannock, P.M., 2011. Response of intertidal populations to climate: effects of extreme events versus long term change. *Journal of Experimental Marine Biology and Ecology*, **400** (1), 132-144.
- 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.
- Wippelhauser, G.S., 1996. *Ecology and management of Maine's eelgrass, rockweed, and kelps*. Augusta: Department of Conservation.